

capacity has been used. Cranial capacity has been (and still is being) used as a "parameter," rather than just a statistic, to explain human behavior in comparison to any other primate behavior. But the well-known cases of microcephalics capable of language, however impoverished, show fairly clearly that human behavior is not going to be related only to brain weight, the number of cortical neurons ("extra" or "vital"), glial/neural ratios, or dendritic branching, but to some aspects of organization of components or neural subsystems. Jerison may want to dismiss these unfortunately complex matters as mere species-specific epiphenomena, but to anthropologists, at least, they are the critical matters. Brain size is obviously an important statistic, but we will never understand human brain and behavioral evolution if we ignore species-specific organization. Indeed, how meaningful is it to say that between gorilla and chimpanzee males there is a matter of 0.24×10^9 "extra" neurons when between STS 60 and STS 5, two gracile australopithecines from Sterkfontein, South Africa, there is a difference of 0.39×10^9 "extra" neurons? Or a difference of 0.62×10^9 "extras" between male and female *Homo sapiens* (pp. 390-393)?

Here, then, is yet another problem. If there is a brain-body weight relationship between different classes, orders, or species of animals at about 0.66 exponent, and this relates to effectiveness of information processing, and there is another regular relation of these "statistics" between species (with an exponent of about 0.2 to 0.3), how is it possible to claim that there is no regular relationship *within* the species? In fact, there are relationships between brain and body weights within species. Pakkenberg and Voigt (10) showed this for *Homo* in a study of Danes, finding the relationship stronger between brain weight and body height than between brain weight and body weight. A partial correlational study in progress in my laboratory shows a much stronger relationship between brain and body weights when height, age, and brain/body weight ratios are controlled. If there is no regular relationship obtaining within the species between brain and body weights, and between brain weight and information-handling capacity, what are the driving forces or evolutionary dynamics that produce the lawful relationships between species or between

higher taxa? Somewhere, there is a hiatus in explanations which claim a set of biological (functional) relationships at supraspecies taxon levels but deny such a relationship within the biological unit (the species) undergoing evolutionary change.

To return to the quotation at the beginning of this review, the fourth step, that of saying that what can't be easily measured doesn't exist, may have been taken. For example, one of the main arguments on which Jerison bases his dislike for the concept of reorganization, and his preference for the use of "biological intelligence" as a concept that can be related to brain size, is that "encephalization of function" is probably a fiction, and therefore should be dismissed from evolutionary arguments (pp. 11-12). Yet on p. 25 he uses both sensory integration and the flexibility and adjustability of behavioral response to this sensory information to talk about cortical function in cats and monkeys with respect to vision and hearing. Perhaps there is a semantic snarl here, but encephalization, or corticalization, of function cannot be so easily dismissed. The clinical and experimental work of the past 75 or more years suggests very securely that cortical lesions have more permanent and serious effects the higher the animal on the phylogenetic scale.

In this review I have tried to focus on a number of underlying assumptions and difficulties in the possible generation of fictional numbers. As we all know, much more quantitative neurohistological research needs to be done, particularly on primates. Lest the reader regard this review as only critical, I would like to emphasize that this book is a useful bringing together of sources and data and presents much substantial work and many provocative hypotheses which deserve the closest attention. Many of the middle chapters on birds, reptiles, amphibians, and primitive and advanced mammals should be of interest to both paleontologists and neuroanatomists. I believe Jerison has taken an advanced step in analyzing what is easy to measure, but I am afraid that as far as human evolution is concerned, he has also taken the wrong subsequent steps. We need much more information to get us out of the realm of fictional numbers we may be left in.

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Biomechanical Adaptations

Primate Locomotion. FARISH A. JENKINS, JR., Ed. Academic Press, New York, 1974. xii, 390 pp., illus. \$34.

Locomotion figures prominently in most accounts of primate phylogeny and is integrally related to the complex social behavior and high levels of intelligence that characterize the order. Yet its analysis has been largely restricted to general observations and broad categorizations. A lack of sufficiently detailed behavioral and kinematic data has made the validity of various proposed phyletic models difficult to judge. This volume is a significant contribution toward the partial elimination of this deficiency in primate studies.

The majority of the 11 contributions are directed at the locomotion of subfossil and extant prosimians or paleogene primates. The general emphasis is thus on the role of locomotion in primate origins and early Cenozoic evolution. Sophisticated techniques (for example, cineradiography, electromyography, three-dimensional photoelastic analysis) are employed by several of the contributors. The basic approaches are largely kinematic or morphological or both. No kinetic data are presented.

The most significant dissent from prevailing general theory is to be found in the contribution by Cartmill. Here the "time-honored" generalization that primate chirodial modifications are attributable entirely to the arboreal substrate is carefully dissected and found to be an insufficient explanation of prosimian adaptation. A review of non-primate arboreal adaptive strategies including those of marsupials and sciuroid rodents forms the basis of Cartmill's argument. Noting that a clawed manus allows an animal to subvert a

large angle between its forelimbs (because friction is not critical to support), he concludes that clawed chiroidia are superior to the friction pads and digital opposability of primates for locomotion on vertical supports and large branches (for example, while the squirrel can successfully traverse a vertical surface, the loris becomes incompetent on smooth-barked trees of diameter greater than 10 centimeters). Additional comparisons document the nonsuperiority of primate chiroidia for running along horizontal supports, hanging beneath slender branches, or leaping across canopy gaps (p. 63).

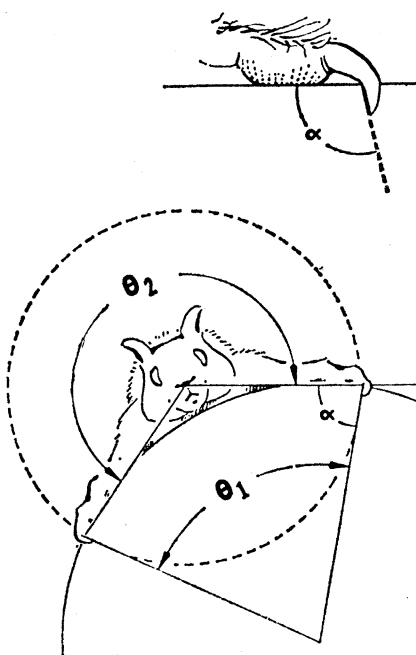
We are therefore entitled to reject that model of primate evolution that envisions the strepsirhine prosimians as having evolved out of treeshrew-like clawed mammals under the selective pressures imposed by arboreal life *per se*.

Cartmill turns to prosimian predatory activity for a more adequate explanation. Many small primates track prey visually and then seize it with their hands. In addition, because of its grasping hind feet a primate such as the loris can move quietly among terminal branches, successfully stalking insects and other small game. The basic locomotor pattern and prehensile chiroidia of prosimian primates may thus be as intimately associated with feeding as with substrate in the strict sense.

Using both cineradiography and a variety of more traditional techniques, Jenkins presents a careful kinematic analysis of tree shrew gait. Applying these data to possible adaptive pathways in the origin of primates, he turns to the often ignored question of substrate variability, emphasizing the transitional nature of the tupaiid niche, which exhibits a blend of both terrestrial and arboreal characters. He concludes (p. 112) that

The adaptive innovation of ancestral primates was . . . not the invasion of the arboreal habitat, but their successful restriction to it.

This observation is particularly noteworthy when combined with Cartmill's that forest floor insects are preyed upon by animals which rely not on vision but olfaction, hearing, and vibrissal contact. Clearly, such modes of prey location would be ineffective in the canopy, and an attractive model of early primate specialization emerges in which visual-chirodial stalking and capture gradually gain dominance and result in the elimination of the terrestrial portion of the original adaptive zone.



Clawed mammal on cylindrical support. θ_1 : central angle subtended by animal on real support. θ_2 : angle subtended on effective support, whose surface is tangent to volar aspect of claws. α : angle of claw penetration. As long as α is 90° or less, the animal is secure, as adduction force is exerted against the claw and the penetrated surface. Without clawed chiroidia, adduction force requires frictional resistance for adhesion to the supporting structure, and only supports of small diameter can be grasped successfully. Clawed mammals effectively adjust support diameter at their convenience. An animal relying solely on friction pads, in order to increase angle θ_1 , can increase body size, but this results in a higher proportional energy cost in vertical locomotion. [From M. Cartmill, in *Primate Locomotion*]

The most striking pedal specializations observed by Jenkins were marked mobility (including pronation-supination and abduction) and a comparatively independent hallux. While the latter is not strictly comparable to its analog in other prosimians (most of the abduction occurred at the metatarso-phalangeal joint), the importance of both these characters is amplified by a detailed analysis of the tarsus of three Paleocene eutherians by Szalay and Decker. Using both estimates of joint motion and reconstructed axes of rotation they document the presence of specialized adaptation for marked inversion in early primates and a clear trend toward increased rotary motion in the calcaneo-cuboid joint. In a second contribution their techniques are extended to Eocene and Malagasy prosimians.

Walker presents a brief review of

prosimian locomotor types along with a synopsis of possibly diagnostic osteological characters. He reiterates the point of view that most if not all Eocene primates utilized vertical clinging and leaping and that it may thus be primitive to the order. In primatology, as in other disciplines, nothing appears to generate new data as rapidly as a major controversy, and the question of vertical clinging and leaping is likely to prove a classic example. Cartmill, Szalay and Decker, and Jouffroy and Gasc (who contribute a cineradiographic description of galago leaping) all suggest substantive contradictions to the vertical-clinging-and-leaping hypothesis.

Perhaps the longest-standing controversy in primatology is the role of suspensory locomotion in hominid phylogeny, a subject which plays a dominant role in the papers by Lewis and Tuttle and Basmajian. Lewis clearly identifies several distinctive characters in the hominoid wrist joint, including articular exclusion of the ulna, ulnar styloid reduction, and the novel inclusion of a meniscus and intra-articular disk. In Lewis's view these carpal modifications are clearly related to suspensory locomotion, but their probable function (increased range of pronation-supination and ulnar deviation) implies that the primary selection involved may well be an enhancement of carpal mobility. His conclusion that the wrist of *Dryopithecus africanus* displayed the hominoid pattern is of some interest since a number of characters in this form are indicative of quadrupedal progression (H. Preuschoft, in *Human Evolution*, M. H. Day, Ed., Barnes and Noble, 1973). Thus *D. africanus* may prove to be the strongest evidence yet available for those who prefer that hominoid carpal modifications be viewed independently of suspensory locomotion.

Tuttle and Basmajian report preliminary results of electromyographic studies of the forearm of a young gorilla. The variety of technical and anatomical difficulties encountered in this pioneering effort are impressive, as are the stepwise solutions developed in the course of the work. Much of this contribution is devoted to an extensive summarization of present opinion concerning the morphological correlates of knuckle-walking. This includes an outline of proposed hominoid locomotor pathways and a thorough synopsis of the present status of each. A now extensive body of data, gathered principally by Tuttle, is reviewed and the sub-

stantive adaptation of the African pongid wrist to knuckle-walking clearly documented.

A useful review of statics in the interpretation of skeletal morphology (Badoux), the results of an extensive comparative analysis of primate scapular morphology (Roberts), and a survey of positional behavior in New and Old World monkeys (Rose) are also included. While the ranges of research and discussion presented in this volume are as broad as its title, much of the material is naturally integrated, giving the book a fairly unified quality. A majority of the contributions contain both valuable data and significant insight, and the book will thus prove vital to anyone interested in primate locomotion.

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Models of Development

Experimental Embryology of Echinoderms. SVEN HÖRSTADIUS. Clarendon (Oxford University Press), New York, 1973. x, 192 pp., illus. \$16.

Developmental Biology of the Sea Urchin Embryo. GIOVANNI GIUDICE. Academic Press, New York, 1973. x, 470 pp., illus. \$32.

Sea Urchin Development. Cellular and Molecular Aspects. LOUIS W. STEARNS. Dowden, Hutchinson and Ross, Stroudsburg, Pa., 1974. xii, 340 pp., illus. \$20.

Studies on sea urchin embryos have provided important cornerstones of developmental biology, and today increasing numbers of researchers are using these organisms as model systems for studying fertilization, cleavage, determination, and morphogenesis. Early experiments probed the organization of the egg and embryo by removal of parts and assessment of the embryos' plasticity—or lack of it—in later development.

These approaches have been especially developed by Sven Hörstadius, and his monograph is a significant, personal, and provocative view of the causal analysis of development—significant because it provides in one place a complete summary of current views of the organization and progressive determination of the echinoderm egg and embryo, personal because much of this

analysis is derived from Hörstadius's own research, which spans almost 50 years and successfully links classical embryology and modern developmental biology, and provocative because a major future challenge is to explain in molecular terms the remarkable organization of the egg as well as the plasticity of the echinoderm embryo.

Hörstadius's monograph briefly recounts the history of experimental embryology. This history is followed by a description of echinoid development and methods for working with these embryos. This chapter will be especially useful to embryologists for its account of methods for removing and transplanting blastomeres. There then follow chapters on the determination of cleavage patterns and on the organization of the egg and embryonic axes. The text is not restricted to sea urchins among the echinoderms, and one chapter covers experiments with the other four echinoderm classes. Finally, experiments on germ layer chimeras and interspecific hybrids are described, and the book ends with a stimulating discussion of determination.

Where Hörstadius's book is primarily a personal review of his own research, Giudice's monograph sets out to review the massive literature of the subject, concentrating on physiological and molecular aspects.

Giudice's book is not solely a compendium of research results. The diverse literature generally is integrated into an interesting and well-written discussion. The first section (175 pages) covers experimental embryology, oogenesis, fertilization, cleavage, and experimental cell dissociation and reaggregation (in which Giudice has been especially active). The second section (225 pages) covers the metabolism of the developing embryo, including one chapter on energy metabolism, three chapters on nucleic acid and protein synthesis, and finally a brief chapter on increases in enzymatic activity during development. The bibliography is extensive, containing almost 1700 references, and includes an addendum covering publications through 1972. A defect, for which the publishers are presumably at fault, is in the indexing. The subject index is sparse (only 4½ pages) and poorly cross-referenced, and there is no author index.

Considering the breadth of his subject, Giudice has done an impressive job of integrating difficult literature. The only substantive shortcoming is in the second section, where he has per-

haps been too equitable and comprehensive in describing good, bad, and redundant research pertaining to nucleic acid and protein synthesis. Overall, however, he has attempted to synthesize conflicting results and point out new and unresolved problems. He has also included many unpublished observations from his own laboratory.

The contribution by Stearns covers the same ground as Giudice's monograph. It is the more readable of the two, but falls short in breadth and comprehensiveness. Its strength lies in the raising of questions and problems. Some of Stearns's points are excellent, as on the mechanism of the acrosome reaction in fertilization. In other areas, as in the chapter on protein synthesis, much verbiage is wasted on inconsequential points.

A question that is not covered in any of these books is whether sea urchins will continue to be available for embryological research. Embryologists have always competed with gastronomes for the roe of the sea urchin, but in the past this competition was on a small scale. Now commercial marketing and increased demands in Japan and Europe have resulted in the development of a large sea urchin fishery in Japan and recently in the United States. In California, the commercial harvest went from 200 pounds in 1971 to almost 2 million pounds in 1973. Japanese embryologists are already experiencing difficulty in obtaining sea urchins for research. If the U.S. fishery continues to grow, American embryologists will soon experience similar difficulties. To preclude this, the fishery should be scientifically managed, and sea urchin preserves should be established near major university and research centers. Otherwise, these magnificent models of embryonic development will be lost.

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Vertebrate System

The Third Eye. RICHARD M. EAKIN. University of California Press, Berkeley, 1974. xii, 158 pp., illus. \$7.50.

Eakin has a national reputation as an excellent electron microscopist and an innovative teacher; this book shows both of these attributes. A short, well-produced and well-illustrated monograph, it summarizes some two decades