The Identity of *Tarsius pumilus,* a Pygmy Species Endemic to the Montane Mossy Forests of Central Sulawesi

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ABSTRACT

In 1917, Henry C. Raven obtained a small-bodied tarsier from upper montane rain forest in the mountains of Central Sulawesi. Miller and Hollister (1921b) designated the specimen as holotype of *Tarsius pumilus,* included two others collected from lowland evergreen rain forest, and pointed to small body size as one of the diagnostic specific characters. Subsequent faunal checklists and taxonomic revisions treated *pumilus* as a subspecies of the widespread Sulawesian *Tarsius spectrum* until 1985 when Niemitz advocated recognition of specific status for *pumilus* based upon the original series and recorded vocalizations. But only one of the three specimens discussed by Miller and Hollister is an example of *T. pumilus,* and the calls said to be those of this species were probably made by *T. spectrum. Tarsius pumilus* is distinctive, but it is known by only the holotype and a second example from montane forest in Central Sulawesi. The morphological and biogeographical limits of the species based upon these two specimens are documented here. The definition of *T. pumilus* is set within a context of morphological and geographical comparisons among *T. bancanus* (Sunda Shelf), *T. syrichta* (southern Philippine islands), and *T. spectrum* (Sulawesi and nearby islands); and subsequent comparisons between these three and *T. pumilus.* Information is provided on habitat and faunal associations of *T. pumilus.* The species is also contrasted in greater detail with morphology, habitats, and regional as well as altitudinal distributions of *T. spectrum.* A hypothesis of phylogenetic relationships among the four species of tarsiers is briefly discussed.

INTRODUCTION

Dense gray mist shrouds the high mountain forests of Central Sulawesi during the day. The air is wet and cold. Sounds are muffled as if they were absorbed by the thick wet

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Fig. 1. Mossy forest on summit of Gunung Nokilalaki, 2275 m, Central Sulawesi. Representative habitat of *Tarsius pumilus*. December 1973.

moss that envelops rocks and rotting tree-falls on the ground, covers trunks and gnarled limbs, and hangs from branches in wet lacy curtains. At night the chill intensifies, the wet persists, the silence continues, broken only by the soft songs of frogs and insects, a low hoot from an owl, and the muffled cry of the *hauntu,* sometimes coming from far off, sometimes from close by—a call announcing the ghost of the mossy forest.

The *hauntu* lives in the wet and cold forests on the slopes of Gunung Nokilalaki, a mist-capped mountain brooding over Lake Lindu in one of the mountain valleys of Central Sulawesi. People living on the shores of the lake have different versions of the *hauntu*'s physical identity. To some the ghost is a beast the size of a macaque, which is clad in shaggy black fur, moves about slowly, lives in the mossy crowns of tall trees, and descends only to the warmth of campfires. To others the ghost is a ferocious demon that looks like a cross between a large dog and a civet. It may live amid the mossy fur and drapes in the canopy or deep within the forest, and when seen is always tensed to strike just beyond the edge of light cast by campfire. For many persons, however, the ghost is neither of these but resembles a small owl, which has wide round eyes and human nails instead of claws. Rarely seen but often heard, it lives within mossy crowns, and will call from above the glowing embers of a cooking fire to remind human intruders that they are forever strangers to the mountain forest.

Myth springs from reality. The shaggy-furred and slow moving *hauntu* resembles the bear phalanger (*Phalanger ursinus*), which is the size of a macaque, has thick and black-ish fur, is arboreal and rarely comes to the ground, and inhabits both lowland and mountain forests. The civetlike demon re-calls a fierce and aggressive predator, the Su-lawesi palm civet (*Macrogalidia muschen-broekii*), the only civet truly native to Sulawesi. It has both the size and appearance of a large dog combined with civet features, is found in lowlands and mountains, hunts on the ground and in trees, and is rarely seen by humans. The third version is recognizable as a tarsier.

Our purpose here is to transform phantom into substance by identifying the morpholog-ical and ecological characteristics of the tar-sier native to the mossy upper montane rain forests of Central Sulawesi. The animal has a name, *Tarsius pumilus* (Miller and Hollis-ter, 1921b); is known by only two specimens, one collected at 1800 m and the other at 2200 m; and is at once recognizable by its small body size and other morphological features. *Tarsius pumilus* is related to the spectral tar-sier, *T. spectrum,* which is common in a va-riety of habitats in terrain that ranges from coasts to mountains where it has been re-corded from the beginnings of lower montane rain forest, but never from higher than 1500 m.

Documenting the characteristics of the pygmy tarsier is part of a larger endeavor tied to identifying the mammalian species diver-sity on Sulawesi, the phylogenetic relation-ships among the native species, and the zoo-geographic relationship of the fauna. To that end, Musser lived and worked during the 1970s in primary forests in the central part of the island where he focused on learning about altitudinal distributions and ecologies of small mammals, mainly rats and squirrels. He encountered the bear phalanger and palm civet in the mossy forests on Gunung Nokila-laki, but not the pygmy tarsier. There is no reason why the tarsier should not be living there; he simply did not see it. Musser worked in the same kind of forest that occurs where the holotype of *T. pumilus* was captured, and the same species of mammals are common to both places. In our accounts of tarsier hab-itats on Sulawesi, we have relied upon his experiences.

Describing the morphology and habitat of *Tarsius pumilus* is but one aspect of mammal studies in Sulawesi. Another is the natural history of the species. We hope our report encourages others to discover the actual al-titudinal distribution of the pygmy tarsier and the interactions between it and its habitat. The species is not extinct. Extensive montane rain forests remain in Central Sulawesi. Field studies will not only illuminate the ecology of *T. pumilus* but will provide data about the ecological and altitudinal relationships be-tween it and the larger-bodied *T. spectrum.* The combined results will contribute to un-derstanding natural histories of the mammal species endemic to Sulawesi, the only place in the world where two species of tarsiers occur on the same island.

Fig. 2. *Tarsius spectrum*. Caught November 7, 1975, in hillside primary forest, 120 m, near Kuala Navusu, Central Sulawesi. Trapped about 10 m above ground on woody vine looping through crown of understory tree. The animal was photographed and released on same day.

SPECIMENS AND METHODS

Specimens studied and cited here are in collections of the American Museum of Natural History, New York (AMNH); the Academy of Natural Sciences, Philadelphia (ANSP); the British Museum (Natural History), London (BM); the Museum of Com-

Fig. 3. Hillside lowland evergreen rain forest near Kuala Navusu, 60 m, Central Sulawesi. Habitat of *Tarsius spectrum*. November 1975.

parative Zoology at Harvard College, Cambridge (MCZ); the Museum Zoologicum Bogoriense, Bogor (MZB); the Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Specimens we examined and localities from which they were obtained are listed below. We use the terms Sungai (stream or small river), Kuala (rivermouth, estuary), Danau (lake), Gunung (mountain), Pegunungan (mountain range), Pulau (island), and Kepulauan (archipelago).

TARSIUS BANCANUS (Sunda Shelf)

1. Southern Sumatra: AMNH 106649.
2. Pulau Belitung: USNM 124992.
3. Borneo: AMNH 41350, 106010, 106754, 200625, 200626, and 202258; ANSP 14090; BM 8.7.17.5, 94.7.2.1, 98.11.31, 0.2.2.5, 51.76, 55.731–55.733, and 52.801; MCZ 6023, 32957, and 35379; USNM 142241–142244, 300916–300918, 317189, and 488081–488085.
4. Pulau Serasan: BM 47.1493.

TARSIUS SYRICHTA
(Southern Philippine islands)

1. Samar Island: BM 97.3.1.1 and 97.3.1.2.
2. Leyte Island: AMNH 187935.
3. Bohol Island: MCZ 39581; USNM 239250.
4. Mindanao Island: AMNH 56782, 166856, 187935, 203296, and 203297; BM 96.7.25.1; MCZ 5975, 33205–33207, 37267, and 54425; USNM 105475, 144643–14645, 218238, 218239, 282639, 282761, 282788, 283069, and 283344.
5. Basilan Island: MCZ 35256.

TARSIUS SPECTRUM
(Sulawesi and nearby islands)

1. Kepulauan Sangihe: BM 1939.1320 and 1939.1321; MCZ 5854; MZB 3288, 6606, and 6607; RMNH cat. u.
2. Northern Peninsula: Manembo Nembo (USNM 217559); Manado (BM 97.1.2.1; MZB 3264, 3269, and 6596); Rurukan, 900–1100 m (AMNH 153561, 196478, 196484, and 196486; BM 97.1.2.2; USNM 83967); Tondano (MZB 6594); Kumar-sot, Kalabat, 250 m (AMNH 196487 and 196488); Molenkapoti (USNM 200279); Gorontolo (RMNH cat. e); Lotta (BM 1939.1322 and 1939.1323); Sungai Paleleh (USNM 200281); Bumbulan (AMNH 153286–153291, 153913–153915; MZB 6595); Toli Toli (USNM 200280 and 200282–200284).
3. Central region: Labua Sore (USNM 218070–218072); Parigi (USNM 218073); Gimpu (USNM 219452 and 219453); Palopo (MZB 3268); Malili (MZB 3263).
4. Southwestern Peninsula: Lombasang, northwest of Gunung Lompobatang, 1100 m (AMNH 153552–153558).
5. Southeastern Peninsula: Wawo, 50 m (AMNH 153560) and Tanka Salokko, 1500 m (AMNH 153559), Pegunungan Mekongga.
6. Pulau Peleng: AMNH 109216–109226, 109360–109370; MZB 4600, 6597–6599, and 6601–6604.
7. Pulau Salayar: RMNH cat. f and s.

TARSIUS PUMILUS
(Central Sulawesi)

1. Rano Rano, 1800 m: USNM 219454.
2. Pegunungan Latimodjong, 2200 m: AMNH 196477.

Values for length of combined head and body, length of tail, and length of ear are those recorded by collectors on labels attached to skins. Length of the third finger (taken from metacarpophalangeal joint to tip of the digital pad) was measured from dry study skins. Cranial and dental measurements were taken with dial calipers graduated to tenths of millimeters. Limits of the measurements are defined below and illustrated in figure 4.

1. Greatest length of skull (GLS): distance from tip of premaxilla to the posterior margin of the occiput.

2. Zygomatic breadth (ZB): the greatest breadth across the zygomatic arches.

3. Breadth across the orbits (BO): the greatest breadth across the orbital margins.

4. Breadth of a single orbit (BSO): the maximum distance between the most medial and lateral margins of a single orbit.

5. Height of a single orbit (HSO): the maximum distance between the most dorsal and ventral margins of the orbit.
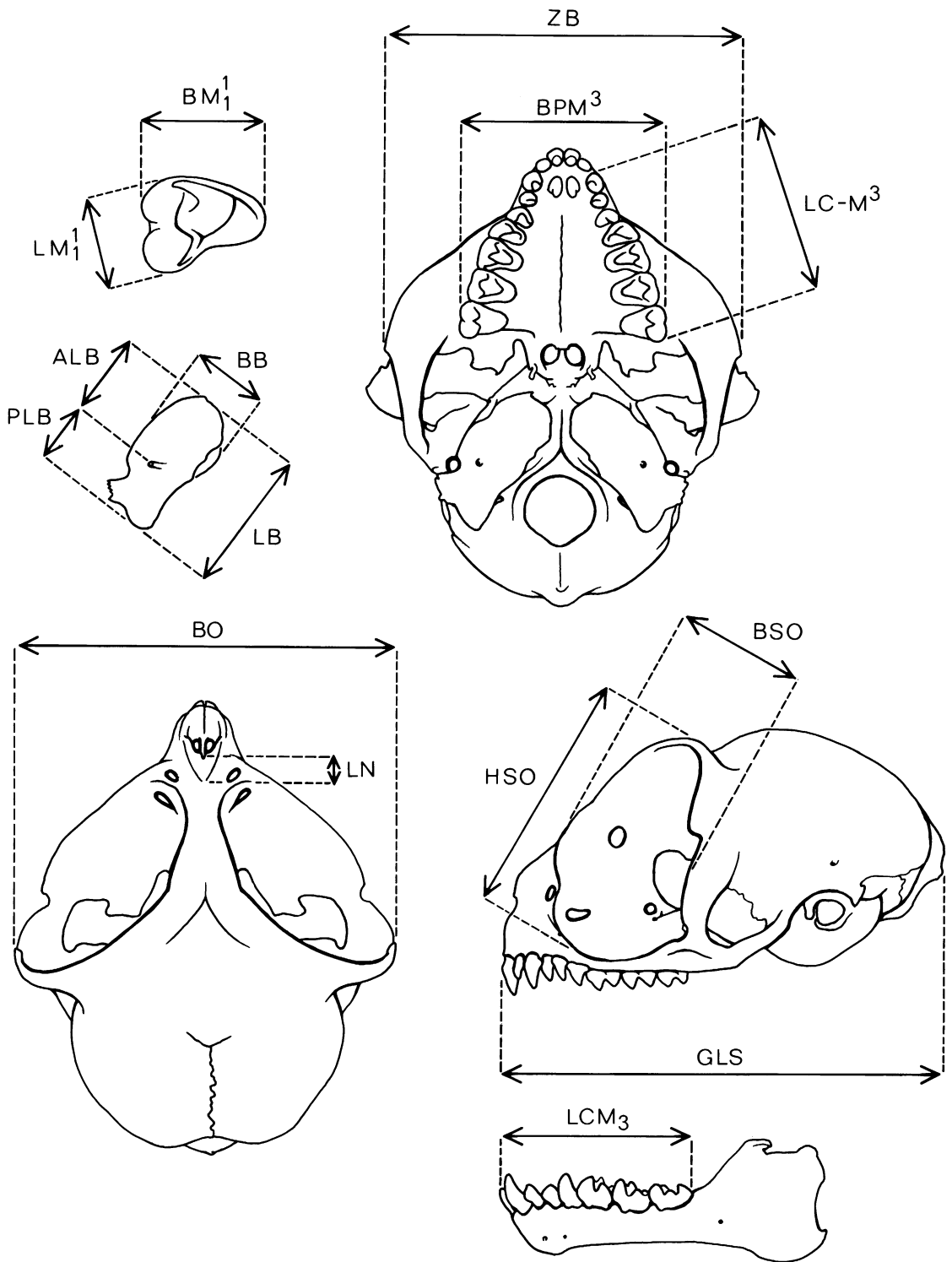
Fig. 4.   Limits of cranial and dental dimensions. See text for definitions and explanations of abbreviations.

6. Length of nasals (LN): the distance between tip of the nasals and the nasofrontal suture.

7. Breadth of bony palate at M^3 (BPM^3): the distance between the buccal edges of the third upper molars.

8. Length of auditory bulla (LB): the maximum length of the bulla.

9. Breadth of auditory bulla (BB): the maximum width of the bulla.

10. Length of anterior part of bulla (ALB): the distance between the carotid foramen and the anterior tip of the bulla.

11. Length of posterior part of bulla (PLB): the distance between the carotid foramen and the posterior tip of the bulla.

12. Length of upper toothrow ($LC-M^3$): the distance between the mesial edge of the canine (C) to the distal edge of M^3, taken parallel to the toothrow.

13. Length of lower toothrow ($LC-M_3$): the distance between the mesial edge of the canine to the distal edge of M_3.

14. Length of M^1 (LM^1): the maximum mesiodistal length of the tooth.

15. Breadth of M^1 (BM^1): the maximum buccolingual breadth of the tooth.

16. Length of M_1 (not illustrated): the maximum mesiodistal length of the tooth.

17. Breadth of M_1 (not illustrated): the maximum buccolingual breadth of the tooth.

Aside from minor metrical distinctions noted in our discussion of regional variation within each species, tarsiers of the same age from all regions within the distribution of the four species are morphologically very similar. For that reason we statistically summarized the values of measurements for a total species sample. The data for *T. spectrum* are an exception because we also subdivided that information into units corresponding to geographic regions of Sulawesi.

We were not concerned with variation due to sex. Tarsiers are not dramatically sexually dimorphic and for our purposes we were able to pool males and females within each sample. Such a procedure may not be valid in a careful study intended to thoroughly analyze individual variation, geographic variation, and variation correlated with sex.

Scanning electron micrographs of teeth are derived from uncoated and unaltered specimens.

HISTORICAL AND TAXONOMIC NOTES

Identifying valid scientific names for the currently recognized species of tarsiers has not been easy. Many early descriptions are deficient in both accuracy of morphological traits—not enough information given to permit determination of the species of tarsier being described—and in locality data. Several descriptions of new taxa were based upon juveniles (Buffon, 1765; Horsfield, 1821; Raf-

fles, 1822, for example), and few holotypes were actually designated. Illustrations were often only poor representations of the living animals. The result was that biologists working and writing in the 18th and 19th centuries renamed the same species several times, confounded different species together under the same name, and gave different scientific names to populations that today are considered to be the same species. Hill (1955) provided a detailed taxonomic history and discussion of these problems. Brief highlights follow.

Tarsiers first became known to Western scientists through the description given to J. Petiver by the missionary J. G. Camel of an animal said to have come from the island of Luzon in the Philippines (Taylor, 1934, and Hill, 1955, explain why the animal could not have been native to Luzon). Petiver published Camel's description in 1705, and named the animal *Cercopithecus luzonis minimus* (fig. 5), which was the basis for Linnaeus' (1758) *Simia syrichta* and thus *syrichta* is the valid specific designation for Philippine tarsiers (Cabrera, 1923; Hill, 1953a, 1955).[3]

[3] Dr. R. D. MacPhee pointed out to us that the genders of *Tarsius* (male) and *syrichta* (female) do not agree. Cabrera (1923) did change the specific name to *Tarsius syrichtus,* but for reasons unstated, both Hill (1953a, 1955) and Niemitz (1977, 1984a) did not adopt this change. According to Article 31 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1985), a specific name must agree in gender with the genus name, if that specific name is an adjective in the nominative singular. If the original author does not state whether the name is to be regarded as a noun or an adjective, and it may be regarded as either, and if evidence of usage is not decisive, it is to be treated as a noun in apposition to the generic name. Linnaeus (1758) coined the specific name *syrichta,* but did not discuss its derivation, or define the part of speech it was meant to be. The word *syrichta* is latinized from the Greek συρικτησ, meaning piper or player on the pipes of Pan. Linnaeus' original binomial for this species was *Simia syrichta,* and it appears from the ending given that the specific name may have been meant either as a noun in apposition or as an adjective in feminine gender to agree with the female *Simia.* The gender of the Greek word is masculine and when transliterated into Latin the termination of the nominative singular ησ becomes *a* as the termination of the grammatical stem for use in forming derivatives; thus *syrichta* is masculine. But the question of gender is irrelevant because συρικτησ is a noun

In 1765, Buffon described a juvenile tarsier ("le tarsier") of unknown provenance. Its naked tarsi indicate, however, that it is also a Philippine tarsier. Buffon did not ally the tarsier with primates or with Linnaeus' *Simia syrichta,* which is understandable given the extremely monkeylike animal figured in Petiver's description (fig. 5). Buffon thought the tarsier might be a jerboa or an opossum. In later editions of his treatise, Linnaeus accepted Buffon's tarsier as an opposum, *Didelphis macrotarsus,* and did not recognize this animal as his *Simia syrichta.*

Erxleben (1777) was the first to link tarsiers with primates, giving them the appellation *Lemur tarsier.* Three years later, Storr (1780) argued for the generic separation of tarsiers from other lemurs and coined the genus name *Tarsius.*

Celebesian tarsiers were first described and given their specific name, *Lemur spectrum,* by Pallas (1778) who studied several specimens in Schlosser's collection (Hill, 1953a, 1955). However, Pallas did not believe that he was describing a new species, but allied his animals with Buffon's tarsier. The identity of Pallas' tarsier with Buffon's was accepted by many authors and the specific name *spectrum* was widely used to refer to all tarsiers. The Celebesian tarsier was not generally recognized as a distinct species until 1804 when Fischer described *Tarsius fuscus* (figs. 6, 7).[4]

[4] Incidentally, Woolard's (1925) classic *Anatomy of Tarsius spectrum* is in all probability not a description of Sulawesian tarsiers but of *T. bancanus.* He based his work upon material from Elliot Smith and Le Gros Clark, who received their specimens from Dr. Charles Hose, who worked in Sarawak (Hose, 1893; Elliot Smith, 1921; Clark 1924). The description of the tail, "no signs of scales" (p. 1076), and his drawings of the cranium showing the short nasals and large orbits indicate characteristics more typical of *T. bancanus* than of either *T. spectrum* or *T. syrichta.*

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and its English translation is a noun phrase. Linnaeus probably used *syrichta* in apposition to the feminine *Simia,* which accords with Article 31 (b) (ii) of the Code of Zoological Nomenclature: "A species-group name that is a simple or compound noun (or noun phrase) in apposition retains the same ending, whatever the gender of the generic name with which it is combined." *Tarsius syrichta* appears to be the correct combination. (We are grateful to Paula Jenkins for helping with this problem.)

PHILIPPINE MONKEY.

Fig. 5. *Cercopithecus luzonis minimus* Petiver (1705). Reproduced from Shaw (1800).

From that time until 1949, the Sulawesian tarsier was redescribed under several names (Meyer, 1896–1897; Miller and Hollister, 1921b; Sody, 1949).

The grounds for accepting Pallas' *L. spectrum* as the first description of a Celebesian tarsier, as Hill has argued for, are actually rather slim. The exact place of origin of the animals studied by Pallas is uncertain, but he believed they came from the East Indies, probably Amboina (now called Pulau Ambou) in the Moluccas, a place that does not harbor any tarsiers today, and probably never did. Pallas claimed that the native name for Schlosser's specimens was *podje,* which is the name given to tarsiers by the people of Makassar (Ujung Pandang), Sulawesi. But there is nothing in the morphological description of *L. spectrum* that would allow us to ally it with any of the currently recognized species of tarsiers. In Hill's opinion, which we provisionally accept, Pallas' name, *Tarsius spectrum,* has priority over other specific names given to Sulawesian tarsiers such as Fischer's (1804) *T. fuscus,* Geoffroy's (1812) *T. fuscomanus,* or Burmeister's (1846) *T. fischeri.*

A third species, *T. bancanus,* was named and described by Horsfield in 1821, based upon animals from the island of Bangka between Sumatra and Borneo (fig. 8). Subsequent discoveries of tarsiers from the nearby island of Billiton (=Belitung), mainland Borneo, Sumatra, and the South Natuna islands are now all considered to belong to *T. bancanus* (Chasen, 1940; Sody, 1949; Laurie and Hill, 1954; Hill, 1955; Niemitz, 1977, 1984a).

Philippine tarsiers were redescribed by Meyer (1894–1895) as *T. philippensis,* by Heude (1898) as *T. carbonarius,* and by Miller (1910) as *T. fraterculus.* Listed as distinct species by Taylor (1934) in his classic monograph on Philippine mammals, these names have been considered synonymous with *T. syrichta* in recent revisions (Hill, 1955; Niemitz, 1977, 1984a).

Tarsius pumilus, the main subject of our study, was unknown until 1921 when Miller and Hollister described it for the first time. It was considered a subspecies of *T. spectrum* by Laurie and Hill (1954), Hill (1955), and Niemitz (1977, 1984a), but Niemitz (1985) has recently advocated returning specific sta-

tus to *pumilus* based upon Miller and Hollister's original list of diagnostic features and analysis of presumed vocalizations of *T. pumilus.*

Taxonomic revisions of the genus *Tarsius* published between 1950 and 1984 thus identify three species: *T. syrichta* from the southern Philippine islands, *T. bancanus* endemic to the Sunda Shelf, and *T. spectrum* native to Sulawesi and nearby islands. The scientific names proposed between 1758 and 1949 that are asssociated with each species are listed by Hill (1955). The identity of a fourth species, the pygmy tarsier, *T. pumilus,* is reported here. Defining the morphological, geographic, and habitat limits of *T. pumilus* requires comparing specimens of it with samples of the other three species. To understand the significance of the differences that distinguish *T. pumilus* from those three, we present first a context of comparisons by evaluating the kinds and magnitude of differences—those published and some we discovered—that distinguish the three large-bodied species of *Tarsius.*

DIFFERENCES AMONG TARSIERS

THE SPECIES

Here we will discuss the characteristics that distinguish *T. syrichta, T. bancanus,* and *T. spectrum.* The contrasts between *T. pumilus* and these three will be covered in the next section. Each species is represented by a small number of specimens from different geographic regions that were pooled so we could obtain a large enough sample from which to evaluate the characteristics of each kind of tarsier. We did examine regional variation in some morphological features within each of the species, especially *T. spectrum,* and we will present those observations later.

Our study concentrated on morphological differences seen in the skin, cranium, mandible, and dentition because most specimens available to us consisted of these elements, and *T. pumilus* is represented only by this kind of material. We also examined other traits, such as geographic distribution and behavior, and tried to evaluate as many as possible of the features used by several authors to distinguish the three species of large-bod-

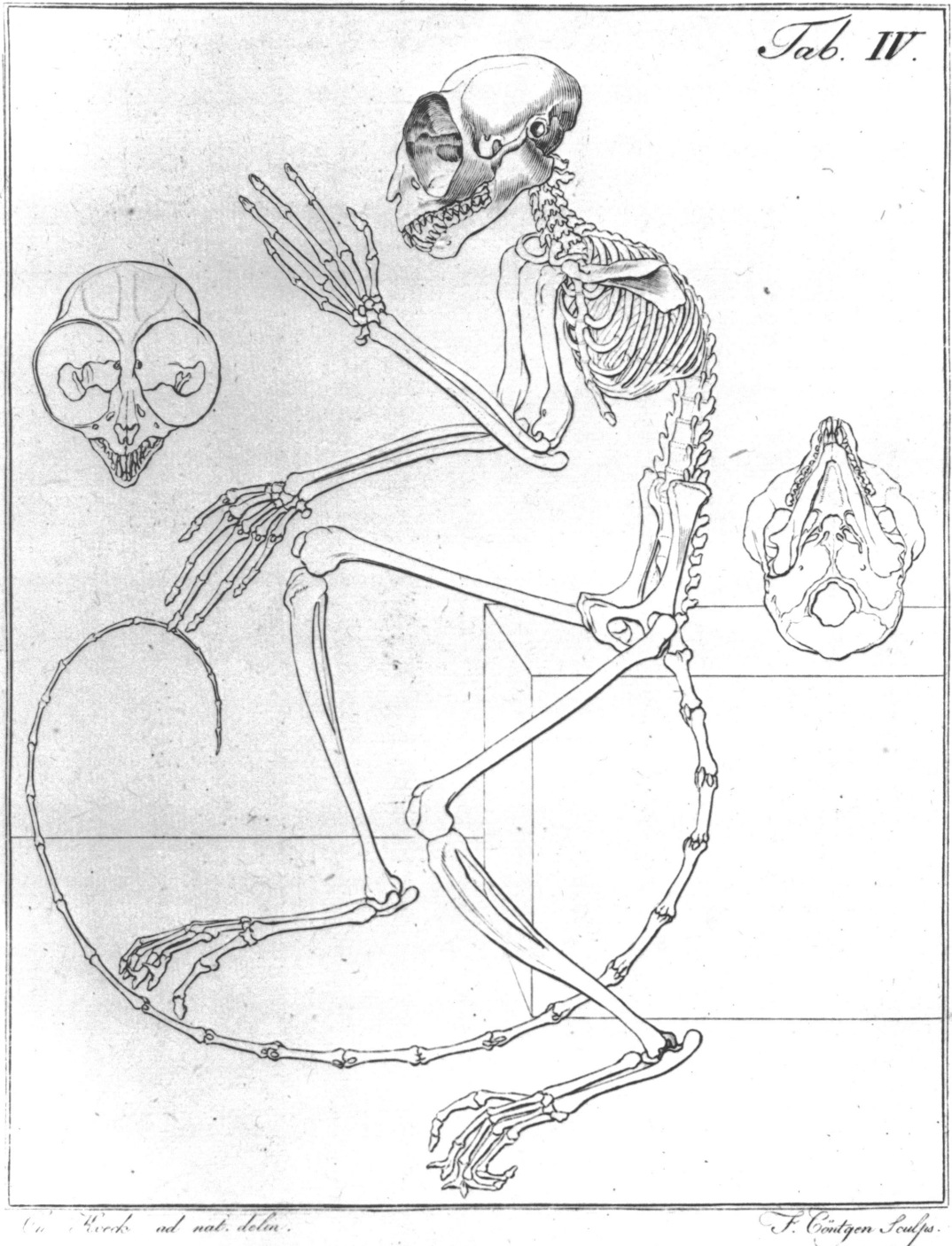Fig. 6.   Fischer's (1804) *Tarsius fuscus,* the Sulawesian tarsier.

Fig. 7.　Skeleton of Fischer's (1804) Sulawesian tarsier, *Tarsius fuscus.*

ied tarsiers. Those characteristics and our evaluation of them are listed in table 1. With the exception of Niemitz's (1977) report, most of the studies were based upon inadequate

TABLE 1

Published Morphological and Behavioral Characters Used to Distinguish *Tarsius syrichta*, *Tarsius bancanus*, and *Tarsius spectrum*

Character	Source	Our assessment
T. SYRICHTA		
Tail naked and smooth	Hill, 1955; Niemitz, 1977	Yes
Tarsi naked	Hill, 1955; Niemitz, 1977	Yes
Dentition more robust	Hill, 1955	Yes (compared with *T. spectrum*)
Relatively shorter limbs	Burmeister, 1846	Yes (compared with *T. bancanus*)
Larger eyes than *T. spectrum*	Burmeister, 1846	Yes
Larger, head length up to 40 mm	Hill, 1955	No
Median upper incisors diverging only at their tips	Hill, 1955	No
Orbits more frontally directed and more widely splayed	Hill, 1955	No
More bluntly pointed incisors than *T. spectrum*	Burmeister, 1846	No
Relatively smaller skull	Burmeister, 1846	No
Manubrium sterni shorter and broader than in *T. spectrum*	Burmeister, 1846	No
14 ribs (compared with 13 in *T. spectrum*)	Burmeister, 1846	No
Shorter and broader scapula than in *T. spectrum*	Burmeister, 1846	Not shorter; axial border longer
Broader pelvis (viewed from above), larger obturator foramen	Burmeister, 1846	No
Lacrimal bone has a wider extension than in *T. spectrum*	Forsyth-Major, 1901	—[a]
Relatively shorter femur and tibia than in *T. spectrum*	Burmeister, 1846	—[a]
T. BANCANUS		
Orbital emargination deeper than in *T. spectrum,* especially above the zygoma	Robinson and Kloss, 1919	Yes (also larger than *T. syrichta*)
Nasals shorter	Robinson and Kloss, 1919	Yes
Nares narrower and more lozenge-shaped in outline with truncate apex	Robinson and Kloss, 1919	Yes
Bullae much dilated anteriorly	Robinson and Kloss, 1919	Yes
Hand much longer	Niemitz, 1977	Yes (but similar to *T. syricta*)
Tail with papillary ridges	Hill, 1955	Yes
Diastema between incisor and canine in *T. b. bancanus*	Robinson and Kloss, 1919	Most specimens
Cranium slightly smaller	Robinson and Kloss, 1919	No
Mandibular condyles longer than broad	Robinson and Kloss, 1919	No
Diastema between canine and cheekteeth	Raffles, 1822	No (observ. based on a juvenile)
Much longer hind limbs	Niemitz, 1977	—[a]
Vocalizations different from *T. spectrum* (no male-female duets)	Niemitz, 1984b	—[a]
T. SPECTRUM		
Orbital rims less projecting, especially dorsally	Hill, 1955	Yes
White spot behind each ear	Hill, 1955; Niemitz, 1977	Yes
Tail scaly	Hill, 1955	Yes
Tarsi haired	Hill, 1955	Yes (not distinct from *T. bancanus*)
Tail hairs thick and dark	Hill, 1955	Yes
Cranial vault less arched, flatter	Hill, 1955	Yes
Lower edge of mandible straighter	Hill, 1955	No
Ascending ramus of mandible broader	Burmeister, 1846	No
Mandibular symphysis more receding	Burmeister, 1846	No

TABLE 1—(*Continued*)

Character	Source	Our assessment
Median upper incisors diverging from roots toward apices of crowns	Hill, 1955	No
More sharply pointed incisors than *T. syrichta*	Burmeister, 1846	No
More laterally directed orbits	Hill, 1955	No
Occiput more projecting	Hill, 1955	No
Longer nail on big toe	Willink, 1905	No
Broader transverse process on 6th cervical vertebra	Burmeister, 1846	No
Relatively longer extremities	Burmeister, 1846	No
Longer and more pointed ears	Hill, 1955; Niemitz, 1977; Burmeister, 1846	—[a]
Two less caudal vertebrae than in other species	Burmeister, 1846	—[a]
Vocaliziations different than in *T. bancanus* (presence of male-female duets)	Niemitz, 1984d	—[a]
Shorter hand	Niemitz, 1977	—[a]

[a] Not examined by us.

sample sizes and we found many of the supposed distinctions to be invalid. These traits, as well as those we discovered, are discussed in detail below.

1. **Geographic distribution.** Each kind of tarsier is found in a distinctive and different zoogeographic region (fig. 8). *Tarsius bancanus* is native to islands on the Sunda Shelf. Specimens have been recorded from mainland Borneo, Pulau Serasan in the South Natuna islands, Pulau Belitung, Pulau Bangka, and Sumatra (Chasen, 1940; Sody, 1949; Hill, 1955; Niemitz, 1984a). The species is also supposed to occur on Pulau Karimata between Borneo and Bangka (Teijsman, 1876) but we have been unable to verify that record. There are old published reports of the species occurring on Java, but Hill (1955) and Niemitz (1984a) explained why those records are not reliable; Chasen (1940) excluded Java from the distribution of *T. bancanus* in his list of Malaysian mammals.

Tarsius syrichta is native to the southern Philippine islands and specimens have been recorded from Samar, Leyte, Bohol, Dinagat, Basilan, and Mindanao (Taylor, 1934; Sanborn, 1952; Lawrence, 1939; Heaney and Rabor, 1982). Niemitz (1984a) also reported the species from Siargo islands, which is near Dinagat, but there are no records of specimens from there. These islands, now isolated from one another, were combined to form what Heaney (1985, 1986) has called Greater Mindanao, the vast expanse of land exposed

during the Late Pleistocene when the sea had dropped to about 120 m below its present level, and earlier during the Middle Pleistocene when seas dropped to about 160 m below present levels.

Tarsius spectrum has been recorded only from the Sulawesi region: the Sangihe islands, just north of Sulawesi; mainland Sulawesi; Pulau Peleng, off the east coast of the mainland; and Pulau Selajar, south of the Makassar arm of Sulawesi (Sody, 1949; Laurie and Hill, 1954). Niemitz reported it from Pulau Savu, a small island between Sumba and Timor but claimed the record is unreliable. We agree.

2. **Body size.** There are no significant differences in body size as measured by length of head and body or greatest length of skull among the three species (table 2; fig. 9). As Niemitz (1977) noted, this facilitates other comparisons among species since no correction for size differences is needed.

3. **Cranial features.** Several traits of the skull distinguish the species of tarsiers. The most obvious difference is in size of the orbits (fig. 10). As measured by either breadth across the orbits or the breadth and height of a single orbit, *T. spectrum* has the smallest orbits of the three species (but still the largest of any non-tarsier prosimian). There is some overlap in orbital breadth between *T. syrichta* and *T. bancanus* (table 2). Thus, as will be evident in most characteristics, there is a cline in absolute orbit size: *T. bancanus* has the
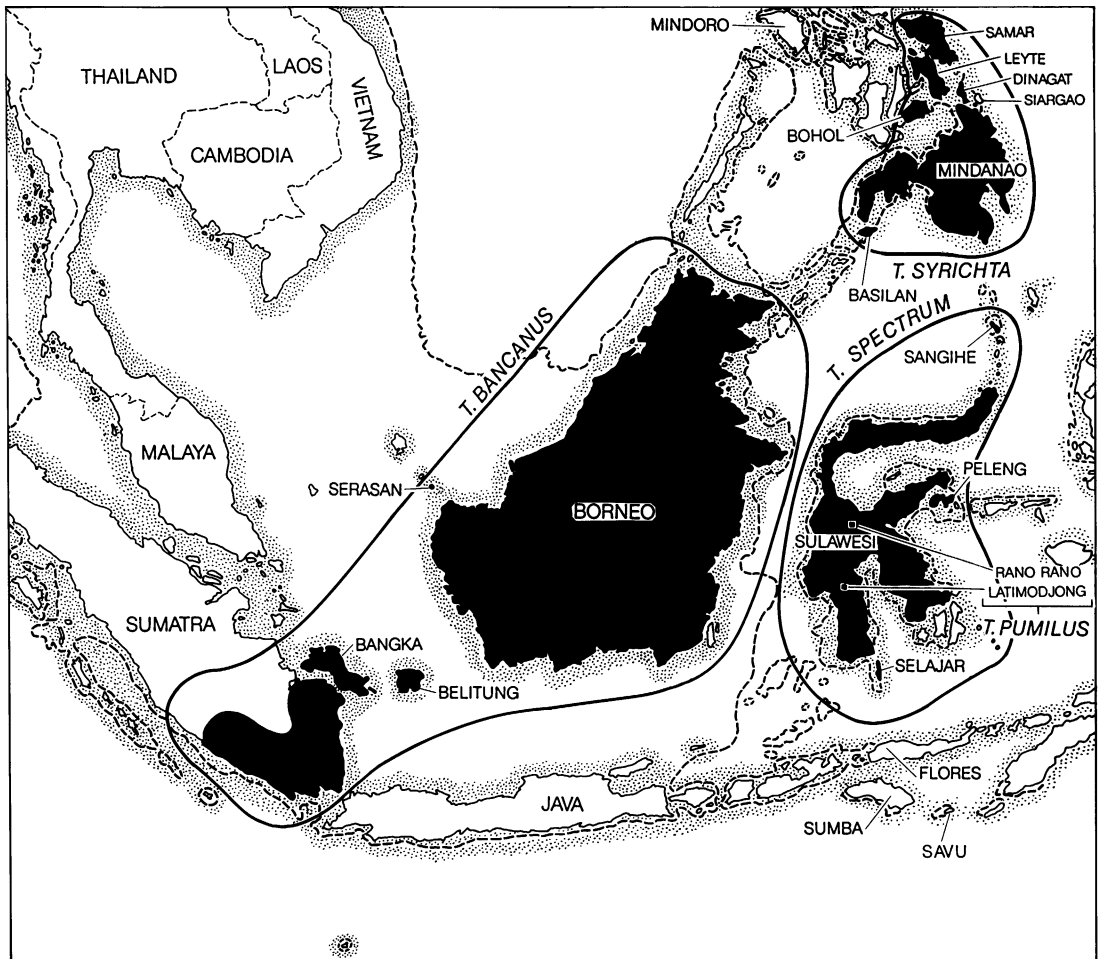
Fig. 8. Summary of geographic distributions of four species of tarsiers. The dashed line indicates the 100 fathom (180 m) bathymetric line.

largest orbits, *T. spectrum* the smallest, and *T. syrichta* is intermediate. All pairwise comparisons are statistically significant with a Student's *t*-test at $p < .01$. Perhaps related to this, *T. bancanus* has a significantly wider skull than *T. spectrum* or *T. syrichta* as indicated by values for zygomatic breadth, but there is no highly significant difference between *T. spectrum* and *T. syrichta* in this regard. Correcting for differences in body size by dividing orbit breadth by greatest skull length does not change the cline: *T. spectrum* has the relatively smallest orbits, *T. syrichta* is intermediate, and *T. bancanus* has the relatively largest orbits (table 3).

Hill (1955) claimed that *T. syrichta* has more frontally directed orbits, and *T. spectrum* more laterally directed ones, but we cannot substantiate this. We measured the degree of convergence (following the definition of Cartmill, 1972) as 47–52° in all tarsiers, with no significant differences among the species. There is no significant difference in interorbital breadth.

Hill (1955) stated that the occiput of *T. spectrum* is more projecting and the cranial vault less arched. It is difficult to evaluate the first claim; we constructed an approximate measure of occiput length by subtracting condylobasal length from greatest skull length;
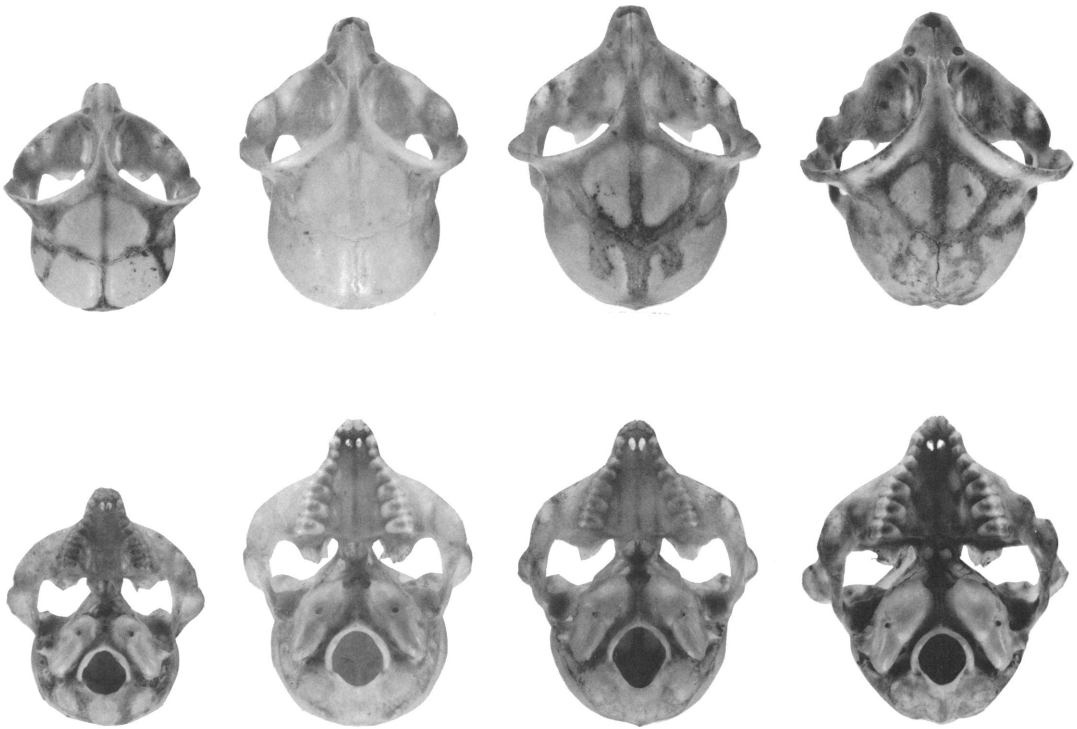
Fig. 9. Crania of adult tarsiers. From left to right: *Tarsius pumilus* (AMNH 196477), *T. spectrum* (USNM 218072), *T. syrichta* (AMNH 203296), and *T. bancanus* (AMNH 106010). Natural size.

differences among tarsiers are not significant. Braincase height is slightly lower in *T. spectrum,* perhaps supporting Hill's second claim.

Tarsius spectrum is easily distinguished from the other two species by its projecting nasal profile (fig. 11); this is associated with significantly longer nasal bones. Robinson and Kloss (1919) noted the relatively short nasals of *T. bancanus. Tarsius syrichta* and *T. bancanus* do not differ in length of nasals, but *T. syrichta* does have a slightly more projecting nasal profile than *T. bancanus.*

4. **Auditory bulla.** There are noticeable differences in the relative size of the bulla, and especially in the degree of hypotympanic sinus inflation. The bulla is significantly shorter in *T. spectrum,* although bullar breadth is equivalent in the three species (table 2). The shorter bulla of *T. spectrum* is attributable to a less inflated hypotympanic sinus. As an approximate measure of this configuration, we compared the length of the bulla anterior to the carotid foramen to the length posterior to it. Although the anterior length is longer
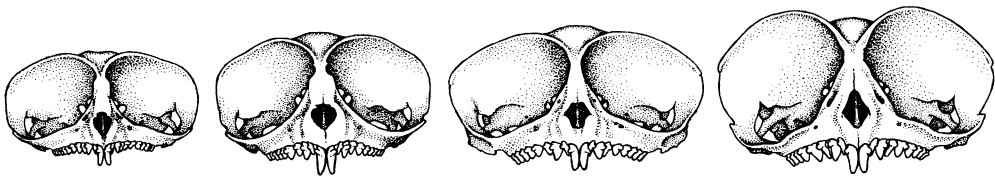

Fig. 10. Orbits of adult tarsiers. From left to right: *Tarsius pumilus* (AMNH 196477), *T. spectrum* (AMNH 196486), *T. syrichta* (AMNH 203296), and *T. bancanus* (AMNH 106010). Drawn to scale. See tables 2 and 3.
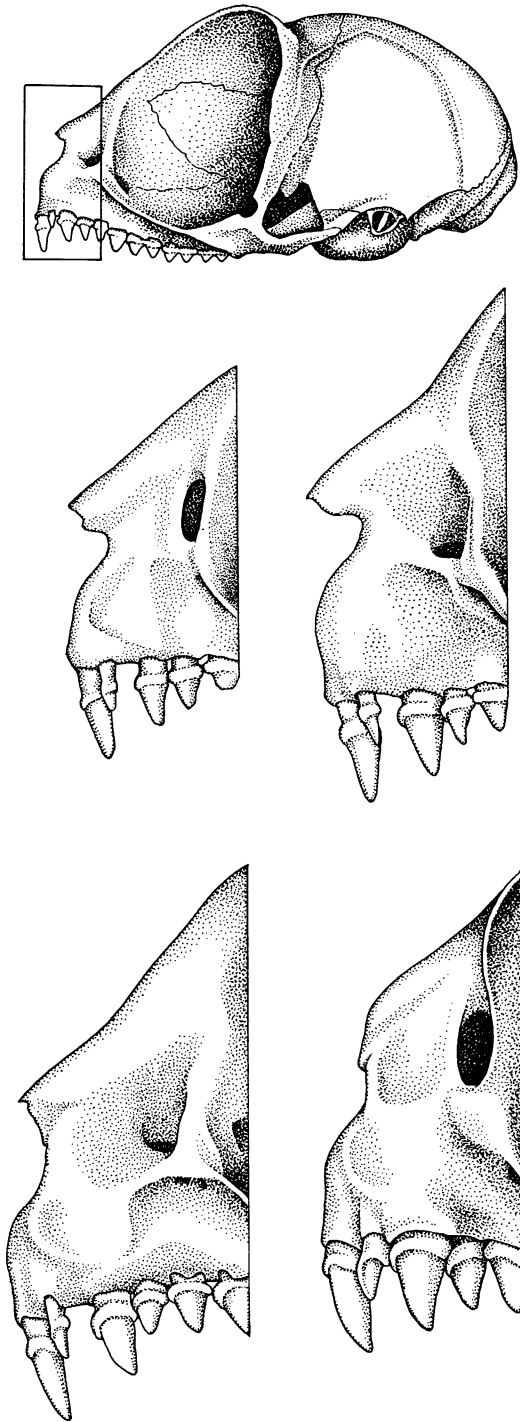
Fig. 11.   Nasal profiles in tarsiers. Top pair: left side is *Tarsius pumilus* (AMNH 196477), right side is *T. spectrum* (AMNH 196484). Bottom pair: left side is *T. syrichta* (AMNH 203296), right side is *T. bancanus* (AMNH 106010).

in all three species, *T. spectrum* shows the least development of the anterior part of the bulla (tables 2, 3; fig. 12). *Tarsius syrichta* exhibits an intermediate development, and *T. bancanus* the largest hypotympanic sinus, although the differences between *T. bancanus* and *T. syrichta* are small.

5. **Mandibular and dental features.** We cannot substantiate any of the several features of the mandible that either Hill (1955) or Burmeister (1846) listed to distinguish tarsiers. Nor do we see the differences in manner of upper incisor divergence also cited by Hill. While we find no significant differences in tooth morphology, there are real differences in absolute tooth size. The area of each molar was measured as the length multiplied by the breadth of the tooth. For all upper and lower molars, all pairwise species comparisons of molar area are statistically significant at $p <$ .01, with the single exception of the second lower molar of *T. bancanus* and *T. syrichta*. We list values for measurements of only first upper and lower molars in table 2.

Again, there is a cline in tarsiers: *T. spectrum* has the smallest relative tooth size, *T. syrichta* is intermediate, and *T. bancanus* has the largest teeth. These differences are also reflected in the lengths of the upper and lower toothrows (canine to third molar) and in the breadth of the palate at the third molar; these three features exhibit the same pattern of variation as molar area. If tooth area is divided by greatest skull length (table 3), the same pattern is observed. There is nothing in the published literature about differences in diet between the species of tarsiers which might explain the variation in relative tooth size.

6. **Tail.** As demonstrated by Hill (1953b) and Sprankel (1965) there are marked differences in traits of the tail that distinguish the three species of tarsiers. These differences concern the amount of tail hair, and histological features of the ventral surface of the tail. The tail of *T. syrichta* is usually described as being naked, but in reality it is covered with very sparse, fine, and short yellowish hairs. The tip of the tail has slightly longer and thicker hairs. There is, however, a naked patch of skin on the ventral surface of the tail. This surface exhibits moderately developed papillary ridges associated with the complete absence of hair follicles, and with
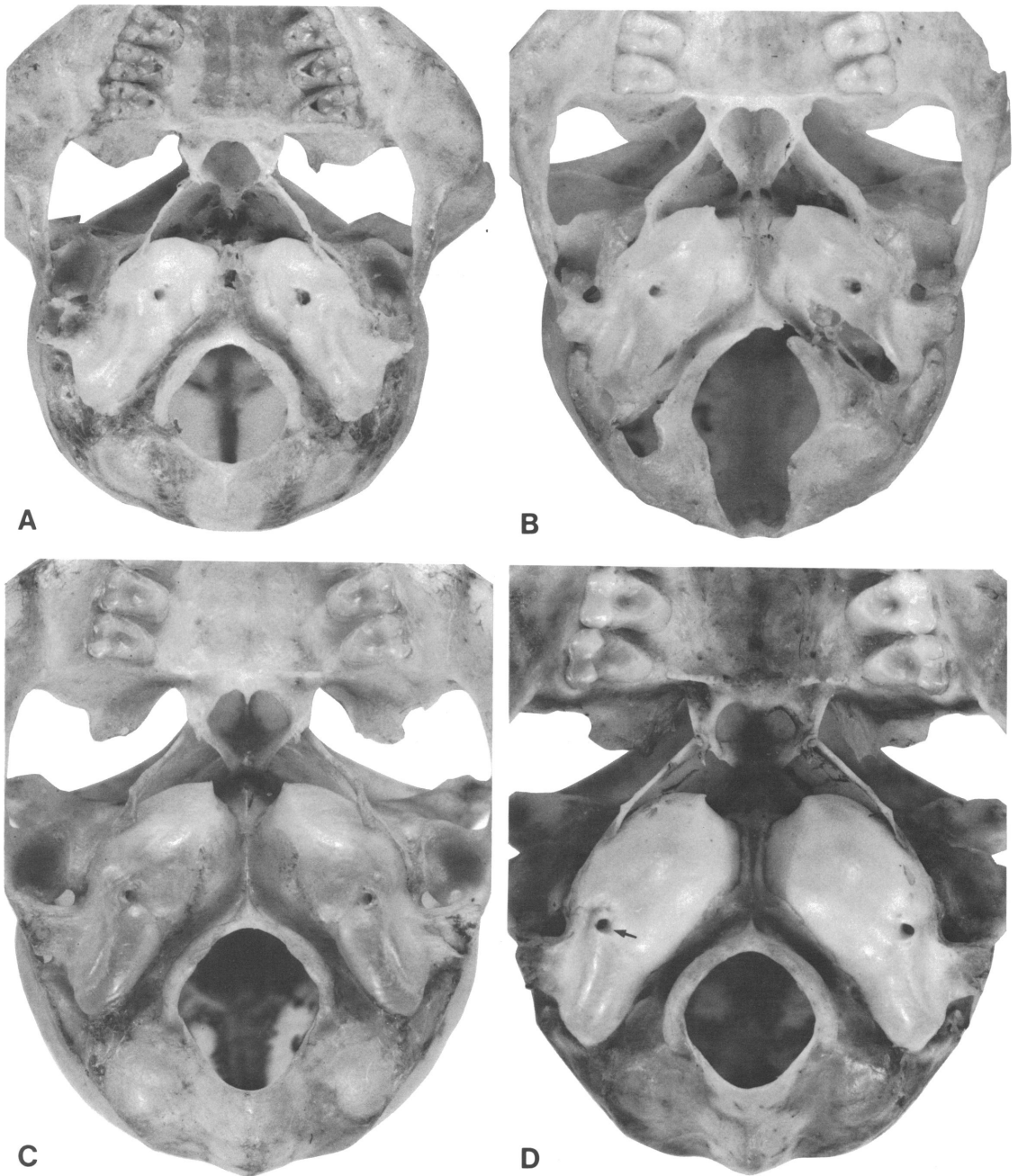
Fig. 12.   Auditory bullae of tarsiers. **A,** *Tarsius pumilus* (AMNH 196477); **B,** *T. spectrum* (AMNH 196484); **C,** *T. syrichta* (AMNH 203296); and **D,** *T. bancanus* (AMNH 106010). Note inflation of portion anterior to carotid foramen (arrow in D) relative to length of segment behind that foramen. See tables 2 and 3. × 3.

a layer of apocrine glands underlying the skin. *Tarsius bancanus* is generally similar to *T. syrichta,* but is even more specialized, showing well-developed papillary ridges. *Tarsius*

bancanus has darker, thicker, and longer hair on the distal tip of the tail.

In *T. spectrum* the entire tail is much more heavily haired than in either *T. bancanus* or

TABLE 2
Measurements (in mm) of Adults from Samples of Four Species of *Tarsius*
(Mean plus or minus one standard deviation, number of specimens in parentheses, and
observed range are listed.)

Measurement[a]	T. pumilus	T. spectrum	T. syrichta	T. bancanus	Sig.[b]
Length of head and body	96.5 (2) 95–98	127.8 ± 8.9 (54) 112–151	127.3 ± 8.1 (6) 118–140	132.2 ± 10.5 (10) 115–147	
Length of third finger	17.4 (2) 16.2–18.6	22.8 ± 1.6 (56) 21.0–26.4	24.9 ± 1.4 (8) 23.1–27.1	27.3 ± 2.3 (11) 21.8–30.4	ABc
Greatest length of skull	30.9 (2) 30.7–31.1	37.2 ± 1.1 (47) 35.5–39.5	38.3 ± 1.2 (11) 36.6–40.0	38.1 ± 1.1 (10) 36.4–39.3	
Zygomatic breadth	24.2 (2) 23.9–24.5	27.1 ± 1.0 (44) 24.9–29.2	27.8 ± 1.2 (11) 24.8–29.0	30.2 ± 1.0 (10) 28.8–31.5	BC
Breadth across orbits	26.4 (2) —	29.0 ± 0.8 (46) 27.4–30.0	31.7 ± 1.2 (11) 29.1–33.5	34.2 ± 0.9 (9) 32.9–35.1	ABC
Breadth of single orbit	14.4 (2) 14.3–14.5	15.8 ± 0.5 (52) 14.9–16.8	17.8 ± 0.7 (12) 16.4–18.8	19.4 ± 0.4 (11) 18.7–20.0	ABC
Height of single orbit	14.5 (2) 14.2–14.7	16.0 ± 0.5 (51) 14.8–16.9	17.9 ± 0.8 (12) 16.0–18.7	19.5 ± 0.5 (11) 18.7–20.3	ABC
Length of nasals	5.2 (2) 4.6–5.7	7.2 ± 0.7 (37) 6.1–8.6	5.9 ± 0.9 (10) 4.1–6.5	5.6 ± 0.3 (10) 5.0–6.0	AB
Breadth of palate at M^3	12.1 (2) 11.9–12.2	14.4 ± 0.4 (47) 13.6–15.3	16.1 ± 0.3 (11) 15.5–16.6	17.4 ± 0.7 (11) 16.1–18.7	ABC
Length of bulla	9.7 (2) 9.6–9.7	11.3 ± 0.4 (53) 10.6–12.0	12.3 ± 0.5 (11) 11.4–13.0	12.5 ± 0.4 (11) 11.9–13.0	AB
Breadth of bulla	5.1 (2) 4.8–5.4	6.6 ± 0.5 (52) 5.7–7.5	6.6 ± 0.5 (11) 5.7–7.3	6.7 ± 0.4 (11) 6.2–7.5	
Anterior length of bulla	4.6 (2) —	6.8 ± 0.4 (50) 5.9–7.8	7.9 ± 0.4 (11) 7.0–8.6	8.4 ± 0.6 (11) 7.6–9.5	ABc
Posterior length of bulla	6.4 (2) 6.3–6.4	5.1 ± 0.4 (50) 4.4–6.6	5.4 ± 0.6 (11) 4.3–6.7	5.2 ± 0.3 (11) 4.9–5.6	
Length of C-M^3	10.6 (2) 10.4–10.7	12.6 ± 0.3 (51) 11.9–13.4	13.9 ± 0.5 (11) 13.1–14.7	14.7 ± 0.4 (11) 13.7–15.2	ABC
Length of C-M_3	10.9 (2) 10.8–10.9	13.4 ± 0.5 (52) 12.1–14.3	14.5 ± 0.8 (11) 13.5–16.2	15.3 ± 0.6 (11) 14.0–15.9	ABC
Length of M^1	1.9 (2) 1.8–1.9	2.3 ± 0.1 (52) 2.0–2.5	2.6 ± 0.1 (11) 2.4–2.8	2.6 ± 0.2 (11) 2.2–2.7	AB
Breadth of M^1	2.9 (2) —	3.5 ± 0.2 (52) 3.2–3.8	4.0 ± 0.3 (11) 3.5–4.4	4.4 ± 0.2 4.0–4.8	ABC
Length of M_1	2.0 (2) 1.8–2.2	2.2 ± 0.1 (49) 2.0–2.5	2.6 ± 0.1 (11) 2.4–2.8	2.8 ± 0.2 (11) 2.4–3.0	ABC
Breadth of M_1	1.9 (2) 1.8–1.9	2.2 ± 0.1 (49) 2.0–2.4	2.5 ± 0.2 (11) 2.2–2.7	2.7 ± 0.2 (11) 2.3–3.0	ABc
Area of M^{1c}	5.4 (2) 5.2–5.5	7.9 ± 0.6 (52) 6.6–9.5	10.2 ± 1.2 (11) 8.4–12.0	11.6 ± 1.0 (11) 8.8–12.5	ABC
Area of $M_1{}^c$	3.7 (2) 3.2–4.2	4.9 ± 0.5 (49) 4.0–6.0	6.4 ± 0.6 (11) 5.3–7.3	7.9 ± 0.5 (11) 7.3–8.4	ABC

[a] Limits are illustrated and explained on pp. 6–8.
[b] Results of Student's *t*-tests. A compares *T. spectrum* with *T. syrichta,* B compares *T. spectrum* with *T. bancanus,* and C compares *T. syrichta* with *T. bancanus.* Capital letter designates significance at $p = .01$ or less, small letter is the significance at $p = .05–.01$.
[c] Area of each tooth is length multiplied by breadth; values are in mm^2.

T. syrichta (compare figs. 13 and 14). The terminal pencil is 30–45 percent of total tail length (Hill, 1953b) as opposed to 17–31 percent in other tarsiers. The hair is dark brown or black. Several authors have described the ventral side of the tail of *T. spectrum* as being scaly (for example, Weber, 1894). Hill (1953b, p. 22), however, has shown that the scaliness does not refer to any condition of the skin itself; the "scales" are "short, blunt, keratinized structures, in groups of three, projecting distally from the edges of the pale transverse cutaneous folds." These structures are simply short, thick hairs. There is individual variation in the extent of this "scaly" patch within *T. spectrum*. In some individuals it covers most of the ventral part of the tail, extending from the base to where the terminal pencil begins, in others it occurs only in small patches, and in one individual (AMNH 153554) we found no "scales" at all.

Hill (1953a) and Sprankel (1965) attributed the specializations of the ventral surface of tarsier tails to their function in body posture. The tail is often braced against a support and helps to prop up the body in the vertical clinging position. Hill (1953a) likened the pattern of *T. spectrum* to the pattern typical of most primitive mammals. Therefore, he believes that *T. spectrum* has the least specialized tail, and *T. bancanus* the most, with *T. syrichta* intermediate. He further argued that the differences between *T. spectrum* and the other tarsiers suggest a diphyletic origin. This hypothesis was questioned by Sprankel (1965), who demonstrated the developement of the papillary ridges of *T. bancanus* from a more *T. spectrum*-like arrangement early in ontogeny.

7. **Pelage.** We agree with Niemitz (1977, 1984a) that there are few characters of the pelage which allow easy distinction of the species. Generally, *T. bancanus* and *T. syrichta* are more yellowish than *T. spectrum*, and their fur appears paler. *Tarsius spectrum* has longer, denser fur but is most easily distinguished by its conspicuous white postauricular spots. We have never seen such spots in either *T. bancanus* or *T. syrichta*.

Tarsius syrichta is distinguished from the other species by its almost naked tarsus (fig. 14). The heel is not covered with dense hair like the rest of the torso. Instead, the foot,

from its proximal end to the toes, is covered with very sparse, fine, and short hair; the skin is clearly visible. There is an abrupt change from the dense hair above the calcaneus to the sparse hair on and below the calcaneus. In *T. bancanus* the leg down to the navicular-cuneiform joint is covered with relatively dense hair like that over the rest of the torso. The fur does gradually thin out over the heel and foot, but it is always thicker than in *T. syrichta*. *Tarsius spectrum* is intermediate in appearance. Generally, the tarsus is rather sparsely haired, as in *T. syrichta*, but the hairs are longer and darker. There is also a fair amount of individual variation; specimens from Bumbulan on the northern arm of Sulawesi, and from the Sangihe islands resemble *T. syrichta* in having nearly naked tarsi; other populations are more like *T. bancanus*.

8. **Limb proportions.** Niemitz (1977, 1979, 1984a) has demonstrated significant differences in limb proportions in the three species. To summarize his findings: *T. bancanus* has the longest hindlimb and hand. *T. syrichta* has shorter hindlimbs than *T. bancanus*, and hands that are intermediate in absolute length between *T. bancanus* and *T. spectrum* (but the same as *T. bancanus* relative to length of head and body, table 3); and *T. spectrum* is the least specialized in these features, having the shortest hindlimbs and hands. Niemitz (1984c) and MacKinnon and MacKinnon (1980) have also demonstrated that *T. spectrum* uses a wider variety of substrate sizes and orientations, and is active over a greater vertical distance than *T. bancanus*. To Niemitz (1979), this suggests that *T. spectrum* is less specialized in its locomotion than either *T. bancanus* or *T. syrichta*, and correlates with the differences in limb structure. The large hands of *T. bancanus* are used to immobilize prey before killing with the incisors, and are of secondary importance in locomotion. The smaller hands of *T. spectrum*, according to Niemitz, suggest more use in locomotion. This may also explain the differences in nail structure which will be described in a later section of our report.

9. **Vocalizations.** Niemitz (1984e) has discussed the differences in vocal communication between *T. bancanus* and *T. spectrum*. *Tarsius syrichta* has apparently not been similarly studied. The most striking difference between the two species is the presence of
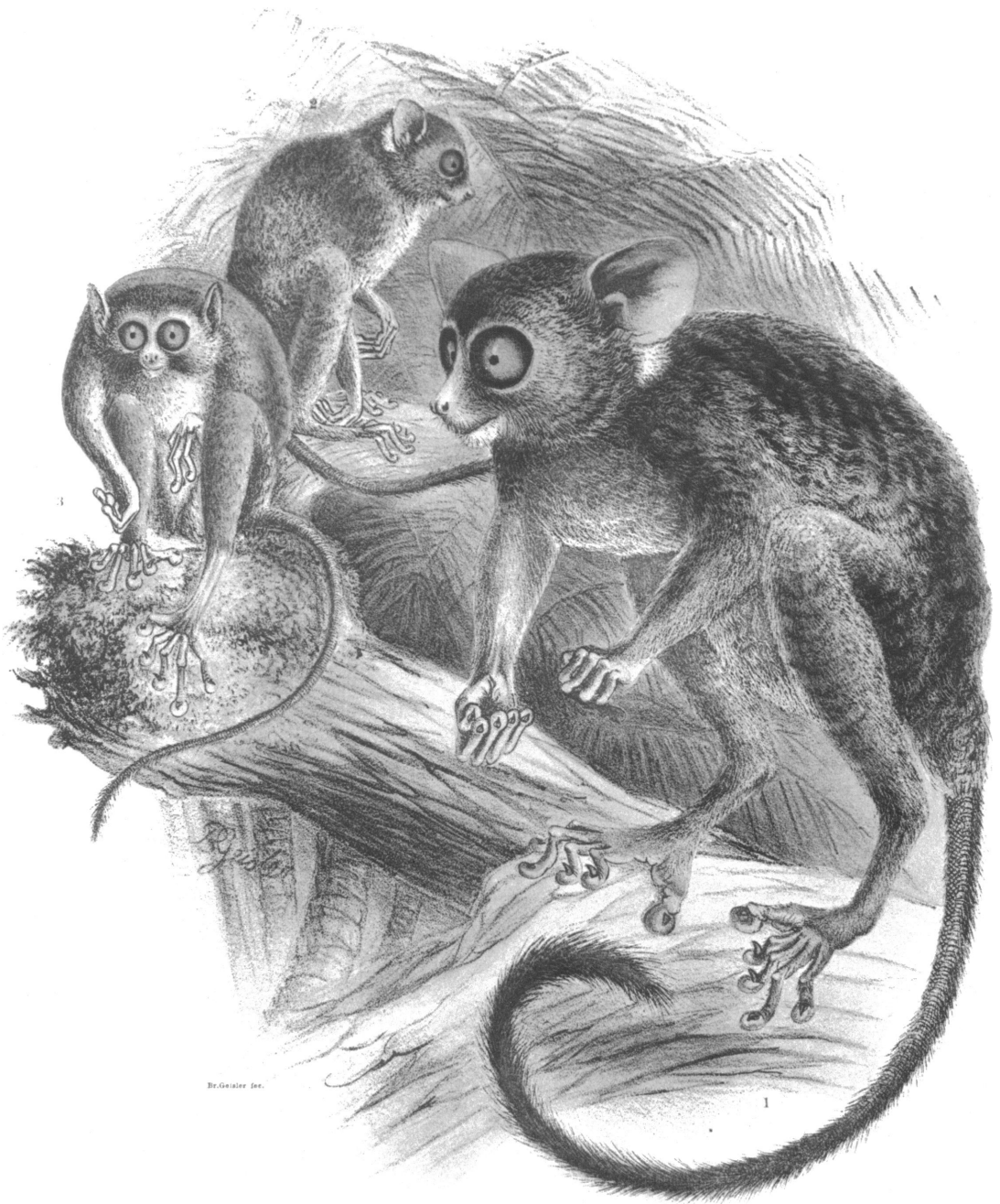
1 - 2 *Tarsius fuscus* Fisch.-Waldh.   3 *Tarsius sangirensis* A. B. Meyer

1 nat. Grösse, 2 circa ⅔, 3 circa ½ nat. Grösse

Fig. 13.   *Tarsius spectrum*. Reproduced from Meyer's (1898/1899) color plate III.

male-female morning and evening duets in *T. spectrum* (MacKinnon and MacKinnon, 1980) and the lack of such duets in *T. bancanus*. Laboratory studies of *T. syrichta* in-
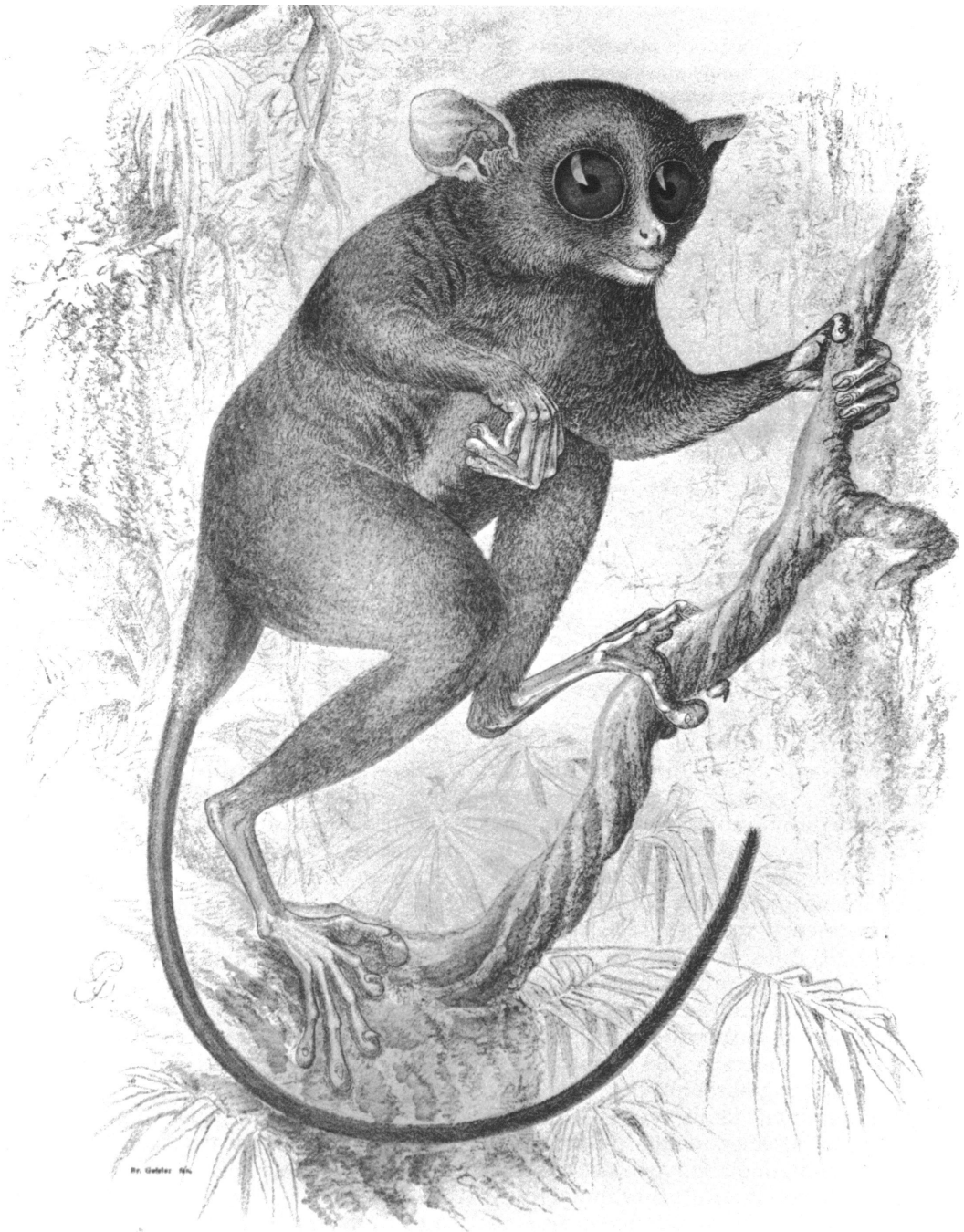
Fig. 14. *Tarsius syrichta.* Reproduced from Meyer's (1896/1897) color plate IV.

dicate that it, like *T. bancanus,* does not have a duet call (Haring et al., 1985). Males and females of *T. spectrum* have different calls; no such difference exists in *T. bancanus.*

10. **Chromosomes.** *Tarsius bancanus* (Klinger, 1963; Poorman et al., 1985) and *T. syrichta* (Chiarelli and Egozcue, 1968) have been karyotyped. The diploid number is 80

TABLE 3
Ratios (in percent) from Samples of Four Species of *Tarsius*
(Mean plus or minus one standard deviation, number of specimens in parentheses, and
observed range are listed. Values are derived from data listed in table 1.)

Ratio	T. pumilus	T. spectrum	T. syrichta	T. bancanus
Length of third finger / Length of head and body	18.0 (2) 17.1–19.0	17.5 ± 1.4 (56) 15.0–21.3	20.0 ± 1.1 (3) 18.9–20.9	20.6 ± 2.0 (10) 17.9–21.3
Breadth across orbits / Greatest length of skull	46.6 (2) 46.0–47.2	42.5 ± 1.4 (47) 39.9–45.4	46.5 ± 1.5 (11) 43.9–49.6	50.7 ± 0.8 (10) 49.4–51.8
Length of nasals / Greatest length of skull	16.7 (2) 14.8–18.6	19.4 ± 2.1 (34) 16.4–23.9	15.2 ± 2.2 (10) 10.8–19.2	14.8 ± 0.7 (9) 13.6–15.6
Anterior length of bulla / Posterior length of bulla	72.4 (2) 71.9–78.0	132.0 ± 10.1 (50) 101.5–154.5	147.3 ± 14.3 (10) 128.4–166.7	161.7 ± 14.2 (11) 138.2–184.8
Breadth of palate at M^3 / Greatest length of skull	39.0 (2) 38.8–39.2	38.6 ± 1.1 (45) 35.7–40.9	42.0 ± 2.0 (11) 39.1–45.1	45.8 ± 1.4 (10) 43.9–48.8
Area of M^1 / Greatest length of skull	17.4 (2) 17.0–17.7	21.4 ± 1.5 (45) 18.2–25.3	26.6 ± 3.5 (11) 21.0–32.9	30.4 ± 2.5 (10) 24.0–32.6
Area of M_1 / Greatest length of skull	12.0 (2) 10.6–13.4	13.1 ± 1.3 (42) 10.7–14.8	16.8 ± 1.7 (11) 13.2–19.9	20.9 ± 1.2 (10) 18.5–22.5

in both species; the majority of chromosomes are acrocentric. To our knowledge neither *T. spectrum* nor *T. pumilus* have been karyotyped.

Considering all of the morphological differences we examined and those described by Niemitz (1977, 1984a), *T. syrichta* and *T. bancanus* are more similar to each other than either is to *T. spectrum* (figs. 9–12). The Sulawesian species differs from the other two in having: (1) longer and more pointed ears; (2) white postauricular spots; (3) scaly segments on the tail; (4) thick and dark tail hairs; (5) shorter hand; (6) less projecting orbital rims and smaller orbits (indicating smaller eyes), both in absolute measurements and relative to skull length; (7) less arched cranial vault; (8) more projecting nasal profile; (9) less inflated hypotympanic sinus; and (10) shorter toothrows and smaller molars, both in absolute dimensions and relative to size of skull. The spectral tarsier is clearly morphologically distinctive compared to the Bornean and Philippine animals, and nobody since the time that Hill's (1953a, 1953b, 1955) studies were published has questioned the specific status of the Sulawesian populations.

That the morphological contrasts between *T. bancanus* and *T. syrichta* reflect genetic isolation is not as strong a hypothesis compared to the picture of *T. spectrum*. Because the Bornean and Philippine populations are never found sympatrically and because they are morphologically very similar compared to *T. spectrum*, Drs. Karl Koopman and Eric Delson have contended to us that available sets of samples may represent two distinctive subspecies—a southern Philippine form and a Sundaic group—and not genetically isolated entities.

We point out that there are consistent differences between the two species in pelage, cranial, and behavioral traits, differences that strongly bolster the hypothesis of Sundaic and Philippine species, not subspecies. Each specimen of *Tarsius syrichta* we examined is clearly distinguished from those of *T. bancanus* by its scantily haired tarsi and tail. There are also histological differences in the ventral surface of the tail (Hill, 1953b; Sprankel, 1965). When adult skulls of each species are compared, *T. bancanus* has absolutely larger orbits than does *T. syrichta* and a greater breadth across the orbits, both in absolute values and relative to greatest length of skull; a bony palate that is absolutely wider, and wider relative to skull length; and longer toothrows with greater molar areas, both in absolute values and relative to size of skull (tables 2, 3). These differences are

significant. In addition, Niemitz (1977, 1979, 1984a) has described significant differences in absolute length of the hand (but no difference in this trait relative to body size) and lower limb segments. Finally, recent results from the laboratory at Duke University Primate Center demonstrate behavioral differences between *T. bancanus* and *T. syrichta* in the amounts of allogrooming, play, scent marking, and in the manner of courtship behavior (Haring et al., 1985). Thus, we accept the samples as representing distinct species, although (as in many such disjunct cases) certainty is not possible.

THE SUBSPECIES

Despite all the published information on taxonomy, geographic distribution, and morphology of tarsiers as well as other aspects of their biology (Hill, 1955; Niemitz, 1977, 1984a), no thorough study has been made on regional variation in morphological and behavioral characteristics within each of the species. We examined, but not in great depth, geographic variation in skin and skull features in *T. spectrum* because we needed to know if all samples of that species were more or less alike or if any of them shared some characters with the small-bodied *T. pumilus*. It is really the identity of the latter that we were trying to assess. We also examined samples of *T. syrichta* and *T. bancanus* from different islands to be sure that the morphological distinctions we noted among the species were valid no matter where the sample originated. Although our analysis of regional variation was incomplete, we provide a few observations.

Niemitz (1984a), the last revisor of tarsiers, recognized two subspecies of *T. bancanus*: the Bornean tarsier, *T. b. borneanus,* and the Sumatran form, *T. b. bancanus.* After discussing insular variation among the samples he examined, as well as published opinions about the distinctions of various subspecies, and providing reasons for not recognizing some of these, Niemitz (1984a, p. 11) wrote that his

> study shows that large sample sizes are necessary in order to establish clear differences. As differences can be found between any statistical populations through an increase of the sample

sizes, reasonable arguments for a definitive establishment of these two subspecies are still lacking. On the other hand, so many measurements tend to indicate differences that a comprehensive study using less fragmentary material is the only way to settle this problem.

No data we collected would change this view.

Although subspecies have been described for the Philippine tarsier, Niemitz (1984a) does not think any of the names indicate morphologically identifiable populations and he does not recognize subspecies in *T. syrichta.* Our material was inadequate and we could not obtain data to either support or modify his conclusion. Heaney and Rabor (1982), however, thought the single large male they reported from Dinagat Island was distinctive in size and fur coloration compared to samples of *T. syrichta* from Mindanao, Leyte, Samar, and Bohol.

Within several species of endemic Sulawesian mammals, such as macaques and rodents, there is geographic variation in features of skin, skull, and dentition which is usually correlated with the peninsular conformation of Sulawesi and the presence of large nearby islands (Fooden, 1969; Musser, 1983–1984, 1987). The pattern of morphological variation in *Tarsius spectrum* may be an exception. In the past, workers have recognized regional variation within *T. spectrum* but the degree of morphological differences among the populations and whether to recognize them as subspecies or not has been variously recognized and differently treated. In his classic monograph, Hill (1955) recognized five subspecies: *T. s. spectrum* from the southwestern and northern peninsulas, *T. s. dentatus* and *T. s. pumilus* from Central Sulawesi, *T. s. pelengensis* from Pulau Peleng, and *T. s. sangirensis* from the Sangihe islands. Laurie and Hill (1954), in their list of land mammals of New Guinea, Celebes, and adjacent islands, also recognized *T. s. sangirensis,* but they incorporated *dentatus* within typical *T. s. spectrum,* and questioned the validity of *T. s. pumilus* and *T. s. pelengensis.*

Niemitz (1984a) explained his reasons for thinking that the diagnostic features of *dentatus, pelengensis,* and *sangirensis* are insignificant in distinguishing them from typical *T. s. spectrum.* The pattern of regional vari-
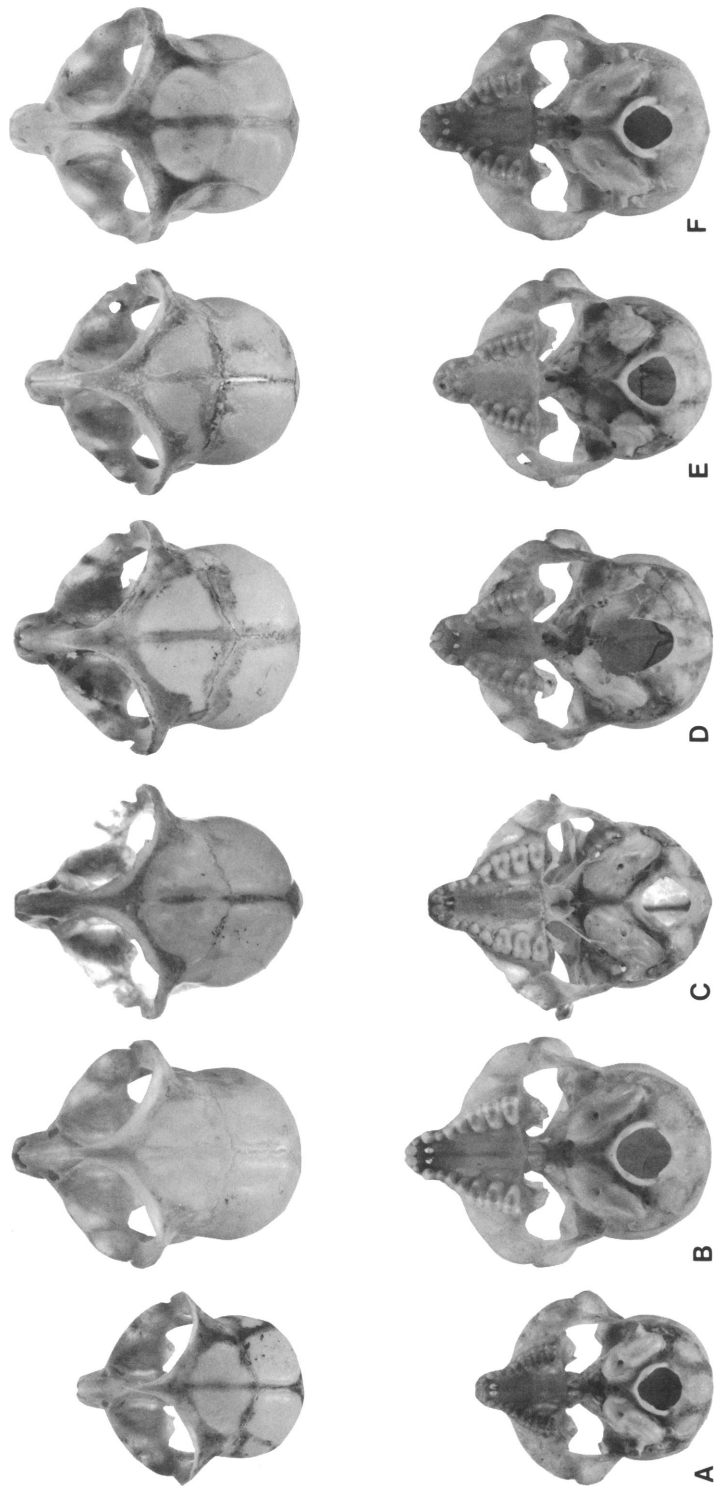
Fig. 15. Crania of adult tarsiers. *Tarsius pumilus*, **A,** (AMNH 196477) from Pegunungan Latimodjong in Central Sulawesi is contrasted with *T. spectrum* from the following regions of Sulawesi; **B,** Labua Sore, northcentral (USNM 218072); **C,** Pulau Peleng (AMNH 109367); **D,** Rurukan, northeastern arm (AMNH 196479); **E,** Lombasang, southwestern peninsula (AMNH 153558); **F,** Wawo, southeastern arm (AMNH 153560). Natural size.

ation in morphological features studied by Niemitz indicated to him that only two subspecies could be recognized: *T. s. spectrum* and the montane *T. s. pumilus* from Central Sulawesi, a form he thought might be specifically distinct.

We agree with Niemitz about *pumilus.* As we explain in the following section, *T. pumilus* is a distinct species but the specimens upon which it is based and their altitudinal distributions are different from what Niemitz envisioned. We also would not formally recognize subspecies in *T. spectrum* but not because there are no significant differences among samples. We see differences but do not know what they mean. We also have very few specimens from the different regions of Sulawesi; our material is clumped, most of it originating from the northern peninsula and from Pulau Peleng. We can only present our view of regional variation based upon these skewed samples (table 4; fig. 15).

Tarsius spectrum sangirensis from the Sangihe islands, between the tip of northeastern Sulawesi and Mindanao in the Philippines, was established by Meyer (1896–1897) on the basis of the tail being less hairy, the tarsi almost completely nude, and no scaly segments on the ventral surface of the tail. These features would align the Sangihe island form with *T. syrichta* rather than with *T. spectrum.* Niemitz (1977, 1984a), however, found the tail to be very scaly, as in typical *T. spectrum.* Elliot (1913), based upon Meyer's (1896–1897) plate, thought that the paler coloring of the face was distinct from *T. spectrum.* Sody (1949) agreed that *T. s. sangirensis* was fairly distinctive. After examining one specimen in the British Museum, Hill (1955) detected little difference between it and mainland samples of *T. spectrum.* Finally, Niemitz (1977, 1984a) claimed that values from skull and body measurements showed little distinction from typical *T. spectrum.*

Results of our study of the Sangihe island specimens in the British Museum and the Museum of Comparative Zoology at Harvard concur with Niemitz's observations. The pelage resembles that of Sulawesian *T. spectrum.* The tarsus is sparsely haired, but some individuals of *T. spectrum* do resemble *T. syrichta* in this regard. The tail, although less

densely haired than in typical *T. spectrum,* is not at all similar to the sparsely haired tail of *T. syrichta.* The typical scaly pattern on the ventral surface of the tail of *T. spectrum* is definitely present in the Sangihe island tarsier. Size of the orbits, length of the toothrows, and morphology of the bullae are more typical of *T. spectrum* than of either *T. syrichta* or *T. bancanus* (compare tables 1 and 4).

The Sangihe island tarsier's distinctive reduction of caudal and tarsal hairiness may warrant its subspecific distinction. The population may also lack the postauricular white spots that are so typical of other *T. spectrum.*

The Central Sulawesian *T. s. dentatus* was established by Miller and Hollister (1921b) as having grayer pelage, a longer tail, larger skull, and larger teeth. Both Sody (1949) and Niemitz (1977, 1984a) disagreed with Miller and Hollister on the distinctiveness of the pelage and on the magnitude of the differences in the three other characters. According to them, tail length overlaps greatly between *dentatus* and *spectrum,* and the skulls and toothrows of *dentatus* are only 2.5 percent longer. We note that though the three specimens from Labua Sore are very gray, both gray and brownish red variants are found in all populations of spectral tarsiers.

Tail length does vary greatly in *T. spectrum,* nevertheless, all three examples of *dentatus* have values in the highest end of the range, and the difference in tail length between *dentatus* and other mainland spectral tarsiers is statistically significant ($p < .05$).

Average skull length is only 1 mm higher in *dentatus,* but again this difference is significant ($p < .05$). These differences are suggestive of a distinctive population, but as both the magnitude of the differences and the sample of *dentatus* are so small, we cannot judge the subspecific status of *T. spectrum dentatus.*

A stronger case can be made for *T. s. pelengensis* from Pulau Peleng. This subspecies was established by Sody (1949) from a series of nine specimens which he claimed had larger skulls and shorter toothrows. Niemitz (1977, 1984a), however, found only a 2 percent difference in skull length, and no difference in length of toothrow. We examined 20

TABLE 4
Measurements (in mm) of Adults from Geographic Samples of *Tarsius spectrum*
(Mean plus or minus one standard deviation, number of specimens in parentheses, and observed range are listed.)[a]

Region	LHB	LT	GLS	BO	LC-M^3	LC-M_3
Northeast Arm (East of Gorontolo: Manembo Nembo, Manado, Kalabat, Rurukan, Molenka-poti)	129.6 ± 8.0 (14) 118–146	216.9 ± 23.9 (14) 185–258	36.5 ± 0.7 (13) 35.5–37.6	28.8 ± 0.6 (13) 27.4–29.5	12.7 ± 0.3 (12) 12.1–13.4	13.6 ± 0.3 (13) 13.2–14.2
Northern Arm (West of Gorontolo: Bumbulan, Toli Toli)	121.9 ± 6.9 (10) 115–135	241.5 ± 15.3 (11) 208–265	36.4 ± 0.8 (6) 35.7–38.0	28.8 ± 0.9 (5) 27.6–29.7	12.5 ± 0.3 (9) 12.2–13.0	13.0 ± 0.5 (9) 12.1–13.8
Central (Labua Sore, Parigi)	123.8 ± 11.8 (4) 112–140	258.8 ± 8.5 (4) 250–260	37.5 ± 0.3 (3) 37.2–37.8	29.4 ± 0.3 (3) 29.1–29.6	13.0 ± 0.3 (3) 12.8–13.3	13.6 ± 0.2 (3) 13.4–13.8
Southwest Arm (Lombasang)	131.6 ± 11.5 (5) 123–151	226.6 ± 30.3 (5) 176–251	36.5 ± 0.8 (4) 35.6–37.1	28.6 ± 0.8 (4) 27.8–29.6	12.2 ± 0.3 (5) 11.9–12.6	12.9 ± 0.4 (5) 12.4–13.3
Southeast Arm (Wawo)	133 (1)	238 (1)	36.7 (1)	29.6 (1)	12.5 (1)	13.0 (1)
Pulau Peleng	134.5 ± 6.5 (20) 115–148	251.1 ± 10.0 (22) 231–268	38.0 ± 0.9 (20) 35.6–39.5	29.2 ± 0.9 (20) 26.1–30.0	12.7 ± 0.2 (20) 12.4–13.2	13.7 ± 0.3 (20) 13.0–14.3
Kepulauan Sangihe[b]	121.5 ± 23.2 (4) 106–156	255.5 ± 15.5 (4) 234–271	38.3 ± 2.0 (4) 37.2–40.0	29.4 (1)	13.8 (1)	13.2 (1)

[a] Abbreviations: LHB, length of head and body; LT, length of tail; GLS, greatest length of skull; BO, breadth across orbits; LC-M^3, length of upper toothrow; LC-M_3, length of lower toothrow.

[b] We measured only one specimen from here; the other values were obtained by Dr. Colin P. Groves.

tarsiers collected on Pulau Peleng. Greatest length of skull is significantly greater ($p <$ .001) in the sample, although again the magnitude of the difference is small (the means differ by 1.5 mm, only a 4% difference). Length of head and body is also greater in the Peleng population ($p < .01$), suggesting a generally larger animal (table 4). There is no difference in absolute length of the upper toothrow, and the lower toothrow is in fact slightly longer ($p < .05$). Given the difference in skull lengths, this suggests relatively smaller upper teeth in Peleng tarsiers; an index of upper toothrow length/greatest skull length does show a significant difference in the relative length of the upper toothrow ($p < .001$), but as expected, no difference in the lower toothrow. There are few differences in pelage to distinguish Peleng from mainland tarsiers. We note, however, that only one of our Peleng animals is at all reddish; the rest are gray with a yellowish tinge.

For the present, we can only comment upon the morphological distinctions we see that separate the samples of tarsiers described as *sangirensis, dentatus,* and *pelengensis*; we cannot resolve the real pattern of regional morphological variation among populations of *T. spectrum,* if any pattern exists. We cannot state, for example, whether populations in the northern peninsula are the same as those in the southwestern peninsula, as have other workers (Laurie and Hill, 1954; Hill, 1955; Niemitz, 1984a). We studied more than 20 specimens from the northern arm but had only seven from the Makassar region. Mean values of external, cranial, and dental measurements are closely similar in these samples (table 4), as is color of pelage. And although we had a large sample from Pulau Peleng, our samples from sites other than the northern and southwestern peninsulas are very small and came from widely scattered regions. Our summary simply reflects our earlier statement that nobody has yet provided an adequate study to determine the pattern of regional morphological variation, if a pattern exists, within *T. spectrum.* Comparisons among large series from many different places that take into account individual, age, and sexual variation are needed to determine the nature of intraspecific morphological variation that may be present.

We are able to report our certainty, verified by examining specimens, that the range of morphological variation in all the samples of *T. spectrum* does not include that seen in the two specimens of the pygmy tarsier, *T. pumilus.* Support for that assertion is contained in the following section.

DEFINITION OF
TARSIUS PUMILUS

Tarsius pumilis was named and described by Miller and Hollister (1921b), based upon three specimens from the mountains of Central Sulawesi. The holotype, USNM 219454, was collected by H. C. Raven on December 31, 1917, from montane rain forest at Rano Rano (1°30′S, 120°28′E), 1800 m. Rano Rano is on the west slope of the mountains ringing the eastern margin of the great Napu Valley, 50 km by air southeast of Danau Lindu (fig. 16). About four months before stopping at Rano Rano, Raven collected in Gimpu, a village at 450 m in lowland tropical evergreen rain forest about 50 km by air southwest of Rano Rano. His collections of birds and mammals made in the vicinity of Gimpu included two small tarsiers (USNM 219452 and 219453), which Miller and Hollister included as examples of *T. pumilus.* These two and the holotype are the only specimens ever identified as *T. pumilus.* Hill (1955, p. 245) wrote that three specimens were known from the type locality and two from Gimpu, a mistake perpetuated by Niemitz (1977).

Miller and Hollister (1921b, p. 104) diagnosed *T. pumilus* as being "In general like *Tarsius fuscus* [=*spectrum*] but very much smaller; upperparts much richer colored, less buffy, more reddish brown; the pelage longer. Spot behind ear buffy rather than white. Tail and feet haired as in *fuscus.* Skull very much smaller than that of *fuscus,* appearing scarcely more than half its bulk (actual relationship about as 12 to 19); mandible particularly small and weak; lower incisors relatively much higher; second unicuspid smaller than first." These characters were considered by Hill (1955) to be diagnostic of a subspecies of *T. spectrum.* Niemitz (1984a) thought so as well but also noted that *pumilus* may be a distinct species. A year later, he (Niemitz, 1985) recognized *pumilus* as a species with a distri-
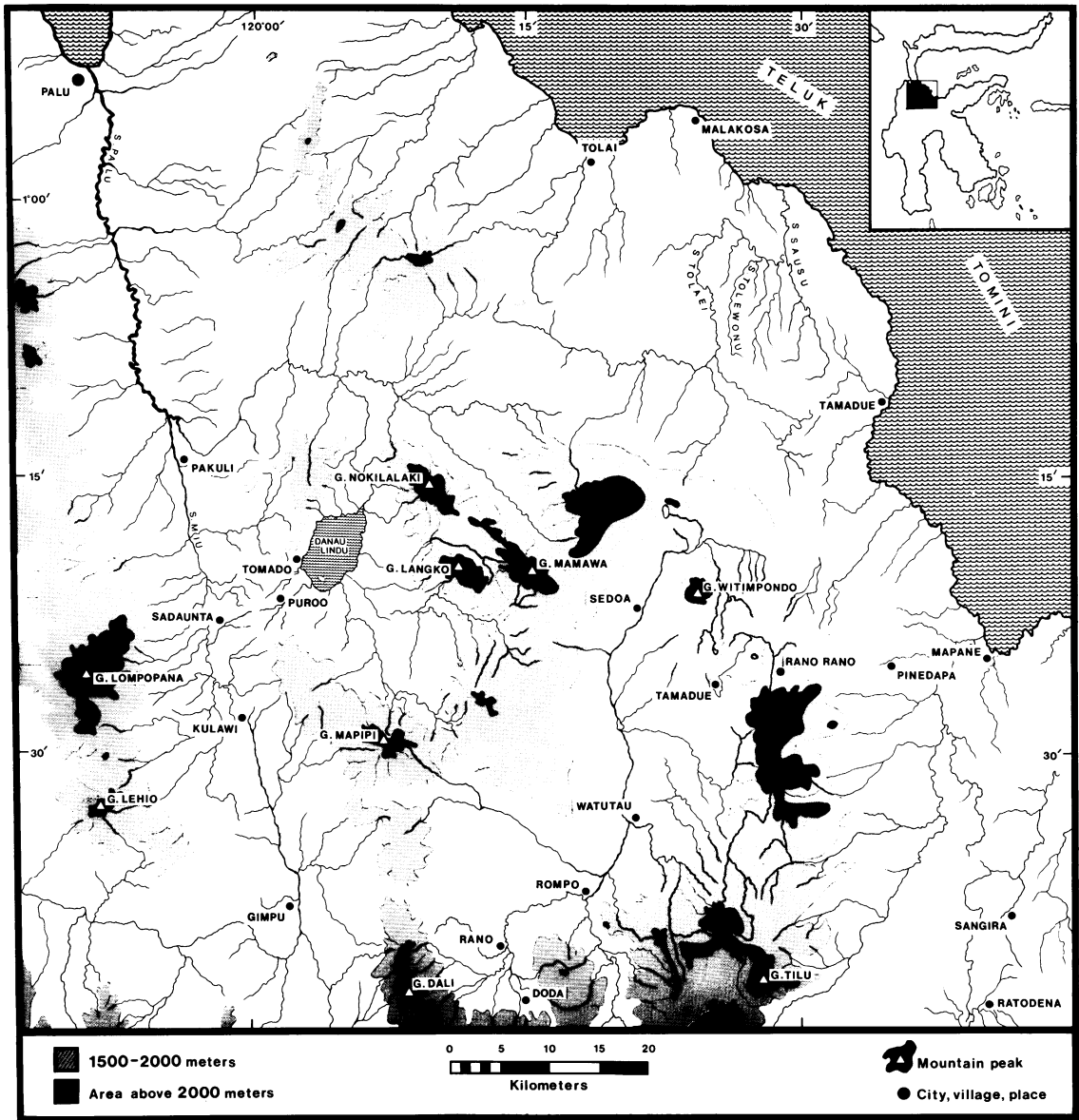
Fig. 16. Central Sulawesi. Indicated are some of H. C. Raven's collecting localities (Gunung Lehio, Kulawi, Gimpu, Rano Rano, Pinedapa, among others) and the areas worked by Musser during 1973–1976 (Sadaunta, Tomado, Gunung Nokilalaki, Malakosa region, Sungai Tolewonu).

bution in the highlands of Central Sulawesi and represented by records from Lore Lindu National Park, Marena, Rano Rano, and Gimpu. As far as we know, neither Hill nor Niemitz ever examined the three specimens upon which *T. pumilus* is based.

That sample is mixed. The holotype of *T. pumilus* represents a small-bodied tarsier with worn molars; it is clearly adult (figs. 17–19). Miller and Hollister's diagnosis of the species could easily have been, and probably was, based upon this specimen. The two animals from Gimpu, however, are juvenile *T. spectrum*. In each, the third molars are unerupted, yet lengths of head and body (88 mm and 80 mm) are almost as great as the adult ho-

lotype, and the dentition, mandible, pelage, and unguae are characteristic of *T. spectrum,* not *T. pumilus.*

In addition to the holotype, we have been able to find only one other example of *T. pumilus.* On June 17, 1930, Dr. G. Heinrich collected an adult female tarsier from moss forest at 2200 m on Pegunungan Latimodjong (3°30'S, 120°05'E; fig. 8), a high part of the mountains in the northern region of the southwest peninsula of Sulawesi. Its stuffed skin and skull (AMNH 196477) have been in the collection of the American Museum of Natural History misidentified as *T. spectrum* for more than 50 years. Except that its fur is brownish gray, the animal is closely similar in morphology to the holotype of *T. pumilus.*

As represented by these two individuals, *T. pumilus* is one of the most morphologically distinctive of the four species of tarsiers. Contrasts between *T. pumilus* and the other three, especially *T. spectrum,* in morphology, altitudinal distribution, habitat, regional distribution, and faunal association are discussed below.

1. **Body size.** *Tarsius pumilus* is strongly distinguished from the other three species of tarsiers by its smaller size (tables 2, 5; figs. 9, 17, 18). Head and body length is only 75 percent that of other tarsiers; greatest skull length is 80 percent. Unfortunately, we have no body weight data. No adult individual of any other species of tarsier overlaps with *T. pumilus* in either length of head and body or greatest length of skull. The other three species of tarsiers overlap almost totally with each other in size.

2. **Cranial features.** Compared with the other three species of tarsiers, *T. pumilus* has the smallest orbits in absolute dimensions (table 2). However, correcting for body size by dividing values for breadth across orbits by greatest length of skull, *T. spectrum* has the relatively smallest orbits. *T. pumilus* and *T. syrichta* are intermediate in relative size, and *T. bancanus* has the relatively largest orbits (table 2).

Tarsius pumilus, like *T. spectrum,* has a projecting nasal profile which distinguishes it from *T. syrichta* and *T. bancanus* (fig. 11). These bones are absolutely shorter in *T. pumilus* but longer relative to greatest length of skull (tables 2, 3).

TABLE 5

Measurements (in mm) of the Two Specimens of *Tarsius pumilus* and the holotype of *Tarsius spectrum dentatus* from Central Sulawesi

| Measurement | T. pumilus | | T. spectrum dentatus |
	USNM 219454[a]	AMNH 196477	USNM 218071
Length of head and body	95	98	120
Length of tail	205	203	270
Length of third finger	16.2	18.6	24.2
Greatest length of skull	31.1	30.7	37.8
Zygomatic breadth	23.9	24.5	27.4
Breadth across orbits	26.4	26.4	29.6
Breadth of single orbit	14.3	14.5	16.2
Height of single orbit	14.7	14.2	15.9
Length of nasals	4.6	5.7	6.7
Breadth of palate at M^3	12.2	11.9	14.6
Length of bulla	9.7	9.6	11.9
Breadth of bulla	5.4	4.8	6.4
Anterior length of bulla	4.6	4.6	6.9
Posterior length of bulla	6.4	6.3	5.2
Length of C-M^3	10.7	10.4	13.3
Length of C-M_3	10.8	10.9	13.8
Length of M^1	1.9	1.8	2.3
Breadth of M^1	2.9	2.9	3.8
Length of M_1	2.2	1.8	2.5
Breadth of M_1	1.9	1.8	2.4
Area of M^1	5.5	5.2	8.7
Area of M_1	4.2	3.2	6.0

[a] Holotype.

3. **Mandibular and dental characters.** The coronoid process of the mandible in *T. pumilus* is closer to the condyle than in the other species of tarsiers; is larger relative to the ramus compared with *T. spectrum* (fig. 19); and is about as high as the condyle, whereas the process in other species is higher than the condyle, especially in *T. syrichta* (fig. 20).

We noted earlier that among the three large-bodied species of tarsiers, *T. spectrum* has the smallest molars relative to skull size. *Tarsius pumilus* has even smaller teeth relative to skull size (table 3). *Tarsius pumilus* differs from all other tarsiers in the construction of its anterior mandibular dentition. Tips of lower incisors are higher relative to the canines. The lower incisors and canines are crowded together so that the mesial edges of the right and left incisors are in full contact
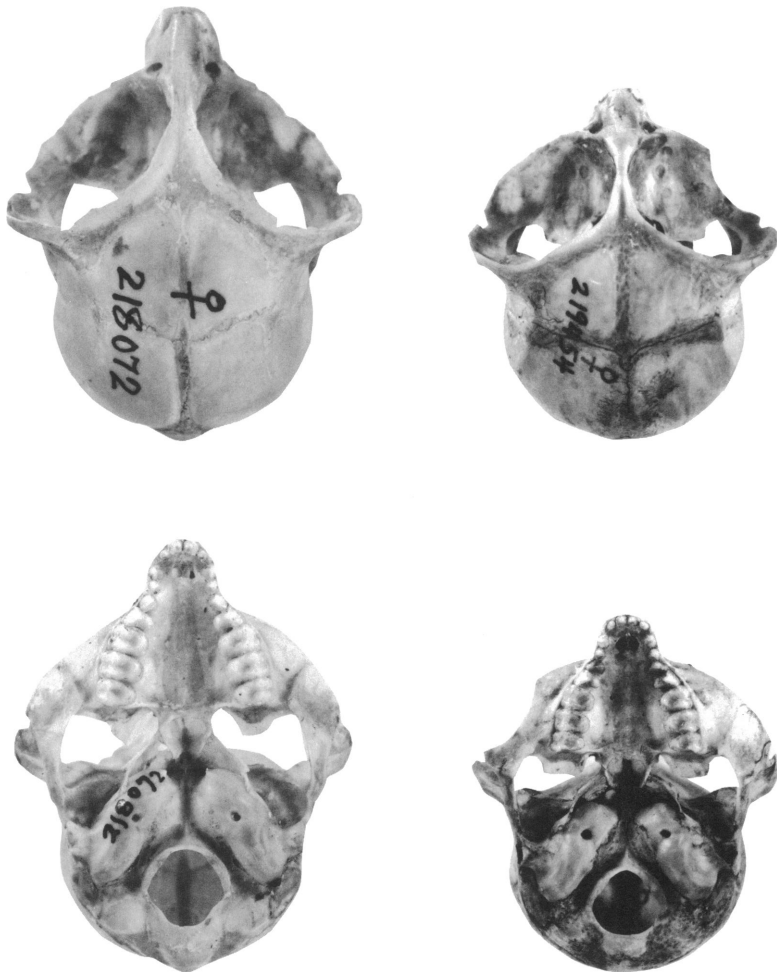
Fig. 17. Crania of adult tarsiers. Left side: holotype of *Tarsius spectrum dentatus* from Labua Sore, Central Sulawesi. Right: holotype of *T. pumilus* from Rano Rano, Central Sulawesi. Measurements are listed in table 5. ×1.5.

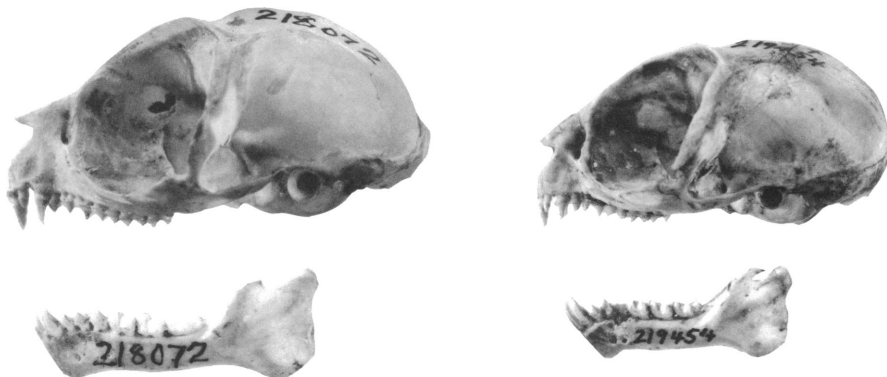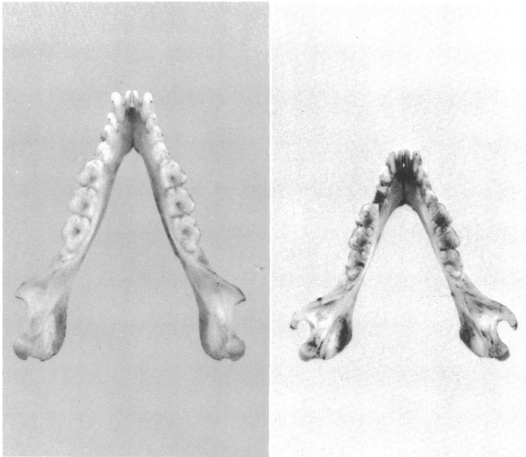Fig. 18. Crania and mandibles of specimens shown in fig. 17. Left: *Tarsius spectrum dentatus*. Right: *Tarsius pumilus*. ×1.5.

Fig. 19. Mandibles of specimens illustrated in fig. 17. Left: *Tarsius spectrum dentatus*. Right: *Tarsius pumilus*. ×1.5.

for their total length in *T. pumilus*, whereas in *T. spectrum*, *T. bancanus*, and *T. syrichta*, there is usually some separation between the incisors (figs. 20, 21). The mesial edge of the canines is compacted against the distal edge of the incisors in *T. pumilus*. In other species of tarsiers there is a fair amount of space between the lower incisors and canines. There are no associated differences in upper canine or incisor morphology.

Tarsius pumilus exhibits marked striations on the lingual ridges of the lower incisor and canine (fig. 22). We examined specimens of it and the other three species under a Scanning Electron Microscope. Only one specimen of *T. spectrum* (AMNH 196484) exhibited even vaguely similar wear, but even in this case, the striations are very faint compared with those in *T. pumilus*. No specimen of *T. bancanus* or *T. syrichta* showed any signs of such wear. These striations strongly resemble in size and location the wear attributed to combing the incisors through fur (grooming) by Rose et al. (1981). We presume that these marks are the result of grooming the fur with the anterior lower teeth in *T. pumilus*. Since *T. bancanus*, *T. syrichta*, and *T. spectrum* are reported to use their front teeth for fur grooming (Niemitz, 1984b, 1984c; Wright, personal commun.), the lack of such striations in these taxa might be attributed to three factors: (1) *T. pumilus* may
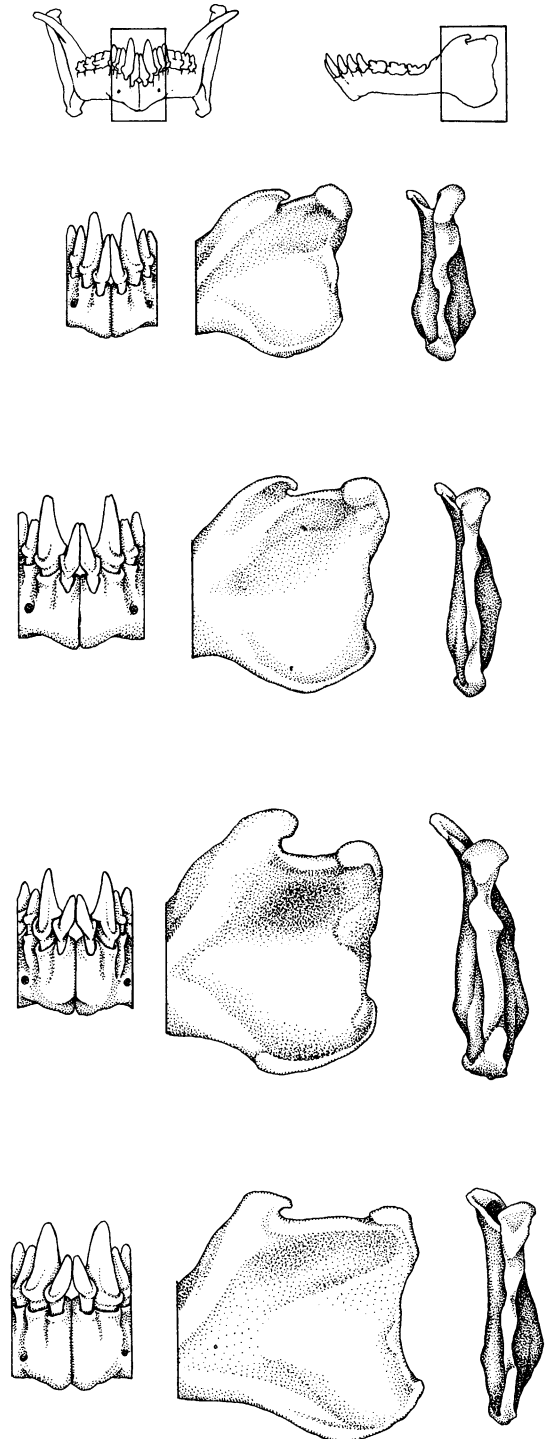
Fig. 20. Mandibles and anterior lower teeth of tarsiers. From top to bottom: *Tarsius pumilus*, *T. spectrum*, *T. syrichta*, and *T. bancanus*. Drawn from same specimens illustrated in fig. 11.
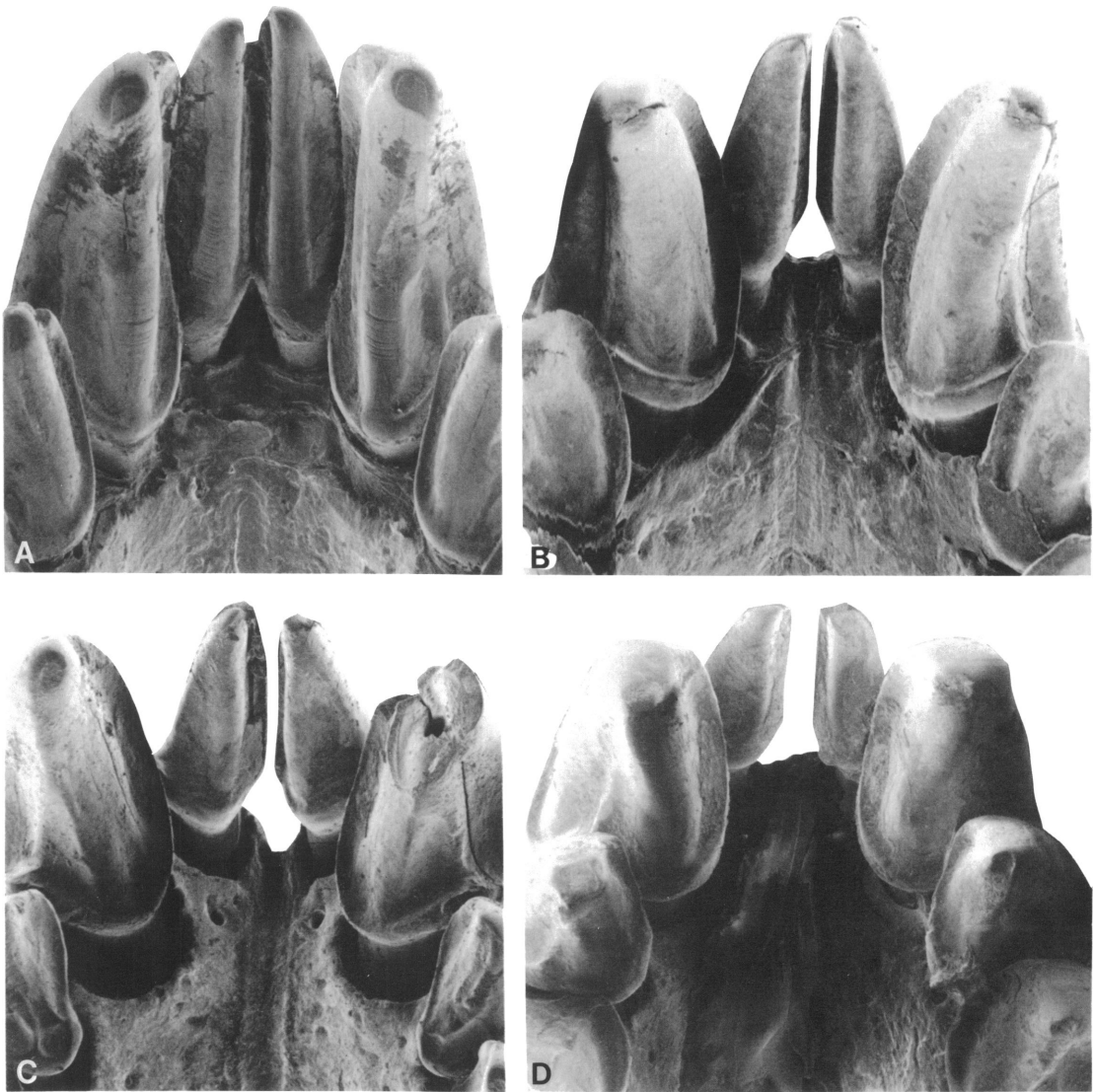
Fig. 21. Anterior lower teeth of tarsiers. **A,** *Tarsius pumilus* (AMNH 196477); **B,** *T. spectrum* (AMNH 196484); **C,** *T. syrichta* (AMNH 203296); and **D,** *T. bancanus* (AMNH 106010. Note horizontal striations on lingual ridges of incisors and canines in *T. pumilus* and absence of these ridges from the other species.

groom more frequently; (2) the longer, thicker pelage of *T. pumilus* may be more likely to mark the teeth; (3) the crowding of the anterior teeth in *T. pumilus* causes the hair to be forced against the teeth more than in other tarsiers.

As an aside, we note that Schmid (1983) used the lack of fur grooming facets in *Tarsius* (no species specified) and their presence in *Necrolemur* as one argument illustrating the wide morphological (and thus presumably

phylogenetic) differences between these two genera. We point out the presence of hair grooming striations in at least one (*T. pumilus*) and possibly two (*T. spectrum*) tarsiers. Lack of such wear is more an indication of differences in anterior dental morphology (and of course, behavior) than a useful phylogenetic character on its own.

Before stressing the importance of the presence of grooming facets in *T. pumilus* too much, we must note that one problem in our

Fig. 22. Lower incisors and canines of *Tarsius pumilus* (AMNH 196477). Top left: horizontal striations near base of left canine (lc). Top right: striations on lingual ridge of left incisor (li).

analysis is that the two examples of *T. pumilus* show a rather extreme degree of molar wear. In both specimens the trigonid is worn

down nearly to the level of the talonid. It is thus possible that we are simply seeing the results of age differences. When evaluating

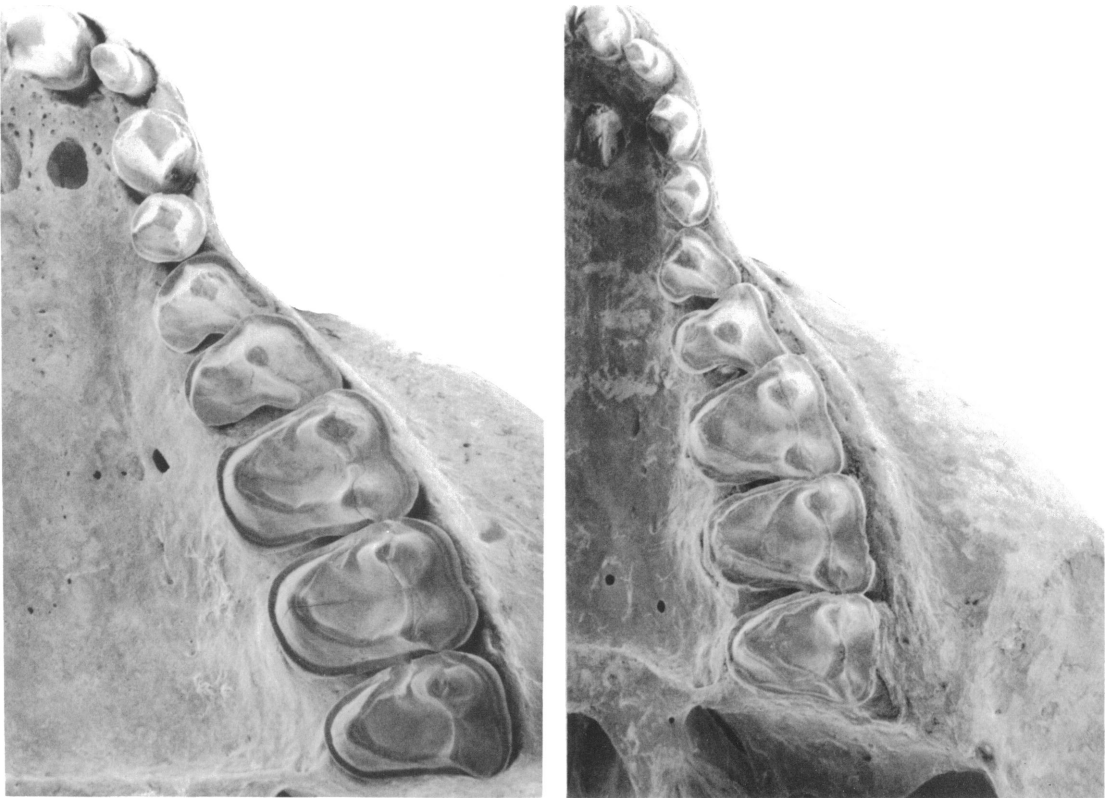Fig. 23. Wear on upper teeth of adult tarsiers. Left: *Tarsius spectrum* (AMNH 196484). Right: *T. pumilus* (AMNH 196477). Contrast the degree of wear shown here with that of the lower teeth in fig. 24.

the other three species, we did examine the anterior teeth of individuals which showed the greatest degree of molar wear. We do note, however, that only 2 of nearly 60 individuals of *T. spectrum,* 3 out of 16 *T. bancanus,* and 1 out of 10 *T. syrichta* show wear even approaching the state of *T. pumilus.* In one specimen of *T. spectrum,* which has a similar degree of wear on the canines and premolars (AMNH 196484), the molars are not worn to the degree seen in *T. pumilus* (figs. 23, 24). Therefore we believe that the degree of molar wear in *T. pumilus* is another distinguishing characteristic of this species. Another possibility is that molar relief of *T. pumilus* is low to start with, but without unworn specimens of *T. pumilus* it is impossible to test this. For the same reason, it is impossible to tell if there are differences in aspects of cusp morphology. There do not appear to be any major differences in premolar or molar morphology, except that *T. pumilus* has the smallest

molars relative to skull length of any species of tarsier (table 3).

The differences in lower incisor morphology and in the degree of molar wear are suggestive of dietary differences between *T. pumilus* and other tarsiers. Uniting the lower anterior teeth into a comblike structure (although the teeth are *not* procumbent in *T. pumilus*) has been associated with two adaptations in primates: gum feeding (Martin, 1972) and fur grooming (Szalay and Seligsohn, 1977). According to Rose et al. (1981), gummivory leaves no distinctive microwear traces on the teeth, so we cannot further evaluate this possibility for *T. pumilus.*

Another potential reason for the restructuring of the anterior lower dentition in *T. pumilus* is the need for a specialized grooming device to care for its slightly longer and thicker pelage. In support of this suggestion we note the presence of deep hair-grooming

Fig. 24. Wear on lower teeth of same specimens shown in fig. 23. Left: *Tarsius spectrum*. Right: *T. pumilus*. Note that wear on incisors, canines, and premolars is about the same in the two species, but the molars of *T. pumilus* are much more worn than those of *T. spectrum*.

striations on the lower incisors and canines of *T. pumilus*.

The reason for the greater degree of molar wear in *T. pumilus* is difficult to discern. Adding significant amounts of gum to the diet would not seem to be able to cause the heavier tooth wear seen in *T. pumilus*. It also seems unlikely that *T. pumilus* could have included significant amounts of plant foods in the diet, given its small body size (Kay, 1975). It is probable that *T. pumilus* includes foods with more abrasive components in its diet.

4. **Bullar morphology.** In *T. pumilus*, the hypotympanic sinus of the auditory bulla is not nearly as inflated as in the other species of tarsiers (fig. 12). There is in fact a cline among tarsier species in the degree of hy-

Fig. 25. Hands and feet of adult tarsiers. Top two: hand and foot of *Tarsius spectrum* (AMNH 153290). Bottom two figures: hand and foot of *T. pumilus* (AMNH 196477). Inset: ventral view of fourth digital pad of foot in *T. spectrum* (left) and *T. pumilus* (right).

potympanic inflation, with *T. bancanus* and *T. syrichta* showing the greatest amount of inflation, *T. spectrum* an intermediate amount, and *T. pumilus* the least. In the other three species of tarsiers, inflation of the hypotympanic sinus is so great that the carotid foramen appears to be pushed towards the back part of the bulla. The length of the bulla anterior to the carotid foramen exceeds the length posterior to it in these species. In *T. pumilus*, however, the anterior length is less than the posterior length (table 2). This difference in bullar morphology cannot be ex-

plained simply as a result of body size, since *T. spectrum* is the same size as *T. bancanus* and *T. syrichta*. The marked reduction in bullar inflation in *T. pumilus* goes against the trend one might expect. Smaller animals need to increase bullar space to maintain similar impedance ratios (Cartmill, 1975). Therefore, the differences in bullar size between *T. pumilus* and other tarsiers, and to a lesser extent among *T. spectrum, T. bancanus,* and *T. syrichta,* possibly reflect functional differences in hearing acuity among the species.

5. **Nails and digital pads.** In tarsiers the "nails show the most advanced degree of degeneration; . . . on most of the digits they are reduced to minute horny plaques" (Clark, 1959, p. 175; see also Clark, 1936). Clark related this development to the greatly enlarged digital pads in tarsiers. There is, however, variation in the degree of reduction of nails in tarsiers. *Tarsius bancanus* and *T. syrichta* show the most advanced degree of ungual reduction and best fit the description given by Clark. The nails of *T. spectrum,* however, are much better developed than those of either *T. bancanus* or *T. syrichta.* They are strongly keeled, and end in sharp points, although the lateral part of the nail is still flattened. The digital pads are large, and the tip of the nail does not extend beyond the digital pad (fig. 25). *Tarsius pumilus* shows an even greater development of the nails. Nails of all the digits of the hand, including the hallux, and the lateral two digits of the foot are strongly laterally compressed and come to a sharp point; they resemble claws more than nails. The digital pads are greatly reduced in size and the tips of the pointed nails extend beyond the edges of the pads (fig. 25). We did not section nails to determine the relative degree of deep matrix and superficial matrix. There is, however, little obvious modification of the distal phalanx. As in other primates, there is no sesamoid bone at the joint between the middle and distal phalanges, and the flexor tubercle is small. As Rosenberger (1977) has argued for callitrichids, these features suggest to us that the clawlike nails of *T. pumilus* are derived for this species and are not primitive retentions from a clawed, nonprimate ancestor.

In primates, sharply keeled nails or clawlike nails develop in several taxa of special-

ized animals: *Daubentonia, Euoticus, Galago inustus,* and callitrichids. All these primates typically use large vertical supports for feeding and/or locomotion. Cartmill (1974) has shown that claws are superior to nails or grasping extremities for locomotion on such large vertical supports. We presume that some similar selection pressures have influenced the development of specialized clawlike nails in *T. pumilus.* We again note that all of these taxa except *Daubentonia* include tree exudates in their diet, and that this gum is collected from the trunks or large branches of trees. *Tarsius pumilus* has been collected from the moss forests of Central Sulawesi. In this environment the trees are usually covered with a thick layer of bryophytes. It is likely that the clawlike nails and small digital pads of *T. pumilus* give it a better purchase on this substrate than would flat nails and large, flattened digital pads.

6. **Vocalizations.** Both Niemitz (1984d) and MacKinnon and MacKinnon (1980) have recorded the vocalizations of tarsiers from Central Sulawesi, and found them to be distinct from the vocalizations of tarsiers living on the northern arm. Niemitz (1984e, p. 138) attributed the Central Sulawesian vocalizations he recorded to *T. pumilus* and wrote that

> The differences of the repertoires of the tarsiers from the north and from Central Sulawesi strongly indicate that they reach beyond the range of mere dialects. They suggest rather to represent vocal systems of nearly related, yet significantly different species, *T. spectrum* and *T. pumilus.* This would indicate a *new species,* since Miller and Hollister (1921) described them only as a subspecies of *T. spectrum.* Only a bit more anatomical material seems to be necessary to verify this assumption and to fully establish this fourth species of tarsiers.

We suspect that the vocalizations recorded from the Central Sulawesian tarsiers are from *T. spectrum* and not *T. pumilus.* The only known specimens of *T. pumilus* come from moss forest between 1800 and 2200 m, and we suspect the species to be altitudinally allopatric to the lowland *T. spectrum,* which has been collected in Central Sulawesi near coasts (Labua Sore, Parigi, Sungai Navusu, Malili, and Palopo) and in the interior up to 450 m (Gimpu). Niemitz (1984e) recorded

vocalizations at Marena, a village at about 500 m between Gimpu and Kulawi in the valley of the Salo Pebatug, which is within the altitudinal range and habitat of *T. spectrum*. Furthermore, Niemitz's (1984a, p. 11, figs. 1–5) photograph of a Sulawesian tarsier that he identified as *T. spectrum pumilus* is a typical *T. spectrum* for it has the large ears and especially the disc-like digital pads, which, as we noted above (and in fig. 25), are much reduced in *T. pumilus*. There is no evidence in the published literature that anyone has ever recorded the vocalizations of the small-bodied, montane *T. pumilus*.

The differences between vocalizations recorded from Central Sulawesian tarsiers and those from tarsiers living on the northern peninsula may actually reflect different dialects. In the northern arm, MacKinnon and MacKinnon (1980) recorded vocalizations they called the Manado form, which was found from the northeastern tip of Sulawesi along the northern arm west to Gorontolo. Beyond Gorontolo and over the rest of the northern arm they recorded another tarsier call. Yet a different call was recorded in the Palu Valley of Central Sulawesi. MacKinnon and MacKinnon noted that some of the regional forms with different calls could also be distinguished by fur color and length. The break at Gorontolo and between the rest of the northern peninsula and Central Sulawesi corresponds to breaks in the distributions of macaque taxa (Fooden, 1969; Groves, 1980).

We separated our specimens of *T. spectrum* into samples from east of Gorontolo and those from west of there. If there are any significant differences in the dimensions we analyzed, our samples were not large enough to show them (table 4). Furthermore, we could not detect significant differences in either pelage color or length. If the difference in calls reflects past geographical isolation, the lack of significant differences in morphology among our samples suggests that genetic isolation did not result from any physical isolation. The slight morphological differences between samples of the tarsier populations from Central and northern Sulawesi, and the altitudinal range in which the calls were recorded, indicate to us that the vocalizations from Central Sulawesi were those of *T. spectrum* and not *T. pumilus*.

7. **Pelage.** The general coloration of the pelage of *T. pumilus* is similar to that of *T. spectrum*. Individuals in both species have either a predominantly gray or a predominantly brownish-red coat. The pelage of *T. pumilus* is denser, longer, and silkier than that of *T. spectrum*. The white postauricular spot which is so typical of *T. spectrum* is, in *T. pumilus*, either buff as in the holotype, or absent as in the American Museum specimen. *Tarsius pumilus* has relatively smaller ears than *T. spectrum*.

8. **Tail and limb proportions.** Relative lengths of the front and hind limbs of *T. pumilus* resemble those of *T. spectrum* and differ from the other two species of tarsiers. The pilosity as well as the morphology of the underside of tails in *T. pumilus* are similar to tail characteristics in *T. spectrum* and unlike either *T. syrichta* or *T. bancanus* (see the previous section for comparisons among the three large-bodied species). About a third of the underside of the tail is scaly in both the holotype of *T. pumilus* and AMNH 196477.

9. **Altitudinal distribution and habitat.** The two examples of *Tarsius pumilus* come from 1800 and 2200 m. Tropical upper montane rain forest occurs at these altitudes (Whitmore, 1984)—the spectacular mossy forest of the high Central Sulawesian mountains.

Tarsius bancanus and *T. syrichta* are lowland animals (Medway, 1977; Taylor, 1934; Sanborn, 1952). *Tarsius spectrum* is represented by specimens and recorded vocalizations from near sea level up to about 1500 m. Most specimens come from between sea level and about 500 m throughout Sulawesi but two tarsiers were taken at 1500 m at Tanka Salokko in the Mekonnga mountains of the southeastern peninsula. In the northern peninsula MacKinnon and MacKinnon (1980) recorded calls of tarsiers living at 1500 m in what they described as moss forest. That altitude falls within the beginning of lower montane rain forest. Although that forest zone has sometimes been listed as a subformation of tropical lowland evergreen rain forest, Whitmore (1984, p. 243) notes that "on all major mountains there is an intermediate Formation, lower montane rain forest . . . below the upper montane rain forest and which itself merges downwards with lowland rain forest . . . ."

No records of tarsier specimens or calls are available to us from altitudes between 1500 and 1800 m. We do not know if the distributions of *T. pumilus* and *T. spectrum* overlap but it is our hypothesis that they probably do not and are altitudinally allopatric, reflecting a pattern common to several species clusters of native Sulawesian mammals whose distributional limits coincide with those of either tropical lowland evergreen or montane rain forest formations (Musser, 1987).

Judged by its altitude, Rano Rano, the type locality of *T. pumilus,* is in the lower portion of upper montane rain forest. Henry C. Raven spent from December 8, 1917, to January 5, 1918, working near Rano Rano in the mountains on the west side of the Napu Valley (fig. 16). Toward the end of November he had trapped in Napu at Watutau and then ascended to Rano Rano where he camped near the summit. From there he would eventually descend to the village of Pinedapa at 30 m and then after several weeks continue to the coastal town of Mapane on the edge of the Gulf of Tomini (Riley, 1924). Raven left no description of the forest at Rano Rano among his fieldnotes. The locality is only about 40 km by air from Gunung Nokilalaki (west of Danau Lindu) where Musser worked in the 1970s studying altitudinal distributions and forest habitats of native rodents. Gunung Nokilalaki and Rano Rano are in the same general mountain region. In moss forests on the slopes of Gunung Nokilalaki, Musser caught the same species of rats and mice that Raven encountered: *Bunomys penitus* (described as *Rattus sericatus* by Miller and Hollister, 1921a), *Melasmothrix naso, Eropeplus canus, Taeromys hamatus* (Miller and Hollister, 1921b, described this as a *Rattus*), *Maxomys musschenbroekii,* and *Rattus hoffmanni.* Samples of each species from the two regions are very much alike in their morphology.

Although incompletely sampled, elements of the same fauna are present on Pegunungan Latimodjong, the other recorded locality of *T. pumilus.* Heinrich collected specimens of *Tateomys rhinogradoides, Eropeplus canus, Bunomys penitus,* and *Rattus hoffmanni.* The shrew rat, *Tateomys rhinogradoides,* also occurs on Gunung Nokilalaki. Specimens of each species are not as similar in morphology

as are those from Gunung Nokilalaki and Rano Rano (see, for example, the differences recorded by Musser, 1982, between samples of the shrew rat), but the differences are slight. We think the forest at Rano Rano, as well as Gunung Latimodjong, also closely resembles that of Gunung Nokilalaki in structure and species composition.

The change from lowland to montane forest in the Gunung Nokilalaki area is dramatic. Whitmore (1984, p. 243), in his book on tropical rain forests of the Far East, could have been describing this region when he wrote that

As one climbs a tropical mountain one successively encounters forests of different structure, physiognomy . . . , and flora. The most dramatic change, partly so because it usually occurs sharply over a short distance, is from mesophyll-dominated forest with an uneven, billowing, canopy surface to microphyll-dominated forest . . . with a lower, flattish canopy surface, the trees more slender, usually with gnarled limbs and very dense subcrowns. This latter Formation is called upper montane rain forest. It is encountered first on knolls and narrow ridge crests with mesophyll forest occupying the valleys, saddles, and broader crests. Upwards it comes to clothe the entire landscape. It is as clearly distinctive on aerial photographs or from an aeroplane as to the traveller on foot.

The upper montane rain forest on Gunung Nokilalaki between 1800 m and the summit (2275 m) is distinctive (figs. 1, 26, 29). The canopy is 10–20 m high; here and there a large tree 20–30 m tall emerges above the canopy but they are rare. Leaves are small, trees are usually without buttresses, large woody vines are absent, trunk climbers are rare, vascular and nonvascular epiphytes are common, and palms are scarce. Species diversity of trees and shrubs is low.

The canopy is formed of just a few species. Oaks (*Lithocarpus*), laurels (*Litsea* and *Cryptocarya*), conifers (*Podocarpus* and *Dacrydium*), magnolias (*Aromadendrom*), and species of *Adinandra, Weinmannia,* and walnut (*Engelhardtia*) predominate. All are intermixed and none form stands as do chestnut (*Castanopsis*) and some oak below in lower montane forest. The understory has greater diversity with myrtles (mostly *Eugenia,* two species of *Tristania*) being most common,

TABLE 6

Minimum and Maximum Ambient Air Temperatures Recorded at Altitudes from Coastal Lowlands to the Summit of Gunung Nokilalaki in Central Sulawesi[a]

(Elevations are in m, temperature data are summarized by mean and observed ranges in parentheses.)

Elev.	Place	Temperature, °F		Number of days	Period
		Minimum	Maximum		
2275	Summit, G. Nokilalaki	51.0 (48–54)	56.6 (52–63)	60	Mar. 4–May 2, 1975
2060	Gunung Nokilalaki	54.7 (51–58)	60.4 (54–65)	60	Mar. 4–May 2, 1975
1730	Gunung Nokilalaki	57.5 (55–60)	64.8 (61–69)	30	Dec. 6, 1973–Jan. 4, 1974
1440	Gunung Kanino	58.4 (52–61)	68.9 (63–76)	32	Jan. 16–Feb. 16, 1975
1150	Sungai Tokararu	61.1 (56–64)	73.9 (69–83)	32	Sept. 12–Oct. 13, 1973
758	Sungai Sadaunta	66.9 (62–70)	75.2 (70–86)	92	Sept. 16–Dec. 16, 1974
290	Sungai Oha Kecil	70.1 (66–73)	78.8 (75–83)	37	July 31–Sept. 5, 1974
136	Sungai Tolewonu	69.8 (67–72)	77.3 (72–81)	57	Jan. 3–Feb. 28, 1976
30	Kuala Navusu	73.6 (72–76)	80.9 (74–87)	95	Aug. 28–Nov. 30, 1975

[a] Each minimum and maximum recording was made during a 24-hour period. Thermometers were placed on or just above the ground beneath the canopy in primary forest. Localities are within the region bounded by the Sungai Miu on the west, Malakosa on the north, Tamadue on the east, and Kulawi on the south (see map in fig. 16). During each duration of recordings, rain fell on about half to three-fourths of the days; relative humidities were about 100 percent in early mornings and late evenings, and dropped to the low nineties and high eighties during the middle of each day. Data are from Musser's fieldnotes.

along with species of *Planchonella,* an occasional *Ficus, Ilex, Eurya, Carallia, Praravinia, Psychotria, Vaccinium, Drimys, Symplocos, Ternstroemia,* and others. Palms are represented by one tree palm (*Areca*) and a few species of rattan (*Daemonorops*). Here and there are tree and vine pandans (*Pandanus* and *Feycinetia*).

The forest is usually open and parklike, and in some areas tangles of rotting tree-falls and piles of rattan clutter the floor. Gingers (*Amomum*), rattan rosettes, small shrubs, saplings, and lacy ferns form a dense knee-high undergrowth (figs. 1, 26). The ground is wet and bare in places, blanketed with leaf litter elsewhere, and covered with sedges in clearings.

When it is not raining, the mountain is immersed in thick, gray mist. The cool air (table 6), combined with relative humidities between 85 and 100 percent, forms a clammy environment, cold and wet, dark with gray mist, an ambience counterpointed by browns, blacks, russet, and dark greens of the vegetation. Conditions are optimal for the luxuriant growth of bryophytes (mostly liverworts, some true mosses) and lichens, the "mossy" component of upper montane forest (Steenis, 1972; Whitmore, 1984).

Moss cloaks the forest (figs. 26, 29). Like a wet, thick, and green fur, it covers rocks and rotting tree-falls, forms thick wet carpets in ground depressions, encases trunks, limbs, and branches all the way from roots up into gnarled crowns. Branches and limbs are also festooned with curtains of hanging moss (*Aerobryum*) and beard-moss (*Usnea,* which is a lichen).

Such a forest is the habitat of *Tarsius pumilus.* It is a very different environment from that typical of lower altitudes in tropical lowland evergreen rain forest (figs. 27, 28) where the canopy is 20–40 m high and broken by many emergent trees 50 to 70 m tall; leaves are large; buttresses are common and large; big woody climbers and smaller trunk climbers are abundant; and nonvascular epiphytes are uncommon (Whitmore, 1984).

Although the range of relative humidities in lowland forest is similar to that in montane formations, the ambient temperatures are greater (table 6) and the environmental sensation is the humid warmth of a greenhouse. Unlike the forboding dark and somber montane rain forest, lowland forests are bright green from the leafy vegetation and mixed with the browns, grays, creams, and sometimes pink and orange of trunks. The forest is dappled with light and shadow. Beneath the canopy there are open, parklike areas intermixed with dense brambles of rattan ro-

Fig. 26.   Mossy upper montane rain forest on summit of Gunung Nokilalaki, 2285 m, Central Sulawesi. December 1973.

Fig. 27. Lowland evergreen rain forest along Kuala Navusu, 30 m, in Malakosa region of Central Sulawesi. November 1975.

settes, clusters of dangling woody vines, and huge impasses formed by tall emergents that had crashed to the forest floor. Where undergrowth flourishes it is waist or head high. Mossy coverings are confined to wet and cool places between buttresses of large trees.

Species diversity in tropical lowland evergreen rain forest in the region encompased by Sadaunta, Danau Lindu, Gunung Nokilalaki, and Malakosa (fig. 16) is spectacular compared with that in mossy forest (Musser, MS). More than 100 species form the canopy and emerge above it (16 in upper montane rain forest), an assemblage that includes the magnolia *Elmerrillia,* several kinds of *Palaquium,* many *Ficus, Dysoxylum, Koordersiodendron, Dracontomelon,* and the diptocarps *Shorea* and *Octomeles,* to name only a few. At least 300 species comprise the understory (compared with about 50 in upper montane forest). Eleven species of tree palms are common (species of *Licuala, Livstonia, Arenga, Pinanga, Areca, Caryotis,* and *Onchosperma*), as are about 12 species of climbing rattan palms (*Korthalsia, Calamus,* and *Daemonorops*). Tree pandans are represented by eight species and the climbing pandan by at least six (one species of each in mossy forest). Eighteen kinds of gingers are found throughout the lowlands and hillsides hill forest. Bamboo is present, often in dense stands. Wild species of bananas (unknown in montane forest formations) are frequently encountered. One species of cycad (unknown in montane forest) occurs at lower elevations.

Above about 1300 m in Central Sulawesi, lowland evergreen forest gives way to lower montane rain forest. Decreases in canopy height, species diversity, buttressed trunks, woody climbers, and ambient temperatures (table 6) are characteristic of this formation. Certain species are found above 1300 m that do not occur lower and the forest structure is dominated by stands of oak (*Lithocarpus*) and chestnut (*Castanopsis*).

The lower limits of this kind of forest mark the upper limits of the known altitudinal distribution of *Tarsius spectrum.* The animal lives in primary forest and other kinds of lowland habitats. In the northern peninsula, for example, MacKinnon and MacKinnon (1980) found it widely distributed in all kinds of terrain and in thorn scrub, primary forest, secondary forest, riverine forest and bamboo, mangrove forest, seashore scrub, and urban gardens (their terms).

10. **Geographic distribution and faunal association.** Specimens of *Tarsius spectrum* have come from most regions of Sulawesi and the species probably occurs everywhere on the island where a wide range of suitable habitats is present. *Tarsius pumilus* is known only from Central Sulawesi and, if present specimens are an accurate indication, its altitudinal distribution is restricted to montane forest habitats.

These records based upon specimens may reflect real distributional patterns on the island. Possibly the pygmy tarsier does not occur outside of Central Sulawesi because it is part of a montane fauna that appears to be endemic to the expansive and mountainous central core. Out of the approximately 122 species of mammals native to Sulawesi, 20 are known only from Central Sulawesi and 13 of these (65%) have not been found in habitats outside of montane rain forest formations (Musser, 1987). In addition to *T. pumilus,* the assemblage includes one species of shrew, *Crocidura* sp. B; one ground squirrel, *Hyosciurus heinrichi*; three kinds of shrew rats, *Melasmothrix naso, Tateomys macrocercus,* and *Tateomys rhinogradoides*; four arboreal rats, *Haeromys* sp., *Margaretamys elegans, Margaretamys parvus,* and a new genus and species to be described; and three terrestrial rats, *Taeromys hamatus, Eropeplus canus,* and *Bunomys penitus.* Some of these species live in lower montane forest but most have been collected only within the mossy upper montane levels.

The distributions of *Tarsius pumilus* and *T. spectrum* in Central Sulawesi also illustrate another pattern common to certain groups of native Sulawesian mammals. Like those two, there are species of other genera in which one is altitudinally replaced by another according to vertical distributions of forest formations or to factors defining special microhabitats within certain altitudinal ranges. This pattern is best demonstrated by the fauna in the central region of Sulawesi (table 7). No such vertical replacement is known on the northern, southwestern, and southeastern arms. The distribution of species in *Bunomys* is a good example. In Cen-

Fig. 28.　Lowland evergreen rain forest near Kuala Navusu, 30 m, Central Sulawesi. November 1975.

Fig. 29.   Mossy upper montane rain forest on summit of Gunung Nokilalaki, 2275 m, Central Sulawesi. December 1973.

TABLE 7

Altitudinal Distributions of Tarsiers, Squirrels, and Rats Occurring in Central Sulawesi

(Numbers indicate altitude in hundreds of meters.)

Taxon	Lowland evergreen forest												Montane forest										
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
TARSIERS																							
Tarsius																							
T. spectrum	—	—	—	—	—	—	—	—	—	—	—	—	—	—									
T. pumilus																	—	—	—	—	—	—	
SQUIRRELS																							
Hyosciurus																							
H. ileile	—	—	—	—	—	—	—	—	—	—	—	—	—	—									
H. heinrichi															—	—	—	—	—	—	—	—	
RATS																							
Margaretamys																							
M. beccarii	—	—	—	—	—	—	—	—															
M. elegans															—	—	—	—	—	—	—	—	—
M. parvus																		—	—	—	—	—	—
Haeromys																							
H. minahassae	—	—	—	—	—	—	—	—															
H. sp.																		—	—	—	—	—	—
Bunomys																							
B. andrewsi	—	—	—	—	—																		
B. sp. A						—	—	—	—														
B. penitus															—	—	—	—	—	—	—	—	—
B. chrysocomus			—	—	—	—	—	—	—	—	—	—	—	—	—	—							
Taeromys																							
T. celebensis	—	—	—	—	—	—	—	—	—														
T. punicans	—	—																					
T. arcuatus														—	—	—	—	—					
T. hamatus													—	—	—	—	—	—	—	—	—	—	—
T. callitrichus						—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

tral Sulawesi, *Bunomys penitus* lives in montane rain forest and is replaced by *Bunomys* species A in the upper half of tropical lowland evergreen rain forest, which in turn is replaced by *Bunomys andrewsi* at lower altitudes in lowland forest. *Bunomys chrysocomus* is sympatric with all three (table 7). In northeastern Sulawesi, only two species of the genus occur: *Bunomys fratrorum* and *B. chrysocomus* (Musser, 1983–1984). *Bunomys fratrorum* is common and extends from lowlands all the way up to montane forest formations. Its vertical range includes habitats and altitudes that encompass three distinct species in the central part of the island.

Much fieldwork in the peninsular arms of Sulawesi is required to determine the real geographic distributions of its native small mammal fauna that is confined to montane rain forest habitats, and to test our suggestion that *T. pumilus* may be endemic to the central part of the island.

Such fieldwork should include gathering more information about the distribution of *Tarsius spectrum* and other species that may have concordant regional and altitudinal ranges. At least two species, *Phalanger celebensis* and the large-bodied squirrel, *Rubrisciurus rubriventner,* have general island and vertical distributions similar to that of *T. spectrum*; both phalanger and squirrel live in forests from coastal lowlands up to the beginnings of lower montane rain forest (Musser, 1987). The ground squirrel, *Hyosciurus*

ileile, may have similar regional and vertical distributions.

11. **Summary.** *Tarsius pumilus* is a distinctive species. It is not simply small body size that sets it apart from the three large-bodied species of tarsiers but a suite of morphological characters involving relative proportions of toothrows, configuration of lower incisors and canines (including presence of lingual wear striations), differential molar wear, bullar morphology, conformation of nails and digital pads, and slightly different pelage. In addition to these features, *T. pumilus* contrasts with *T. spectrum,* its Sulawesian congener, by having proportionately wider orbits. The pygmy tarsier also differs from the other three species in its montane habitat, known distribution possibly confined to Central Sulawesi, and the associated montane mammal fauna of which it is a part.

Mossy forest habitat is unique to *Tarsius pumilus* and some of its diagnostic morphological features are undoubtedly results of co-evolution with that kind of forest. Its long and dense pelage, for example, is probably an adaptation to the cool and wetter ambient conditions at high elevations on Sulawesi, as is possibly small body size. The clawlike nails and very small digital pads likely give *T. pumilus* excellent purchase on mossy substrates. The greater degree of molar wear might be related to the kinds of foods available in mossy forest; possibly *T. pumilus* eats mostly arthropods with heavily keratinized exoskeletons. The other three species of *Tarsius* include arthropods in their diets but they also feed on a variety of vertebrate species (MacKinnon and MacKinnon, 1980; Niemitz, 1984b). The significant reduction of bullar inflation may reflect reduced auditory acuity. Night in mossy forest is quiet and usually only broken by the soft calls of insects, frogs, and owls. Perhaps heightened auditory acuity is unnecessary when sounds are carried clearly in the sharply cold and wet night air.

There is much to learn about the biology of *Tarsius pumilus* that only extended work in the field and laboratory can provide. There are also questions to be answered about its phylogenetic relationships to other species of tarsiers, a subject we briefly discuss in the next section.

PHYLOGENY AND DISPERSAL

It is difficult to sort out the relationships among the four species of tarsiers. The group comprises closely related taxa, has virtually no fossil record, and no close living relatives to use as a reasonable outgroup. We are analyzing a limited number of features, some of which may be functionally related, and which exhibit variation in a quantitative rather than qualitative sense.

Our hypothesis of relationships divides the living species into two groups: the Celebesian tarsiers (*T. spectrum* and *T. pumilus*) and the Sundaic and Philippine species (*T. bancanus* and *T. syrichta*). *Tarsius spectrum* and *T. pumilus* are linked by three features, the polarities of which, unfortunately, are difficult to determine. All are characteristics of the pelage: generally darker, longer fur; a white or pale brown postauricular spot; and the modified hairs of the ventral tail which form the "scales." This last trait, although certainly unusual for a primate, may be primitive for tarsiers; Sprankel (1965) noted that the development of friction skin on tails of *T. bancanus* and *T. syrichta* includes a *T. spectrum*-like stage.

Tarsius syrichta and *T. bancanus* are more similar to each other than are *T. spectrum* and *T. pumilus.* Differences between them tend to be quantitative rather than qualitative. They are united on the basis of four traits: increase in relative hand and leg length, a reduced nasal profile, reduction of the amount of hair in the terminal pencil of the tail, and a patch of friction skin on the ventral surface of the tail. On the basis of developmental evidence, Sprankel (1965) considered this last trait to be a very recent acquisition and a derived feature compared with the tail skin of *T. spectrum.* In most features (orbit size, tooth size, bulla inflation, and limb proportions) *T. syrichta* is less extreme than *T. bancanus.*

Although the evidence is limited, we believe the *T. spectrum–T. pumilus* group to be more primitive than the *T. syrichta–T. bancanus* group. Characters that best support this hypothesis are the increase in bullar size from *T. spectrum* to *T. syrichta* to *T. bancanus* (although we interpret the extremely small bulla of *T. pumilus* as an apomorphy of this

species, not the most primitive condition), and the increase in hand and leg lengths. Both of these features, which are more extremely expressed in *T. syrichta* and *T. bancanus,* are considered to be derived based upon comparison with other primates. Other *T. spectrum–T. syrichta–T. bancanus* morphoclines which are explained by this phylogenetic hypothesis are increase in orbit size and tooth size, and reduction in length of nasal bones. These are not strong characters to use in constructing the hypothesis because their polarities are difficult to determine. For example, *T. spectrum* has the smallest orbits of the four species; *T. bancanus* has the largest. Based upon a comparison with other primates, the smaller orbits of *T. spectrum* are more likely to be primitive than the large orbits of *T. bancanus.* But since *T. pumilus* and *T. syrichta* have the same size orbits, this polarity requires that *T. pumilus* share a common ancestor more recently with *T. bancanus* and *T. syrichta* than with *T. spectrum,* or that it independently acquired large orbits, perhaps as a consequence of dwarfing. The other possibility, and the one we adopt here, is that the ancestral tarsier had orbits the size of *T. pumilus–T. syrichta,* and the smaller orbits of *T. spectrum* are an apomorphy of this species. No evidence allows us to clearly choose between these alternatives. It is also impossible to say whether relatively large or small tooth size is primitive, since both increases and decreases in tooth size occur in other primates.

Our phylogenetic hypothesis is compared with several theories of dispersal that are outlined below.

1. The species on the Sunda Shelf and the Philippines are derived from populations on Sulawesi. This is the hypothesis favored by Niemitz (1977, 1984d) and Groves (1976). It has two variants: *T. syrichta* and *T. bancanus* are independently derived from *T. spectrum* (Niemitz, 1977) or the ancestor first went to the Philippines (through the Sangihe and Talaud islands) and then to Borneo (Groves, 1976; Niemitz, 1984d). This hypothesis is problematic in light of the distribution of other mammals. There is no evidence that any fauna of either Borneo or the Philippines is derived from Sulawesi (Musser, 1987). Some Sulawesian mammals may

be derived from ancestors common to Bornean forms. Fooden (1969), for example, would derive the endemic Sulawesi species of *Macaca* from an ancestral population related to the pig-tailed macaque, *M. nemestrina,* which lives on Borneo, Sumatra, Pulau Bangka, peninsular Thailand and Malaysia, and also occurs in Indochina. Macaques on the Philippines are derived from another species group, *M. fascicularis,* which now ranges over the Sunda Shelf and southern Indochina and probably had a wide distribution in southern Asia (Delson, 1980; Fooden, 1980). Evidence so far indicates that the greater part of the mammal fauna native to Sulawesi is primarily Asian derived (Groves, 1976), but there is no strong evidence for Sulawesi as a source area for any other mammalian groups (Musser, 1987). If tarsiers have dispersed in this manner, they are the only mammals which have done so.

Even though *Tarsius syrichta* is morphologically more primitive than *T. bancanus,* it seems much more likely that the dispersal was from the Sunda Shelf to the Philippines, not the other way (Groves, 1984; Heaney, 1985, 1986). *Tarsius bancanus* must have acquired its specializations after this dispersal, or these features are reversed in *T. syrichta.*

2. *T. spectrum*-like ancestors arrived at all three island groups and became isolated from each other at about the same time; the similarities of *T. syrichta* and *T. bancanus* are convergences. This scheme seems unlikely to us because of the close morphological resemblance between *T. syrichta* and *T. bancanus.*

3. A *T. spectrum*-like ancestor got to the eastern part of the Sunda Shelf and to Sulawesi where it remained isolated from the Sundaic population. *Tarsius spectrum* and *T. pumilus* were derived from this Sulawesian population. The Sundaic population evolved into a *T. bancanus–T. syrichta* form, which later dispersed to the southern Philippines (possibly to Greater Mindanao; see Heaney, 1985, 1986), where it evolved into *T. syrichta.*

The last two scenarios fit best with the zoogeographic relationships of other mammals dispersed among the three regions (Heaney, 1986; Musser, 1987). Number two is the simplest explanation and requires fewer past dispersal events. Number three reflects hypoth-

eses proposed for the dispersals of other mammalian groups: macaques (Fooden, 1969, 1980; Delson, 1980) and pigs (Groves, 1981, 1984), for example. In both cases, the evidence points to Sulawesian, Philippine, and Sundaic species being similar because of derivation from a common ancestor.

In addition to the tarsiers, other elements of the Sulawesi fauna have an ancient aspect to them. Anoas and the babirusa may have their closest links with the Miocene-Pliocene Siwalik fauna (Groves, 1976, 1981, 1984). *Sus celebensis* retains many features that are primitive for *Sus* and may have been derived from an ancestral stock living during the early Pliocene (Groves, 1981). Groves has suggested that the *S. celebensis* lineage was in the Malaysian region and got to Sulawesi before the late Pliocene migration of the *S. verrucosus–S. barbatus* lineage to the Sunda Shelf. The macaques of Sulawesi belong to the *silenus-sylvanus* group, the most primitive species group of this genus (Fooden, 1969, 1980). The origins of most of the native shrews, squirrels, and rats are also to be found in a now largely extinct Asian fauna (Musser, 1987).

In summary, recent analyses of the Sulawesi mammals (Cranbrook, 1981; Groves, 1984; Musser, 1987) indicate a probable derivation from a mainland Asian fauna no earlier than the Late Miocene or Early Pliocene, followed by relative isolation of Sulawesi, leading to the evolution of a derived, largely endemic fauna, which contains two species of tarsiers.

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