
The 61st Wenner-Gren Symposium at Burg Wartenstein was an important event for both primatologists and mammalogists as a whole, so that the publication of the contributions in their final form has been eagerly awaited.

The book begins with a remarkable ‘pre-conference’ paper by Simpson; very concisely, objectively, and without passion, the author expresses his views on taxonomic schools, methods of phylogenetic inference, and the relationships between classification and phylogeny.

An illustration of these problems and their difficulties is given in McKenna’s contribution entitled ‘Toward a Phylogenetic Classification of the Mammalia’. This ambitious topic largely exceeds the scope of the Burg Wartenstein reunion, and could have provided subject matter for one or several symposia. Although other criteria are mentioned, the cladistic analysis essentially bears on dental characters, for which original interpretations are given. The phyletic tree of the mammals put forward by McKenna goes much farther than what has been attempted until now; it will have to be backed up, discussed, and necessarily reworked, but it is a starting point for further work, the usefulness of which cannot be denied. However, the creation of numerous higher taxa and also of new taxonomic categories seems premature and dangerous. Was it really necessary, for instance, to erect a superlegion (Kuehneotheria) for Kuehneotherium alone? Is it legitimate to consider this genus as the sister group of the whole of the other Theria (Trechnotheria), while none of the latter is known to have lived at the same time as Kuehneotherium, which could well occupy a directly ancestral position? Many choices (for example the position of the Delta-theridia) are still in large part arbitrary. Even for the Ungulata, which the author declares he could not classify dichotomically, and for which few new terms have been introduced, the proposed rearrangement is questionable and unpractical (where, for instance, should be placed the Didolodontidae, which would no longer be condylarths, but which belong to none of the orders included in the ‘mirorder’ Meridiungulata?).

The 15 other contributions are more directly concerned with the phylogeny of the Primates, which is investigated with the help of various criteria: morphology and development of the skeletal and dental system in recent and fossil forms (Szalay, Starck, Cartmill, Tattersall and Schwartz, Delson and Andrews), soft anatomy (Luckett, Campbell, Novack), biochemistry (Goodman, Kohn), physiology, ethnology and ecology (Eisenberg, Charles-Dominique, Martin, Tuttle), geographical dispersion (Szalay). The amount of new evidence is considerable; light is thrown on many problems, some of which are solved, while others are posed. It is to be regretted that no synthesis of the symposium has been attempted as a conclusion.

Szalay brings forth new evidence, founded on basicranial anatomy, for rooting the Primates in the early erinaceomorphs. Two authors (McKenna and Goodman) revive the taxon Archonta, erected by Gregory in 1910, which include Primates, Scandentia, Dermoptera, and Chiroptera.
It is satisfying to notice that the term ‘Prosimii’ seems to have finally been abandoned, at least as a taxon. The Plesiadapiformes = Paromomyiformes are recognized as an early radiation, which sets them apart from the remainder of the Primates. Some problems remain, concerning the inclusion within this group of the Microsyopidae (advocated by Bown and Gingerich) and of the African genus Azibius (proposed by Sudre): Szalay disagrees on both points.

On the basis of various criteria, all the contributors admit the division of the rest of the Primates into Strepsirhini and Haplorhini (Gingerich’s very divergent opinion has not found any defenders here).

Many problems posed by the Strepsirhini are clarified, through anatomical, biochemical, and even ethological observations (Cartmill’s anatomical work is especially remarkable). The so-called ‘anterior carotid’, in particular, can no longer be considered as a neoformation (observations due to Cartmill, whose conclusions are accepted by Szalay), and therefore the inclusion of the Cheirogaleidae in the Lorisoida can hardly be advocated any more; it is, however, maintained by Szalay and by Tattersall and Schwartz, but rejected by Goodman (immunodiffusion). In my opinion, from the bulk of present evidence, the most likely phylogenetic diagram seems to be that in Cartmill’s figure 13B (p. 344), which also simplifies paleobiogeographical problems. Therefore, I abandon the phylogenetic hypotheses I had contemplated for the Strepsirhini (J.hum.Evol. J: 332-337, 1974) as a logical consequence of the interpretation proposed by Szalay and Katz in 1973 for the so-called lorisoid carotidian circulation.

It should be noted, however, that Tattersall and Schwartz maintain a very divergent position, which they have already defended elsewhere [Anthrop. Pap. Am. Mus. nat. Hist. 52: 139-192, 1974]: they set the Indriiformes’ (Indriidae + Daubentoniidae) apart from the rest of the Strepsirhini; their interesting observations on craniomental anatomy must, of course, be taken into consideration, but some of their interpretations are questionable (for example, the assimilation of the first upper tooth of Daubentonia to a canine does not fit the fact that this tooth is emerging from the premaxilla, in front of a locus occupied by a deciduous incisor, which is followed by a deciduous canine inserted in the maxilla; [see Peters Abh.K.Akad.Wiss.Berl, f. 1865, publ. 1866, p. 2, fig. 8]), and, above all, the phylogenetic insertion of the aye-aye between recent and fossil Indriidae (fig. 5, p. 309) is not convincingly demonstrated; it is even contradicted by Goodman’s immunological studies. However, Szalay seems to agree on this point with Tattersall and Schwartz (see his figure 19, p. 123, in which one will notice, incidentally, a probably material mistake concerning the vertical extension of the Adapidae).

As a matter of fact, the Strepsirhini illustrate in a striking way the need for paleonto-logical evidence, and the drawbacks created by its absence, in such problems; the discovery of some fossils in the Tertiary of Madagascar and in the Paleocene-Eocene of Africa would, no doubt, enable us to eliminate some hypotheses and guide the choice among others.

Today there is less cause for discussion about the Haplorhini. Their monophyly is largely sustained by several observations, among which those by Luckett (placentation and fetal membranes) and by Goodman (immunodiffusion) stand out.

Szalay offers us an important contribution on the Tarsiiformes, including a praiseworthy essay on phylogenetic relationships between the known genera.

Concerning the Anthropoidea (which I prefer to call the Simiiformes), their monophyly also seems to meet with a wide consensus. Divergences remain concerning their affinities with the Tarsiiformes, of which they may represent either the sister group, or a lateral
offshoot; only the discovery of ante-Oligocene Simiformes, which, in my opinion, could be expected in Africa, will settle the question.

Anyway, an increasingly large number of authors admit that Platyrrhini and Catarrhini constitute a natural whole, instead of two groups having separate roots in Laurasian ‘Prosimii’. This implies that the ancient Atlantic was crossed by the founders of one or the other of these groups of monkeys. Szalay admits this, but prefers a W-E crossing, that is, a derivation of the Catarrhini from South American ancestors (this seems hardly defensible, taking into account the diversity already existing among the Oligocene monkeys from the Fayûm, and also what is known about paleocurrents; see, for instance, Berggren and Hollister, p. 171, fig. 17; in Hay (ed.) Studies in paleogeography, Soc. Econ. Paleont. Miner., Spec. Publ. No. 20, 1974).

The phylogeny of the Catarrhini is widely discussed by Delson and Andrews. A paper by Tuttle is devoted to the Hominoidea, and more precisely to the problems of brachiation and parallelism. This brief account reveals again how interesting a synthesis of this important symposium would have been. Considering the theme that was being discussed, other contributors could have been called upon: I think it would have been good to allow such a scientist as Gingerich (with whose interpretations I do not always agree, but whose observations and independence of thought I appreciate) to defend his original views. One could also have wished for a larger part to be allotted to paleobiogeography (limited here to a short outline by Szalay), with the stress being put on the weight of this type of evidence in phylogenetic reconstructions, and on the important part played in evolution by geographic, as well as genetic and ecological, factors.

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Since Sir Arthur Keith’s studies at the turn of this century, the hylobatid (or lesser) apes have figured prominently in theories on the evolution of hominid orthograde positional behavior. And since C.R. Carpenter’s documentation of monogamous matings in gibbons, anthropologists and other social scientists have joined biological scientists in scrutinizing available information about them. Rumbaugh’s series on Gibbon and Siamang contains new data and useful syntheses for scientists in many disciplines.

The three volumes reviewed here consist of research papers and reviews about the morphology (2: Schultz; Frisch; Biegert; Donisch; 3: Lorenz; 4: Andrews and Groves), natural history (3: Ellefson), behavior of free-ranging captives (3: Brockelman et al.; 4: Carpenter; Baldwin and Teleki), taxonomy (4: Creel and Preuschoft), evolution (2: Darga et al.; Simons and Fleagle; Frisch), psychology (2: Parker; Gossette; 4: Abordo), vocalizations (3: Tembrock; 4: Goustard) and reproduction (2: Arnold) of selected species. Volume 4 contains a general subject index to volumes 1-4. This indicates that additional volumes will not be forthcoming in the near future.
Some chapters are overwritten or otherwise insufficiently edited. In addition to typographical errors, occasional factual mistakes occur. For instance, Andrews and Groves (4:176) incorrectly state that William K. Gregory was the first explicit proponent of the ‘brachiator’ theory of human origins. Sir Arthur Keith clearly has priority to this theory. Also the chief method of chimpanzees for moving in trees probably is not knuckle-walking (Andrews and Groves, 4:179). Although they sometimes knuckle-walk on large horizontal branches, chimpanzees commonly grip branches with the hands and climb versatilely on a variety of supports.

The contribution that should attract the widest readership is Ellefson’s ‘A natural history of white-handed gibbons in the Malayan Peninsula’ which constitutes the bulk of volume 3. It is his doctoral thesis based on a field study of Hylobates lar in 1964 and 1965. The chapter begins with Frederick Engels then passes on to confirm most of C.R. Carpenter’s basic observations on the social organization, maintenance behavior and ranging pattern of H. lar in Thailand. After a 5-month survey of 27 localities in West Malaysia, Ellefson spent 16 months at Tanjong Triang on the eastern coast where a small gibbon population had been isolated for approximately 50 years and where the forest had been selectively logged. The sex ratio was dramatically skewed in favor of males. There were 2 unmated adult males and 4 out of the 5 youngsters were males (3:49).

Ellefson fully habituated 2 groups, partially habituated a third group and the 2 unmated males, and failed to habituate the fourth group at Tanjong Triang. One of the major contributions from Ellefson’s study is further clarification of locomotor and other positional behavior in free-ranging gibbons. He stressed that arm-swinging (or brachiation) is only one component in a complex repertoire of movements that also includes climbing, bipedal running, and leaping (3:68). He did not distinguish between vertical dropping and leaping or indicate the relative frequency of hindlimb versus forelimb propelled ‘leaps’.

Intergroup altercations, characterized by prolonged male calling, display-swinging and chasing, were frequent at Tanjong Triang. Ellefson observed 126 conflicts, only one of which included fighting (3:102). Three groups were involved simultaneously in 22 of the conflicts (3:110). About 20 percent of the conflicts ended prematurely because of Ellefson’s presence (3:51). Whether his presence deterred fighting in some of the other conflicts is unknown. Ellefson explains that one advantage of these male contests is that the females and youngsters can feed in the no-gibbon’s-land during a fracas (3:115). Despite the length of Ellefson’s study, the precise mechanism for new group formation in H. lar remains obscure. Ellefson could do little more than expand upon Carpenter’s speculations about this matter (3:117-120).

Ideally, studies on free-ranging captives might assist to clarify the social dynamics of hylobatid groups and especially the manner of new group formation. But colonies founded with nonferal animals (3: Brockelman et al. p. 139) and former medical experimental subjects (4: Baldwin and Teleki, p.26) hold little promise for definitive results. While some hypotheses might be formulated on the basis of these captives, they must be tested on natural populations. Since many provocative hypotheses already have been derived from the naturalistic studies of Carpenter, Ellefson, Chivers, and other hylobatologists, the most productive strategy might be to concentrate our resources on longitudinal studies at feral localities. Or we should found behavioral research colonies with several natural family groups from the same region. Captives are probably more relevant to problems about functional morphology and maintenance behavior (4: Carpenter; Baldwin and Teleki; 2: Parker; 3: Lorenz) than social dynamics.

Book Reviews
Abordo’s lucid review of research on ‘the learning skills of gibbons’ (4:106-134) reveals that knowledge on the psychology of hylobatid apes has progressed slowly since Yerkes and Yerkes called for more research on them in 1929. While a few experiments on hylobatid cognitive capacities (notable among which are those of Beck and Rumbaugh and Gill) have been conducted with gibbons, none have employed siamangs (4:129).

Although some anthropologists, sociologists, and students of guerezas, howling monkeys and even titi monkeys might disagree with Goustard’s opening remark that ‘The gibbons are by far the noisiest of all Anthropoidea...’ (4:136), all persons interested in primate communication will welcome his and Tembrock’s (3:176-205) efforts to objectively describe by means of sonographic analysis the calls of captive Hylobates concolor, H. lar, H. moloch, and Symphalangus syndactylus. From these studies it appears that the vocalizations of hylobatid apes, like those of many birds and monkeys, might serve as discrete taxonomic characters. However, further field studies are essential before they can be used confidently by taxonomists and before we will know their functions in the social communicative system of each species. There is no complete consensus about hylobatid taxonomy and phylogeny among the several authors in the series who variously examined morphological features or employed biomolecular cladistic perspectives. Schultz (2:51) reiterates his longstanding judgements that (1) the Hylobatidae are a separate family of the Hominoidea and (2) among the Hylobatidae, the separate genus Symphalangus has the closest resemblance to the Pongidae, especially Pongo. Frisch (2:56), Darga et al. (2:159), Biegert (2:183) and Andrews and Groves (4:174) agree that the Hylobatidae belong in the Hominoidea. Chiarelli’s suggestion (based on karyological features) that the Hylobatidae belong in the Cercopithecoidea (1:98) is not supported by dental, dermatoglyphic and other morphological features or by ‘the bulk of the protein and DNA evidence’ (Darga et al., 2:159).

Frisch, Biegert, and Darga et al. seem to support separate generic status for the siamang. While Andrews and Groves (4:174) accept that there are good grounds for its generic status, they continue to refer to the siamang as Hylobates symphalangus. Creel and Preuschoft (4:280) infer from a thoroughgoing, handsomely illustrated multivariate study on the cranial morphology of wildborn lesser apes that Symphalangus is probably only a subgenus of Hylobates.

The evolutionary origins of the Hylobatidae are also obscure and subject to dispute. Simons and Fleagle (2:145), Biegert (2:183), and Andrews and Groves (4:173-174) favor a relatively early furcation of the hylobatid lineage from stem Hominoidea. Frisch (2:84) casts doubt on the idea that Aeolopithecus chirobates is the earliest hylobatid. Because of the variability in fossils designated Limnopithecus and Pliopithecus and their broad contemporaneity, Frisch (2:93) concludes that no fossil species appears to be more closely related to extant lesser apes than the others do. Per contra, Simons and Fleagle (2:141) are somewhat more favorably disposed toward species of Limnopithecus being ancestral both to Pliopithecus and collaterally to extant lesser apes.

We have much to learn about the Hylobatidae. Hopefully, some readers of Gibbon and Siamang will be stimulated to conduct psychological, naturalistic behavioral, paleontological, biomolecular and functional morphological studies which will advance our knowledge of these fascinating creatures a bit further.

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