movement variables, including fixation locations, saccade sizes and directions, and velocities (*9*). Typically, fixations were analyzed for 8 to 20 repeated trials, each of which consisted of clearing the baited apple board. Fixation plots of normal monkeys showed a clustering of fixations at points where the apple pieces appeared on the board (Fig. 1, B and E). Both the 17-slot apple board and spontaneous eye movements yielded quite different clustering patterns.

In accordance with previous reports (*1, 3*), the effects of either frontal eye field or collicular lesions on visually guided saccadic eye movements were not dramatic. Ablation of the frontal eye fields produced a partial neglect; animals tended to leave some of the sites on the apple board unpicked and looked at peripheral targets less frequently. This effect was temporary; after 1 to 3 weeks, recovery was virtually complete, and fixation patterns and latencies became comparable to performance before the lesion was made (Fig. 1, B to D).

Superior colliculus ablation in otherwise intact monkeys produced several subtle deficits, which recovered little; the animals were able to make visually triggered saccades but accuracy decreased, as did the number, size and velocity of saccades (Fig. 1F).

In contrast, ablation of both the frontal eye fields and the superior colliculi produced a remarkably dramatic deficit: animals virtually ceased making organized saccades. They seemed to have lost the ability to target their eyes on visual stimuli. Monkey 1 was able to perform saccadic eye movements only within a limited range and showed low accuracy in targeting. This effect did not recover with time (Fig. 1H). We have kept animals for longer than 1 year without observing improvement. The extent and distribution of the remaining eye-movement activity varied among animals and appeared to be a function of spared tissue in the superior colliculus. In some animals the deficit was more pronounced than for monkey 2 (Fig. 1, E to H).

Figure 2 shows the histological reconstruction of the lesions for monkey 2. The collicular lesion in the right superior colliculus was more extensive than that in the left. Tissue sparing was especially evident on the left lateral margin of the superior colliculus (sections 3 and 4)—representing the lower right visual field near the vertical meridian—and near the midline (sections 5 and 6)—representing the upper vertical meridian. The residual eye-movement activity of monkey 2 appears to correspond to the tissue spared in the colliculi. Animals in which the superior colliculus was removed only partially or only superficially (leaving intermediate and deep layers intact) showed less pronounced deficits.

Although animals with the combined bilateral lesions could move their eyes only within a restricted range and targeted inaccurately, they attended to the entire visual field. Except for the period 1 to 3 weeks after the frontal eye field was ablated, they picked all or most of the apples on the board without directing their gaze correctly. When their heads were free, they oriented head and body toward items of interest.

We also examined several other kinds of oculomotor performance in these animals. Smooth pursuit and optokinetic nystagmus as elicited by moving objects and gratings showed a narrowed range corresponding to the deficit seen on the apple board task. The range of the vestibulo-ocular reflex, produced by rotating the monkey while the head was fixed, was also reduced immediately after surgery but recovered considerably over a period of several weeks or months. With the head free, eye movements induced by the vestibular system as compensation for a head movement were evident; however, such compensation was not typically preceded by saccadic targeting, as it is in intact animals.

These findings suggest that two pathways, one via the frontal eye fields and the other via the superior colliculi, are responsible for producing visual targeting by eye movement; when only one is damaged, the other can remain effective; when both are disrupted, organized saccadic eye movements are virtually abolished.

PETER H. SCHILLER
SEAN D. TRUE
JANET L. CONWAY

Department of Psychology,
Massachusetts Institute of Technology,
Cambridge 02139

References and Notes

1. R. Latto and A. Cowey, *Brain Res.* **30**, 25 (1971); *ibid.*, p. 1; K. V. Anderson and D. Symmes, *ibid.* **13**, 37 (1969); E. G. Keating, *ibid.* **67**, 538 (1974); T. Pasik, P. Pasik, M. B. Bender, *Arch. Neurol.* **15**, 420 (1966); D. Kurtz and C. M. Butter, *Soc. Neurosci.* **2**, 1122 (1976); R. H. Wurtz and M. E. Goldberg, *J. Neurophysiol.* **35**, 587 (1972).
2. D. Denny-Brown, *Proc. R. Soc. Med.* **55**, 527 (1962); K. Welch and P. Stuteville, *Brain* **81**, 341 (1958).
3. D. A. MacKinnon, C. G. Gross, D. B. Bender, *Acta Neurobiol. Exp.* **36**, 169 (1976).
4. P. H. Schiller and F. Koerner, *J. Neurophysiol.* **34**, 920 (1971); D. L. Sparks, R. Holland, B. L. Guthrie, *Brain Res.* **113**, 21 (1976); R. H. Wurtz and M. E. Goldberg, *J. Neurophysiol.* **35**, 575 (1972).
5. E. Bizzi, *Exp. Brain Res.* **10**, 69 (1968); C. W. Mohler, M. E. Goldberg, R. H. Wurtz, *Brain Res.* **61**, 385 (1973).
6. D. A. Robinson, *Vision Res.* **12**, 1795 (1972); _____ and A. F. Fuchs, *J. Neurophysiol.* **32**, 637 (1969); P. H. Schiller and M. Stryker, *ibid.* **35**, 915 (1972).
7. P. H. Schiller, *Brain Res.* **122**, 154 (1977).
8. D. A. Robinson, *IEEE (Inst. Electr. Electron. Eng.) Trans. Bio-Med. Eng.* **10**, 137 (1963).
9. S. D. True and R. W. Sjoberg, *Brain Theory Newsl.* **3**, 142 (1978).
10. Supported by NIH grant 2 RO1 EY00676, NSF grant BNS76-82543, and NIH grant 1 T31 GMO7484.

2 April 1979; revised 5 July 1979

Early Hominid Population Densities: New Estimates

Abstract. *Proportional faunal representations in excavated fossil occurrences (Shungura Formation, Omo, Ethiopia) are very similar to modern sub-Saharan mammalian faunal proportions in a variety of environments. Early hominids comprise between 0.6 and 1.6 percent of the excavated assemblage, corrected to reflect numbers of individuals. With allochthonous faunal localities for comparison, direct analogies to modern fauna suggest early hominid population densities of between 0.006 to 1.7 individuals per square kilometer. Calculations based on population densities of modern large mammals indicate that population densities of early hominids were between 0.001 and 2.48 individuals per square kilometer.*

In terrestrial biotopes, biomasses of herbivores, carnivores, and further links in the food chain are progressively smaller (*1*). Furthermore, among animals there is a tendency for herbivores to be more numerous, and for primary, secondary, and tertiary carnivores to be respectively less abundant (*1*). These ecological relationships can be used, in conjunction with faunal excavations, to reconstruct aspects of hominid Pliocene paleoecology.

The paleobiological significance of an excavated fauna depends on the particular agents responsible for its accumulation and the depositional environment in which it occurs; that is, its taphonomic history. Excavations in the lower Omo Basin, Ethiopia, considered here, have been reported (*2*). They occur in both high-energy depositional environments, such as point-bar and abandoned-channel deposits, and in relatively low-energy environments, such as backswamps and alluvial plain deposits.

Large accumulations of disarticulated and fragmentary bones, occurring in well-sorted and large grain-sized sediments, as in localities L.1 and L.398, (Table 1), are considered to represent allochthonous faunas, accumulated by attritional death over some length of time and transported from the environments in which death occurred (*3*). Such localities therefore provide a generalized view of the fauna, which can be utilized in paleoecological reconstruction, considering that, minimally, inhabitants of distal environments and small mammals would be underrepresented. Lower-energy depositional environments, in contrast, such as L.345 and (to a lesser extent) L.338y and L.626, incorporate bones that are more complete, less abraded, and partially articulated, indicating a more autochthonous fauna, more likely related to one paleohabitat (*4*).

The five excavated faunal samples considered here range in age from 2.8 million years ago (L.1) to 1.9 million years ago (L.626) (*5*). Their respective ages (million years) and stratigraphic units within the Shungura Formation are 2.8 for L.1, units B9 to B12; 2.5 for L.345, unit C9; 2.2 for L.338y, unit E3; 2.1 for L.398, unit F1; and 1.9 for L.626, units G12 and G13.

Identified taxa of large mammals are summarized in Table 1 by numbers and percentages. Consideration of small mammal remains (body weight less than 10 to 15 kg) is omitted because of their underrepresentation due to destruction by carnivores, fluvial transport, weathering and other taphonomic agents (*6*). Nonmammalian remains are also omitted.

In the L.1 and L.398 assemblages, virtually no significant associations or articulations of bones are demonstrable (*2*). This fact in conjunction with the high-energy deposition, militates against any of the remains belonging to the same individual. A modified "minimum numbers" approach (*3, 7*) has been employed in which all identifiable specimens were counted as individuals unless articulation, close proximity, or morphology indicated otherwise. Characteristics such as dental wear, size, or degree of long bone fusion often indicated that different body parts of the same taxon (for example, isolated second and third molars) could not have derived from the same individual. A strict minimum numbers approach based on most common skeletal elements (*7, 8*) has the disadvantage of grossly underestimating numbers of individuals in the more numerous taxa (such as bovids).

Table 1 shows numbers of individuals and percentages of the total of excavated taxa. Results are comparable from all five excavations and suggest an ecological "pyramid of numbers" [see figure in (*2*)], with herbivores at the base and carnivores at the top. Large, probably nonherd animals with relatively low population densities (rhinocerotids, deinotheriids, and stegodontids) would also occupy positions near the top of the

Table 1. Numbers and percentages of specimens belonging to large mammal taxa (corrected for individual numbers) from Omo excavations.

	L.1		L.338y		L.345		L.398		L.626	
	No.	%	No.	%	No.	%	No.	%	No.	%
Bovidae	180	.282	89	.244	12	.164	261	.306	92	.582
Giraffidae	30	.047	2	.005	0	0	30	.035	1	.006
Camelidae	2	.003	1	.003	0	0	0	0	0	0
Equidae	17	.027	2	.005	0	0	11	.013	6	.038
Rhinocerotidae	4	.006	0	0	0	0	1	.001	0	0
Hippopotamidae	22	.034	118	.323	12	.164	213	.249	31	.196
Suidae	61	.096	49	.134	2	.027	111	.130	11	.070
Elephantidae	21	.033	14	.038	1	.014	43	.050	0	0
Deinotheriidae	5	.008	0	0	0	0	2	.002	1	.006
Stegodontidae	1	.002	0	0	0	0	0	0	0	0
Cercopithecinae	248	.389	83	.227	46	.630	162	.190	13	.082
Colobinae	17	.027	0	0	0	0	1	.001	0	0
Hominidae	4	.006	3	.008	0*	0*	14	.016	1	.006
Felidae	3	.005	1	.003	0	0	5	.006	2	.013
Mustelidae	0	0	3	.008	0	0	0	0	0	0
Viverridae	22	.034	0	0	0	0	0	0	0	0
Hyaenidae	1	.002	0	0	0	0	0	0	0	0
Total	638	1.00	365	1.00	74	1.00	854	1.00	158	1.00

*L.345 (a)-11, a hominid parietal was found at this locality but it likely derives from a stratigraphic level slightly higher than that excavated. If this specimen were in situ, the hominid percentage of the fauna ($N = 74$) would equal .014.

Table 2. Ratios of total population numbers of large mammalian taxa in modern African environments and in faunal excavations at Omo.

	Modern (*12*)						Fossil				
	Savanna*	Savanna†	Savanna‡	Savanna§	Woodland‖	Forest¶	L.1	L.338y	L.345	L.398	L.626
Hippopotamid/bovid	.33	.59	.0007				.12	1.33	1.00	.82	.34
Elephantid/hippopotamid	.21	.21					.95	.12	.08	.20	
Elephantid/bovid	.07	.12		.0002			.12	.16	.08	.16	
Suid/bovid	.04	.07	.04		.06		.34	.55	.17	.43	.12
Suid/elephantid	.62	.60					2.90	3.50	2.00	10.09	
Colobine/bovid						12.44	.09			.004	
Cercopithecine/bovid						2.86	1.38	.93	3.83	.62	.14
Rhinocerotid/bovid			.002	.0002			.02			.004	
Equid/bovid			.35	.19	.26		.09	.02		.04	.07
Giraffid/bovid			.02	.003	.03		.17	.02		.11	.01

*Rwindi-Rutshuru area, Uganda; open savanna near forest, or wooded savanna. †Queen Elizabeth National Park, Uganda; open savanna near forest, or wooded savanna. ‡Nairobi National Park, Kenya; open savanna with *Acacia* stands. §Serengeti National Park, Tanzania; open savanna. ‖Henderson Ranch, Zambia; open woodland. ¶Tano Nimri Forest, Ghana.

Table 3. Hominid population densities as estimated from other large mammals obtained from the equation $d_h = d_a(e_h/e_a)$. The number of estimates is based on available modern population densities (*12*).

Estimates	No.	Hominid individuals per square kilometer	
		L.1	L.398
Bovid	6	.01 to 1.05	.03 to 2.58
Elephantid	3	.001 to .32	.002 to .55
Hippopotamid	3	.005 to 1.45	.002 to .52

pyramid. However, the trophic pyramid is not perfect, as the actual population numbers of large herbivores living in habitats distal to the depositional environment (camelids and equids) are likely underrepresented, and those living in proximal habitats may be overrepresented (hippopotamids). As noted above, small mammals, such as colobines with a body weight of about 9 kg (*9*), are also greatly underrepresented (see Table 2).

To test the reliability of the use of excavated faunal numbers in reflecting actual population sizes, a comparison was made between population ratios of large mammal species in modern sub-Saharan Africa and in the Omo excavations (Table 2). The fossil ratios show a close correspondence to the modern ratios in a variety of environments. Two factors are responsible for the observed variance. In some cases a greater taxonomic diversity likely accounts for higher representations in the fossil assemblages. Suids and giraffids are relatively more prevalent in the fossil situations because more taxa of these families were present in the African Pliocene than are present today (*10*). Ratios of hippopotamids to bovids are slightly higher, especially in the autochthonous faunas, since hippopotamids are residents of the proximal depositional community (the river) and therefore are more likely to be fossilized (*11*).

The allochthonous faunas, probably accumulated by attritional death (L.1 and L.398), show the closest approximation to the modern analogs in the elephantid-bovid, hippopotamid-bovid, and elephantid-hippopotamid ratios. These two localities probably best reflect overall faunal population numbers.

On the basis of simple analogy with modern population densities of large mammal taxa found in similarly rare numbers in excavated assemblages (Table 1), early hominid densities would be in the range of the following (individuals per square kilometer): 0.006, Serengeti black rhinoceros (*12*); 0.04, Seronera leopard (*13*); 0.09, Nairobi Park black rhinoceros (*12*); 0.1, the sum of the Serengeti lion and cheetah (*13*); 0.1, the sum of the Kruger Park lion, leopard, and cheetah (*13*); 0.12, Serengeti spotted hyena (*14*); 0.27, Ngorongoro lion (*13*); 0.38, Lake Manyara lion (*13*); 0.45, the sum of the Nairobi Park lion and cheetah (*13*); and 1.7, Ngorongoro spotted hyena (*14*). The estimated range is 0.006 to 1.7 hominid individuals per square kilometer.

A second method of assessing early hominid population densities depends on the use of numbers of individuals of abundant excavated large mammal taxa. This calculation proceeds on the assumption that population densities of fossil mammalian taxa were the same as modern densities of the same or closely related taxa. With the ratio of excavated number of hominid individuals to excavated number of individuals of mammalian taxon "a," and the known modern population density of the latter, fossil hominid population densities can be calculated by

$$d_{\mathrm{h}} = d_{\mathrm{a}}\,(e_{\mathrm{h}}/e_{\mathrm{a}})$$

where d_{h} is hominid population density, d_{a} is population density of modern mammalian taxon "a," e_{h} is number of excavated individuals of hominids, and e_{a} is number of excavated individuals of mammalian taxon "a."

Using bovid, elephantid, and hippopotamid excavated numbers of individuals from the allochthonous localities (L.1 and L.398) and the available modern population densities for these three groups from the parks listed in Table 2 (*12*), one obtains the following results listed in Table 3. The range of densities, 0.001 to 2.58 individuals per square kilometer, is similar to the range obtained by direct analogy, 0.006 to 1.70.

It is difficult to state conclusively to which hominid taxon or taxa these numbers are to be referred because of the fragmentary nature of the remains. *Australopithecus africanus* is the sole taxon in the early Omo deposits (L.1), but both gracile (*Homo* sp.) and robust (*A. boisei*) are present in stratigraphic member F (L.398) (*15*).

The rarity of hominid skeletal elements raises the question of possibly greater destruction by taphonomic processes in comparison to other taxonomic groups, such as rhinocerotids or carnivores, known to have been environmentally rare. This is unlikely. Hominids, as large animals (18 to 91 kg) (*16*), are in the same size range as 8 of the 11 Omo carnivore taxa counted in Table 1 (*17, 18*). Only the lion-sized (100 to 168 kg) (*9*) *Homotherium* is larger (*18*), and only the very rare *Felis caracal* (13 to 15 kg) (*9*) and mellivorine mustelids (about 9 kg) (*9, 17*) are smaller.

Inhabitation of distal environments at Omo also cannot explain the rarity of hominids. Modern humans and carnivores (*9*) must drink daily, and early hominids were probably also closely tied to fresh water (*19*). Both hominids and carnivores would be expected to have died in similar frequencies in areas favorable for deposition near the Omo River.

Although population densities of early hominids and carnivores appear similar, behavioral and dietary extrapolations are not necessarily warranted on this basis alone. For example, the population density of the frugivorous, early-hominid-sized (34 to 41 kg) (*9*) *Pan troglodytes*, in the Tano Nimri Forest, Ghana, is 0.09 individuals per square kilometer (*12*).

NOEL T. BOAZ

Department of Anthropology,
New York University,
New York 10003

References and Notes

1. G. L. Clarke, *Elements of Ecology* (Wiley, New York, 1954).
2. D. C. Johanson, M. Splingaer, N. T. Boaz, in *Earliest Man and Environments in the Lake Rudolf Basin*, Y. Coppens, F. C. Howell, G. L. Isaac, R. E. Leakey, Eds. (Univ. of Chicago Press, Chicago, 1976), pp. 402–420.
3. M. R. Voorhies, *Wyo. Univ. Contrib. Geol. Spec. Pap. 1* (1969).
4. J. A. Shotwell, *Ecology* **36**, 327 (1955).
5. F. H. Brown, J. de Heinzelin, F. C. Howell, *Quaternaria* **13**, 247 (1970).
6. A. K., Behrensmeyer, D. Western, D. E. D. Boaz, *Paleobiology* **5**, 12 (1979).
7. J. A. Shotwell, *Trans. Am. Philos. Soc.* **53**, 3 (19 → D. K. Grayson, *Am. Antiq.* **43**, 53 (1978); R. Klein, in *Fossils in the Making*, A. K. Behrensmeyer and A. Hill, Eds. (Univ. of Chicago Press, Chicago, in press).
8. These were determined either by using body parts as to side (left or right) or single body parts characterized with no respect to side.
9. J. Dorst, and P. Dandelot, *A Field Guide to the Larger Mammals of Africa* (Collins, London, 1972).
10. H. B. S. Cooke, in *Earliest Man and Environments in the Lake Rudolf Basin*, Y. Coppens, F. C. Howell, G. L. Isaac, R. E. Leakey, Eds. (Univ. of Chicago Press, Chicago, 1976), pp. 251–263; J. M. Harris, in *ibid.*, pp. 264–267.
11. There are also two to three hippopotamid species present, possibly serving to raise the hippopotamid-bovid ratio [S. C. Savage, in *Earliest Man and Environments in the Lake Rudolf Basin*, Y. Coppens, F. C. Howell, G. L. Isaac, R. E. Leakey, Eds. (Univ. of Chicago Press, Chicago, 1976), pp. 238–250].
12. F. Bourlière, in *African Ecology and Human Evolution*, F. C. Howell and F. Bourlière, Eds. (Aldine, Chicago, 1963), pp. 43–54.

13. G. B. Schaller, *The Serengeti Lion* (Univ. of Chicago Press, Chicago, 1972).
14. H. Kruuk, *The Spotted Hyena*. (Univ. of Chicago Press, Chicago, 1972).
15. N. T. Boaz, thesis, University of California, Berkeley (1977).
16. R. J. Thompkins, *Kroeber Anthropol. Soc. Pap. (Univ. Calif. Berkeley)* **50**, 85 (1977).
17. F. C. Howell, and G. Petter, in *Earliest Man and Environments in the Lake Rudolf Basin*, Y. Coppens, F. C. Howell, G. L. Isaac, R. E. Leakey, Eds. (Univ. of Chicago Press, Chicago, 1976), pp. 314-331.
18. M. G. Leakey, in *ibid.*, pp. 302-313.
19. A. K. Behrensmeyer, *Yearb. Phys. Anthropol.* **19**, 36 (1976).
20. Support for the Omo Research Expedition was provided by the National Science Foundation, the Leakey Foundation, the National Geographic Society, and the Wenner Gren Foundation. The excavations were performed by N. T. Boaz, G. G. Eck, D. C. Johanson, J. Kaumbulu, M. Splingaer, H. B. Wesselman, and other members of the Omo Research Expedition (F. C. Howell, director). I thank especially D. Boaz and E. Meikle for assistance.

8 January 1979; revised 30 April 1979

Antennal Hair Erection in Male Mosquitoes: A New Mechanical Effector in Insects

Abstract. *Male* Anopheles *mosquitoes erect their antennal hairs prior to mating. The erectile mechanism resides in a unique annulus at the base of each hair whorl. It appears that the insect regulates the degree of hydration of this annulus. When the annulus is made to swell the attached hairs are pushed to their erect position.*

Male mosquitoes are sexually attracted to the flight sound of the female. The long fibrillae (hairs) on a male's antennae are set in resonant vibration by the female's hum. This vibration, transmitted via the shaft of the antenna, stimulates receptor neurones (scolopidia) in the bulbous antennal base (*1*). Sound can only be perceived when the antennal hairs stand nearly perpendicular to the antennal shaft. In many species of mosquitoes the antennal hairs of the male are recumbent against the antennal shaft during most of the day and night and are erected only for a few hours, usually about dusk. Mating is limited to the period of antennal hair erection since this is the only time that males can perceive the females (*1*-*3*). Erection of each whorl of hairs is under direct neural control (*3*). We report here the structure and properties of the effector mechanism that erects the antennal hairs of *Anopheles stephensi*. This mechanism is of a type heretofore unknown in animals but similar to that used by *Mimosa*, Venus's-flytrap, and certain grasses to fold their leaves (*4*).

Antennal hairs are arranged in 12 evenly spaced whorls along the length of the antenna. Each whorl is attached to the periphery of a doughnut-shaped annulus that is, in turn, suspended from the antennal shaft by a stiff chitinous flange (Fig. 1). The annulus stains intensely blue with methylene blue at pH 7. In addition, it stains a very pale blue with Mallory's trichrome. These staining reactions differ radically from those of chitin and from those of the antennal cuticle; they indicate that the annulus is rich in basophilic protein (*5*).

A deep slit runs along the distal face of the annulus. In antennae with recumbent hairs this slit is tightly closed (Fig. 1A), whereas in antennae with erect hairs the slit is widely agape (Fig. 1B). Measurements on sections of 35 antennae with hairs erected to various degrees revealed a direct proportionality between the angle of gape of the annulus and the angle between the hair and the antennal shaft.

Three types of cells are present in the space immediately below each hair whorl. A tormogen cell and the cell body of a sensory neuron occur at the base of each hair (*6*) (Fig. 1D). In addition, large irregular cells are attached to the entire inner surface of the annulus. The appear-

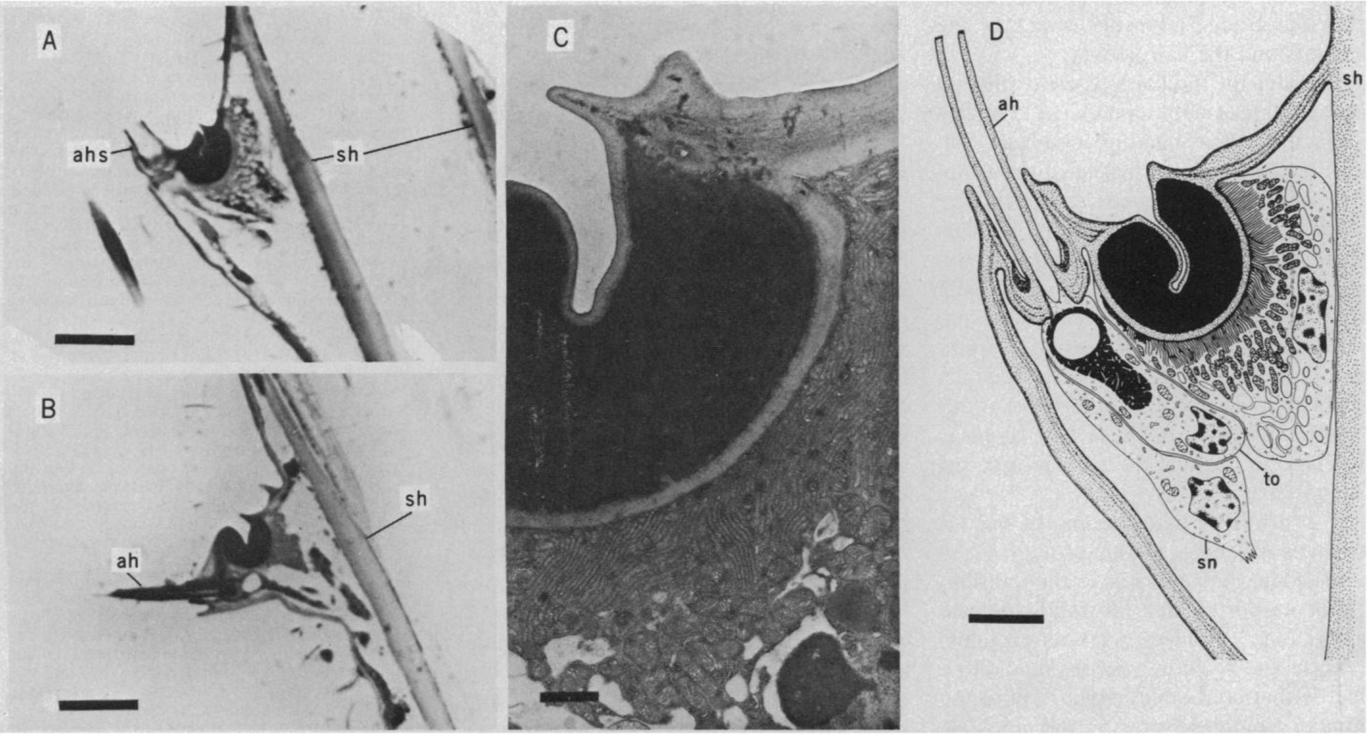

Fig. 1. (A) Thin section through one hair whorl of an antenna with recumbent hairs. (B) Section through antenna with erect hairs. Note that slit in dark-staining object (annulus) at base of hair is now open. Scale bar, 10 μm. (C). Electron micrograph of a portion of annulus and its subtending cell. Scale bar, 1 μm. (D) Diagrammatic reconstruction, based on electron micrographs, of the erectile mechanism of an antennal hair. Scale bar, approximately 5 μm. Abbreviations: *ah*, antennal hair; *ahs*, hair socket; *sh* skeleton of antennal shaft; *sn*, cell body of sensory neuron of hair; and *to*, tormogen cell of hair.