SLOTH HAIR: UNANSWERED QUESTIONS

Annette Aiello

Smithsonian Tropical Research Institute, P.O. Box 2072, Balboa, Panama

In: G. Gene Montgomery, Editor, "The Evolution and Ecology of Armadillos, Sloths, and Vermilinguas." 451 pp. Smithsonian Institution Press. Washington. (1985)

Abstract
Hair of tree sloths *Bradypus* and *Choloepus* differs in form and structure from that of all other mammals and may be specialized to accomodate the unicellular algae which grow in it. Conjectures are made concerning the possible relationship(s) between sloths and their algae.

Abstracto
El pelo de los perezosos arbóreos *Bradypus* y *Choloepus* difiere en forma y estructura del de todos los otros mamíferos y puede ser especializado para acomodar la algas unicelulares que crecen en él. Se hacen conjeturas respecto a las posibles relaciones entre los perezosos y sus algas.

Resumo
O pelo de preguiças *Bradypus* e *Choloepus* difere em forma e estrutura do pelo de todos od demais mamíferos e pode ser especializado para acomodar algas unicelulares que nele crescem. Conjecturas são feitas a respeito da possível ou possíveis relações entre preguiças e suas algas.

Among the many odd features of tree sloths *Bradypus* and *Choloepus* perhaps the oddest of all is their hair which, with its algal infestation and peculiar structure, is unlike the hair of any other mammal. Algae have been noted in or on the hairs of several other mammals, most notably inside the hairs of polar bears in captivity (Lewin and Robinson, 1979), but have not been found in wild polar bears, nor do they occur commonly in the few other mammals in which they have been observed.

Green-tinged hair is a consistent feature of 3-toed sloths *Bradypus* living under natural conditions, and the algae responsible for the color are already present on the hairs of animals a few weeks old (Britton, 1941). A number of unrelated alga species have been implicated; Thompson (1972) cultured algae representing four phyla (Chlorophyta, Chrysophyta, Cyanophyta, Rhodophyta) from the hair of *Bradypus*. Although no proof has been provided nor alternatives explored, most biologists assume that the sloth/alga association is of mutual benefit, the alga obtaining shelter and the sloth gaining camouflage. A 3-toed sloth with dry hair appears brownish grey, while a wet animal takes on a green tinge (Beebe, 1926).

HAIR STRUCTURE

Ridewood (1901) described the hair anatomy of eleven living and one extinct species of xenarthrans: *Bradypus tridactylus*, *Choloepus didactylus*, *Myrmecophaga tridactyla* (as *M. jubata*), *Tamandua tetradactyla*, *Cyclopes didactylus* (as *Cyclothurus*), *Chlamyophorus truncatus* (as *Chlamydophorus*), *Euphractus sexcinctus* (as *Dasypus*), *Chaetophractus villosus* (as *Dasypus*), *Tolypeutes matacus* (as *T. conurus*), *Dasypus novemcinctus* (as *Tatusia novemcincta*), *Dasypus pilosus* (as *Tatusia pilosa*), and *Mylodon listai* (extinct).

Typical mammalian hair and that of many xenarthrans, is composed of a central medulla surrounded by a cortex that contains pigment granules, and is enclosed within a thin, fairly uniform, scaly cuticle. The hair structures (cuticle, cortex, and medulla) can be distinguished by selective staining. However, *Bradypus* and *Choloepus* hairs have neither medulla nor pigment granules.

Not only do the hair structures of *Bradypus* and *Choloepus* differ from those of other mammals (other xenarthrans included), but the hairs of the two genera differ as well (Fig. 1). The most obvious external characteristic of *Bradypus* hair is its transversely cracked surface, and in *Choloepus* the striking feature is the fluted appearance due to 8 to 11 longitudinal ribs. *Bradypus* has both over-hair (guard hairs) that harbors algae, and soft underfur which is algae-free. *Choloepus* does not have underfur. In this paper, "hair" will refer to over-hair unless otherwise noted.

Bradypus tridactylus hairs are oval in cross-section and consist of a solid cortex surrounded by a thick extra-cortical layer which harbours algae (Ridewood, 1901). Ridewood interpreted the extra-cortex as "...the cuticle itself, enormously thickened and distinctly cellular, instead of more or less homogeneous and structureless.....a layer not represented, or at least not in this form, in the hair of any other mammal."

The hairs of *Choloepus didactylus* consist mainly of cortex, permeated by irregular branching tubes that may represent a diffuse medulla (Ridewood. 1901). The cuticle enclosing the cortex is thickest at the summits of the above-mentioned ribs, but becomes thinner on the sides and disappears at the bottoms of the grooves except for intermittent cuticular bridges joining rib bases. Within the grooves are strands of extra-cortex in which algae live, and it is Ridewood's view that, as in *Bradypus*, this "extra-cortex" is an elaboration of the cuticle itself.

ALGAE

While many accounts of *Bradypus* hair are vague as to the location of algae, or imply that the colonies are located on the hair surface, Sonntag and Duncan (1922) reported that the algae of *Bradypus tridactylus* are found between the cuticular scales. My observations agree with theirs. In spite of the illusion that the algae rest on the hair surface, they are invisible under the scanning electron microscope, an instrument sensitive to surface structure rather than to color contrast.

Grassé (1955) states that the algae are located in the transverse cracks of *Bradypus* hairs. Hairs which I examined (Table 1) had algae growing right up to the edges of the large cracks, but the tissue within the cracks was pale and appeared to be free of algae. That algae do not inhabit these fissures is not surprising; wetted hairs soak up water as does a sponge, swell slightly, and the cracks close. Algae within a closed crack would have little access to light.

My observations indicate that hairs of *B. variegatus* pass through a distinct age sequence (Fig. 1). Young hairs were white, gray, brownish, or black, and lacked the deep transverse cracks of older hairs. The first traces of algae were seen on these young hairs as tiny dots or very narrow transverse green lines. Older hairs had larger, wider algal colonies and obvious transverse cracks. In apparently older hairs, the cracks were deeper, and the cortical layer could be seen. Upon wetting, even the larger cracks closed considerably. When dry, such hairs gave the effect of beads on a string. The oldest hairs were badly deteriorated; the spongy cuticle had worn off on one side exposing the full length of the cortex. These very old hairs did not appear to have living algae, indeed, only young and middle-aged hairs supported healthy algal colonies. Either algae colonize very narrow cracks in young hairs, or the algae themselves initiate the cracks. Once a crack exceeds a certain depth, algae cease to grow in it. In either case, perhaps the algae hasten the deterioration of *Bradypus* hairs.

The hair of the other *Bradypus* species was similar. *B. tridactylus* hair which I studied was not prominently cracked and may have been from a young or newly molted individual. Hair of *B. torquatus* was essentially like that of *B. variegatus* (Fig. 1). The hair of all three *Bradypus* species readily absorbed water in all parts including the cortex, and the surface of *B. tridactylus* hairs became mucilaginous and sticky when wet.

Choloepus hairs were also wettable, cortex included, but they did not swell when wet. It was not clear whether in *Choloepus* the algae rested upon the surface of the spongy cuticle in the grooves, or were embedded in it. In either case the algae were confined to the

Table 1. Origin of specimens from which hair was obtained. GML refers to Gorgas Memorial Laboratory, Panama. NMNH refers to the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Species	*Country of Origin*	*Collection Data*
Bradypus variegatus Schinz	Panama, Ancon	29 June 1982; A. Aiello and G. Montgomery.
Bradypus torquatus Desmarest	Brasil, Bahia, nr. Ilheus	NMNH (US 259473).
Bradypus tridactylus L.	Guyana	NMNH (US 256676).
Cabassous centralis (Miller)	Panama	GML
Choloepus didactylus (L.)	Venezuela, T.F. Amazonas, Belen	NMNH (US 388206).
Choloepus hoffmanni Peters	Panama, Arraijan	Dead on Road, Dec. 1982; A. Aiello and R. Cortez.
Cyclopes didactylus (L.)	Panama, Barro Colorado Island	1983; Bonafacio de Leon.
Dasypus novemcinctus L.	Panama	GML
Myrmecophaga tridactyla L.	Panama	GML
Tamandua mexicana (Saussure)	Panama, Cerro Galera	Dead on Road; 1 Dec. 1982; A. Aiello.
Tamandua mexicana (Saussure)	Panama	GML

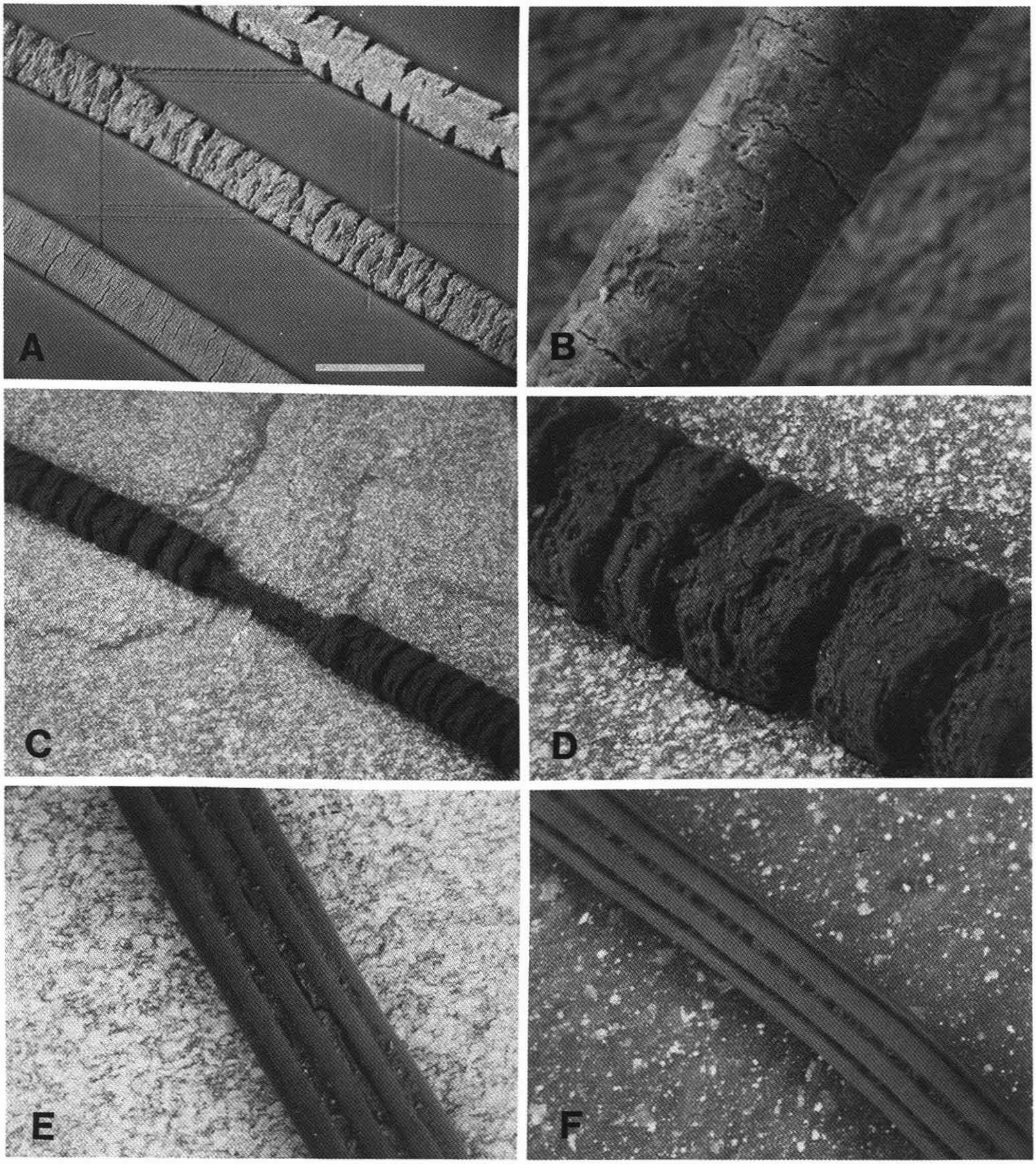

Figure 1. Hair of tree sloths. A. *Bradypus variegatus* Schinz. Three hairs at different stages of deterioration are shown: bottom hair is young and has a few narrow transverse cracks; center hair is older and has larger more numerous cracks; top hair is very old, has deep cracks, and the full length of its cortex is exposed. Scale bar = 0.60 mm. B. *Bradypus tridactylus* L. Hair showing moderate transverse cracking. Scale bar = 0.10mm. C and D. *Bradypus torquatus* Desmarest. Hair has deep transverse cracks and in C a portion of the cortex is partly exposed. Scale bars = 0.40mm and 0.10mm respectively. E. *Choloepus hoffmanni* Peters. Hair with five longitudinal ribs showing. Each rib is enclosed within a scaly cuticle. Scale bar = 0.10mm. F. *Choloepus didactylus* (L.). Hair with four longitudinal ribs showing. Each rib is enclosed within a scaly cuticle which extends across the grooves at frequent intervals and joins the bases of adjacent ribs. Scale bar = 0.10mm.

grooves, and it appears that the hair is better designed than that of *Bradypus* to control the extent of algal colonization.

DISCUSSION

The hair of *Bradypus* and *Choloepus* is apparently specialized to encourage a symbiotic relationship with algae. The hair structures which harbor algae are different, but possibly homologous; no other mammals have either comparable hair structure or algae. Nevertheless, the algae may be accidental guests, or they may be sloth hair parasites which take advantage of the sheltered humidity beneath the hair cuticle and also benefit from the sunbathing activity of their hosts.

If the algae are parasites, then why do sloths have spongy hair that soaks up water and encourages their colonization? Thermal insulation has been suggested (group discussions at STRI). Sloths have difficulty maintaining an even body temperature; exposure to heat raises, and to cold lowers a sloth's temperature (Britton and Atkinson, 1938; Montgomery and Sunquist, 1978; McNab, 1978, 1985).

Certainly, thick fur would be of insulative value to such an animal, but while I agree that the fine fluffy underfur of *Bradypus* probably serves this purpose, I question that spongy, water-absorbing hair would serve as insulation, at least in wet season; more likely it promotes evaporative cooling, and is thus detrimental.

It seems more likely that sloth hair has evolved its unique structure to encourage algal colonization. If so, why?

Camouflage is the reason usually given. But while a green-tinged sloth is perhaps better hidden, the green color is present only during rainy periods, and any sloth is very well concealed by screening vegetation, regardless of its body color.

Would an animal develop such specialized hair for the purpose of half-time improvement of its already excellent camouflage?

The sloth may obtain nutrition or a particular trace element from the algae. Indeed, many leaf-eating animals have difficulty obtaining sufficient nitrogen and it is difficult to explain how the sloth manages to collect enough of this element. It has been suggested (Hoke, 1976) that sloths may prevent certain dietary deficiencies by inadvertently partaking of an occasional ant along with their usual leaves. There are at least two possible methods by which a nutrition transfer from alga to sloth might take place.

Nutrients might be transferred by the sloth licking its hair. While many mammals lick their hair, sloths have not been observed to engage in this activity (Tirler, 1966). Even if they do, it certainly is not a frequent event and nutrition transfer in this way is unlikely.

The nutrients might move into the sloth through the hair itself. Unlike the hair of other mammals, sloth hair (spongy cuticle, and cortex) soaks up water, and even if only one portion is in contact with water, after some minutes the entire length of the hair is moist. Chemicals might diffuse along the hair to the skin surface, and then be absorbed through the skin. The spongy hair structure would promote this process. An analogy can be made to orchid roots, which absorb water and minerals through an outer layer (velamen) of spongy, algae-harbouring epidermal cells. See Dressler (1981) for references about orchid roots.

Dependence upon either algae or an occassional ant or both for trace nutrients might help explain why *Bradypus* does not survive long in captivity; if the algae are not healthy or if, as discussed by Hoke (1976), ants are not available, the sloth would eventually die. *Choloepus*, with its less extensive algal colonies and absence of underfur, is much more active than *Bradypus*. From what can be inferred from its food choices in captivity, it has a more varied diet than *Bradypus*. If sloths do depend upon their algae for proper nutrition *Choloepus* would probably be less dependent on algae than *Bradypus*.

The hair of at least two species of extinct ground sloths was not specialized. Ridewood (1901) examined hairs of *Mylodon listai* from Patagonia and found that they lacked a medullar layer, had a thick scaly cuticle, and showed no trace of a spongy cuticle. They did not at all resemble hairs of tree sloths but instead were very similar to those of modern *Tamandua* and *Daspus*. Ridewood did not mention anything about algae or algal-like bodies. Hausman (1929, 1936) reported that *Nothrotherium shastense* did not have underfur, and that the hairs had medulla (sometimes double), cortex, pigment granules, and scaly cuticle, and "...did not seem to be fundamentally different from those of... modern animals." Alga-like "ovate bodies" were scattered on the surface of these hairs. From the description and illustrations these bodies were solitary, not in algal colonies as in *Bradypus* and *Choloepus*. It is not at all clear that they are the remains of algae, but could be some other form of unicellular life.

SUMMARY

The tree sloths *Bradypus* and *Choloepus* have hair that is strikingly different in form and structure from hair of other xenarthrans (extinct or extant) and other mammals, and is probably specialized to encourage colonization by various unicellular algae. Whether the sloth gains camouflage or nutrition or both from its algae is not yet clear. Certainly this intriguing relationship deserves much more attention than it has received.

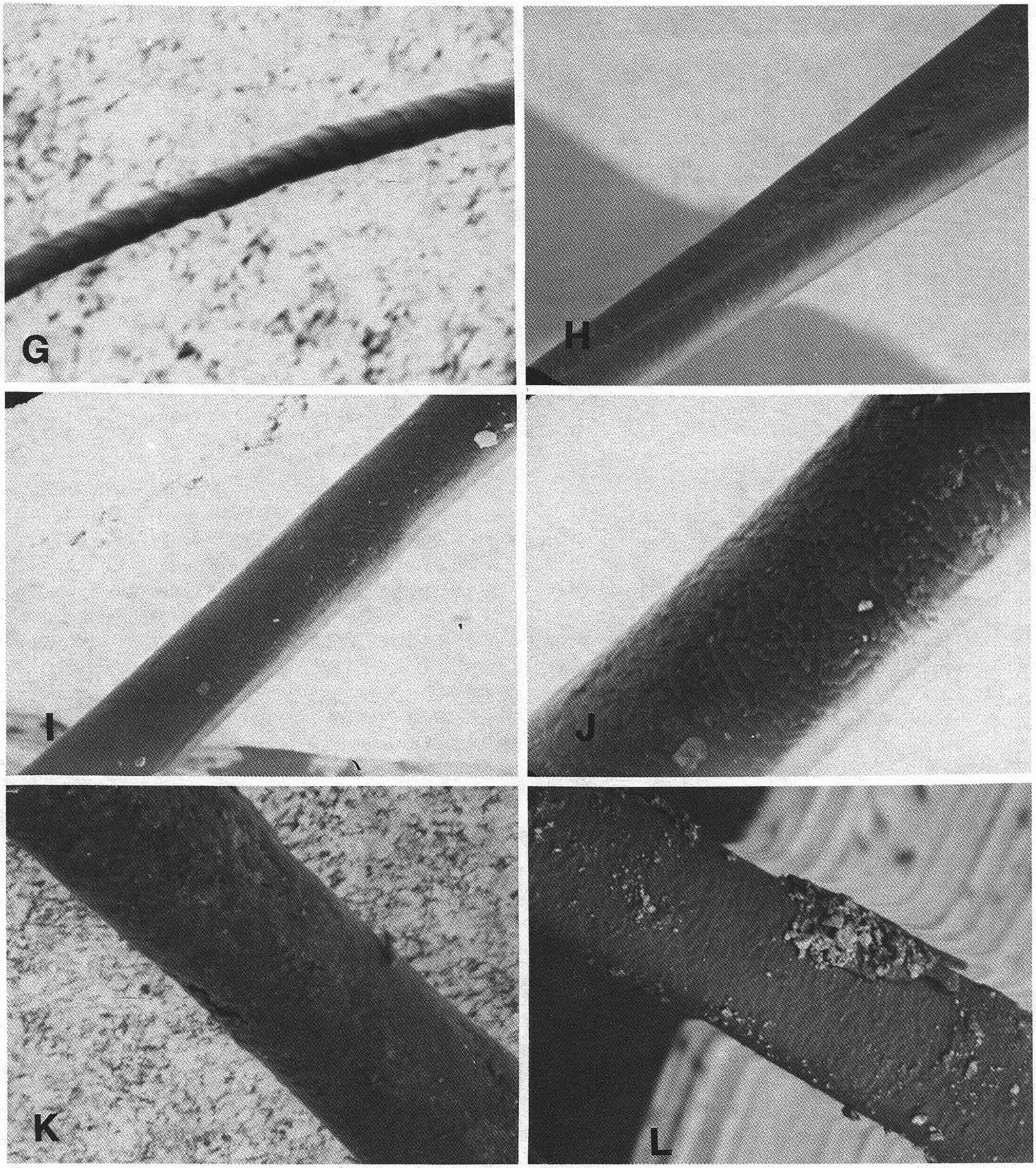

Figure 2. Hair of vermilinguas and armadillos. G. *Cyclopes didactylus* (L.). The hair is much finer than that of other xenarthrans and the cuticle scales are relatively few and large. Scale bar = 0.04mm. H. *Myrmecophaga tridactyla* L. The hairs are compressed and have a broad longitudinal groove on each side. Scale bar = 0.10mm. I and J. *Tamandua mexicana* (Saussure). The scales of the cuticle overlap closely and have ragged edges. Scale bar = 0.10mm and 0.04mm respectively. K. *Cabassous centralis* (Miller). The hairs are covered with debris, but the cuticle scales show through in several places. Scale bar = 0.10mm. L. *Dasypus novemcinctus* L. The hairs have bits of loose debris, but the closely overlapping cuticle scales show clearly. Scale bar = 0.10mm.

ACKNOWLEDGMENTS

I am grateful to G. Gene Montgomery for his encouragement and advice during this project, and to Estorgio Mendez of Gorgas Memorial Laboratory, Panama, Dr. Charles Handley, U.S. National Museum, Washington, D.C., and Patricia and Michael Fogden for their generous donations of hair samples. G. Gene Montgomery and Donald Windsor read the manuscript. Colonel Richard Barrere, U.S. Army, Tropic Test Center, Panama, allowed use of the scanning electron microscope, and the library of the Smithsonian Tropical Research Institute obtained copies of literature not available in Panama.

LITERATURE CITED

Beebe, W.
1926. The three-toed sloth *Bradypus cuculliger cuculliger* Wagler. Zoologica, 7: 1-67.

Britton, S.W.
1941. Form and function in the sloth: Quart. Rev. Biol., 16(1) 13-34.

Britton, S.W. and W.E. Atkinson.
1938. Poikilothermism in the sloth. J. Mamm., 19(1): 94-99.

Dressler, R.L.
1981. The orchids: natural history and classification. Harvard University Press, Cambridge, Massachusetts, 332 pp.

Grassé, P.P.
1955. Ordre des Edentates. Pp. 1182-1246 *In*, Traité de zoologie anatomie, systématique, biologie. Mamminféres. (P.P. Grassé, editor). L'académie de Médecine Edituers, Paris. 17(2): 1171-2300.

Hausman, L.A.
1929. The "ovate bodies" of the hair of *Nothrotherium shastense*. Am. J. Sci., (ser.5)18(106): 331-333.

1936. Further studies of the hair of the fossil ground sloth (*Nothrotherium shastense*), and of its problematical "ovate bodies." Am. J. Sci., (ser.5)31(181):223-228.

Hoke, J.
1976. Discovering the world of the three-toed sloth. Franklin Watts, New York. 88 pp.

Lewin, R.A., and P.T. Robinson.
1979. The greening of polar bears in zoos. Nature, 278(5703): 445-447.

McNab, B.K.
1978. Energetics of arboreal folivores: physiological problems and ecological consequences of feeding on an ubiquitous food supply. Pp. 153-162, *In* The ecology of arboreal folivores. (G. Gene Montgomery, editor). Smithsonian Institution Press, Washington, D.C. 574 pp.

McNab, B.K.
1985. Energetics, population biology, and distribution of xenarthrans, living and extinct. (this volume).

Montgomery, G.G. and M.E. Sunquist.
1978. Habitat selection and use by two-toed and three-toed sloths. Pp. 329 to 359, *In* The ecology of arboreal folivores. (G. Gene Montgomery, editor). Smithsonian Institution Press, Washington, D.C. 574 pp.

Ridewood, W.G.
1901. On the structure of the hairs of *Mylodon listai* and other South American Edentata. Quart. J. Micros. Soc. (n.s.), 44: 393-411.

Sonntag, C.F., and F.M. Duncan.
1922. Contributions to the histology of the three-toed sloth (*Bradypus tridactylus*). J. Royal Mic. Soc., :37-46.

Thompson, R.H.
1972. Algae from the air of the sloth *Bradypus*. Supplement to J. Phycol., 8:8.

Tirler, H.
1966. A sloth in the family. Walker and Co., New York, 47 pp.