

- ford Univ. Press, Stanford, Calif., 1965), chap. 17; D. R. Thomas and E. Barker, *Psychonomic Sci.* **1**, 119 (1964).
9. H. M. Hanson, *J. Exp. Psychol.* **58**, 321 (1959); W. K. Honig, D. R. Thomas, N. Guttman, *ibid.*, p. 145; D. R. Thomas, *ibid.* **64**, 24 (1962).
 10. As commonly employed, the term "proprioception" refers to kinesthetic stimulation emanating from the muscles and joints and sensations from the vestibular system [see F. Geldard, *The Human Senses* (Wiley, New York, 1953), p. 233]. Observations of the pigeons standing on the tilted floor indicated that their heads were maintained in an upright position, suggesting that the kinesthetic receptors are the major mediating system operative in this experimental situation.
 11. Supported in part by NIH research grant RO 1-HD-00903-05, under the direction of D.R.T. Norma Haggberg, John Erdner, Richard Davis, and David Centa aided in the collection of the data. A paper based on this study was read by D.R.T. at the May 1966 meetings of the Midwestern Psychological Association in Chicago, Ill.

12 May 1966

Taxonomic Status of Tree Shrews

The report by A. S. Hafeigh and C. A. Williams, Jr. (1) again raises the question of the taxonomic status of the tree shrews. A comment on their findings and on those of other recent studies seems appropriate. Van Valen (2) has reexamined the evidence, with the exception of the neuroanatomical evidence, which has been thought to indicate a primate status for the Tupaiidae and has added some from his own studies. He concluded that "... a special tupaiid-primate relationship is possible but unlikely and that the similarities between Recent tupaiids and primates are probably convergences and primitive retentions." McKenna (3), after examining much of the anatomical evidence, concluded that the tupaiids should be regarded as lepidote-like insectivores, and that among living nonprimates the tupaiids are the closest primate relatives.

I have reexamined the neuroanatomical evidence (4). With the exception of relative brain size, all of the characteristics cited by Le Gros Clark (5) may be directly related to the fact that tupaiids, other than *Ptilocercus*, have an elaborate visual system. Tree shrews, other than the nocturnal *Ptilocercus*, are diurnal animals adapted to an arboreal or scansorial way of life. Many of the characteristics listed by Le Gros Clark as indicative of primate affinity, such as presence of a calcarine sulcus, advanced development of certain elements of the thalamus, and downward displacement of the rhinal sulcus, are

found in an arboreal, nocturnal marsupial, *Trichosurus vulpecula* (6). A great deal of emphasis has been placed on the presence in the tree shrew of a laminated, dorsal lateral geniculate nucleus. Laminated, dorsal lateral geniculate nuclei are found in all primates. They are also found in some nonprimates, including *Trichosurus vulpecula*. Three separate studies (7) reveal that in *Tupaia glis* uncrossed fibers from the retina terminate in the innermost and outermost laminae of the ipsilateral nucleus (laminae 1 and 5), while crossed fibers terminate chiefly in laminae 2 and 4 (with a somewhat less pronounced projection to laminae 3) in the contralateral dorsal lateral geniculate nucleus. This is the direct opposite of the situation found in every primate which has been examined (5). This strongly suggests to me that the elaborate visual system on which many of the arguments for a primate status for the tree shrews have been based is a result of convergent evolution.

The fact that *Tupaia* has serum albumin more like that of primates than that of insectivores such as the hedgehog, as reported by Hafeigh and Williams, is not a new finding. Goodman (8) has already reported this finding and has given the same possible explanation for it as that suggested by Hafeigh and Williams. However, he also reported that with antisera to hedgehog and tree shrew sera, hedgehog and tree shrew sera showed more correspondence to each other than to any of the other nonprimates and primates tested. When the cross reactions of the lower primates and nonprimates with antisera to human serum proteins other than albumin (gamma globulin and alpha₂ macroglobulin) were tested, the lemur and galago developed larger cross reactions than did the tree shrew and nonprimate mammals. The major genera of primates, including anthropoids and prosimians, but excepting the tree shrew, *Tupaia glis*, accept passive sensitization by human atopic reagins whereas none of the nonprimates do (9).

Much has been made of the fact that tree shrews supposedly possess a hemochorial placenta similar to the anthropoid primates (10). Hill (11) has shown that several species of *Tupaia* have an endotheliochorial placenta unlike that of any primate.

The relationships of various primates

and nonprimates to man have been examined in a study of the homologies of their polynucleotide sequences (12). In this study, the competition of unlabeled DNA fragments from various primate and nonprimate sources was examined. Human DNA labeled with C¹⁴ and unlabeled human DNA embedded in agar was the indicating system. It was determined that anthropoid ape DNA fragments competed 94 to 100 percent with the labeled human DNA; New and Old World monkey fragments, 83 to 88 percent; and prosimian fragments, 47 to 65 percent. The competition of DNA from tree shrews was only 28 percent as compared to that from the African hedgehog which was 19 percent and that from the mouse which was 21 percent. This data essentially agrees with the generally accepted views on primate relationships.

I have attempted to indicate the large number of recent studies whose results indicate that a close relationship between tupaiids and primates is unlikely. The finding mentioned by Hafeigh and Williams and previously discovered by Goodman is inconsistent with the bulk of recent evidence. There is no doubt that the inclusion of the tree shrew as the most primitive primate in the morphological sequence: tree shrew - lemur - tarsier - ape - man is an attractive picture. Its innate attractiveness may have been in large measure responsible for its acceptance.

C. B. G. CAMPBELL

Department of Neurophysiology,
Walter Reed Army Institute of
Research, Washington, D.C. 20012

References and Notes

1. A. S. Hafeigh and C. A. Williams, Jr., *Science* **151**, 1530 (1966).
2. L. Van Valen, *Evolution* **19**, 137 (1965).
3. M. McKenna, *Folia Primatologica* **4**, 1 (1966).
4. C. B. G. Campbell, *Evolution*, in press.
5. W. E. Le Gros Clark, *The Antecedents of Man* (Edinburgh Univ. Press, Edinburgh, 1959).
6. F. Goldby, *J. Anat.* **75**, 197 (1941); A. D. Packer, *ibid.* **75**, 309 (1941); personal observations.
7. J. Tigges, *Folia Primatologica* **4**, 103 (1966); C. B. G. Campbell, J. A. Jane, D. Yashon, *Anat. Rec.* **154**, 348 (1966); M. Glickstein, W. Calvin, R. W. Doty, *ibid.* **154**, 348 (1966).
8. M. Goodman, in *Classification and Human Evolution*, W. L. Washburn, Ed. (Aldine, Chicago, 1963).
9. L. Layton, *J. Allergy* **36**, 523 (1965).
10. W. Meister and D. D. Davis, *Fieldiana: Zool.* **35**, 73 (1956).
11. J. P. Hill, *J. Zool.* **146**, 278 (1965).
12. B. H. Hoyer, E. T. Bolton, M. Goodman, in preparation.
13. B. H. Hoyer, B. J. McCarthy, E. T. Bolton, *Science* **144**, 959 (1964).

6 May 1966