Z. Morph. Anthrop.	71	2	157—163	Stuttgart, August 1980

Gradistic views and adaptive radiation of platyrrhine primates

By **Alfred L. Rosenberger**, New York

Summary: The classical view of a platyrrhine level of organization, more primitive than a catarrhine grade and representing the ancestral anthropoid morphology and adaptive pattern, is an unnecessary and unwarranted generalization. Gradistic clusters and rankings of living ceboids are contestable on phenetic and adaptive grounds, and conflict with arguments of morphocline polarity. The two major ceboid clades, cebids and atelids, traceable to the late Oligocene, inhabit complimentary adaptive zones involving alternative dietary regimes. Some adaptive specializations of the living genera are quite ancient and are evident in related fossil forms.

Zusammenfassung: Die klassische Sicht, nach der das platyrrhine Organisationsniveau ursprünglicher als eine catarrhine Erscheinungsform sei und Vorläuferformen anthropoider Morphologie und adaptiver Muster repräsentiere, ist eine unnötige und unzulässige Verallgemeinerung. Gradistische Clusterung und Reihung rezenter Ceboiden sind bestreitbar auf der Grundlage morphologisch-phylogenetischer und adaptiver Merkmale und stehen in Widerspruch zu ihren morphoclinen Positionen der Gruppen. Die beiden Zweige der Ceboidea, die Cebiden und die Ateliden, die bis ins späte Oligozän zurückverfolgt werden können, bewohnen gleiche adaptive Räume, wobei sie sich hinsichtlich ihrer Ernährungsweise unterscheiden. Einige adaptive Sonderbildungen rezenter Genera sind stammesgeschichtlich ziemlich alt und lassen sich bereits bei den entsprechenden fossilen Vorformen beobachten.

Because they are poorly represented in the fossil record, and because systematists have largely relied on the fossil record for motivating phylogenetic hypotheses and evolutionary interpretations, the neontologically-based concept of grade or level of organization has strongly influenced evolutionary and taxonomic studies of the platyrrhine primates. This is clearly evident in the widely accepted, highly split classifications of Napier & Napier (1967), Hershkovitz (1977) and others. In another sense, gradistic argument has apparently substituted for phyletic analysis in appraising the relationships and histories of Old and New World monkeys and the category Anthropoidea generally. This has led to the often implied or cited, but never documented, conclusion that anthropoids are not strictly monophyletic (Cachel, 1978) but represent a convergently achieved grade of organization instead. A more influential example of this approach is the Huxleyian alignment of primate morphology into a series of "trends" and primate lineages into a sequence of "grades" (e. g., LeGros Clark, 1963; Napier & Napier, 1967; Hershkovitz, 1977), yielding the picture of an ascending adaptive scale of primate evolution that posits platyrrhines as the primitive link between the catarrhines and "prosimians".

Several such applications of the grade concept, as they pertain to issues of platyrrhine evolution, will be examined in this paper. Additionally, I will present an abstract of an alternative framework for examining the adaptive radiation

0044-314X/80/0071-0157 $ 1.75

of the ceboids. Given the many recent advances in evolutionary biology, both in theory and in method, the philosophical basis of the grade concept clearly warrants a serious reconsideration. While this cannot be attempted here, it is hoped that critical analysis of its use will reveal some of its weaker points and suggest other, perhaps more heuristic, ways of looking at the same data. Unless indicated otherwise, the classification adopted is from SZALAY & DELSON (1979) and ROSENBERGER (1979 a, b) and groups the living Ceboidea as follows – Cebidae: Cebinae *(Cebus, Saimiri)*, Callitrichinae *(Callithrix, Leontopithecus, Saguinus, Callimico)*; Atelidae: Atelinae *(Ateles, Brachyteles, Lagothrix, Alouatta)*, Pitheciinae *(Pithecia, Cacajao, Chiropotes, Callicebus, Aotus)*. A full elaboration of many of the points presented, and more complete documentation, is given elsewhere (ROSENBERGER, 1979 b).

Discussion

The platyrrhine grade

As a taxon, the platyrrhines were usually negatively defined relative to modern cercopithecoids (and hominoids) by 19th century authors, who noted such features as: their complement of three premolars; ring-like ectotympanic bone; inflated auditory bulla; broad internarium and laterally facing nostrils; lack of ischial callosities and cheek pouches; pendulous or prehensile tail. This practice continues today (CLARK, 1963) and has become further emphasized in the interests of paleogeographic theories of platyrrhine origins. The form of this comparison goes hand in hand with the assumptions that New and Old World monkeys, as monkeys, represent successively higher levels of organization and that apes evolved from monkeys. This phyletic conception of the catarrhines is contradicted by cladistic analyses which demonstrate that cercopithecoids are highly derived in dental, postcranial and soft anatomy, and are a comparatively recent lineage which differentiated from a hominoid-like stock (SZALAY & DELSON, 1979). The recovery of good Oligocene catarrhine material (SIMONS, 1972) contests such a gradistic ranking by illustrating that early undoubted catarrhines cannot be distinguished by the traditional suite of craniodental characters and are in fact more similar to some platyrrhines than to eucatarrhines in certain postcranial features (CONROY, 1976). An even more basic objection is that the analysis is based on a minimal number of subjectively chosen morphological criteria and taxa. Given the expansive range of morphologies evident among platyrrhines (and catarrhines!), I doubt that one can easily define a platyrrhine adaptive grade that would not approach a meaningless generalization. At best we might attempt a reconstruction of some ancestral platyrrhine characteristics and, by functional analysis and analogy, postulate what some of their biological roles and adaptive significances might have been. But this has yet to be done.

Some (e. g., CONROY, 1978) regard the similarities of Fayum catarrhines and ceboids as an affirmation of a platyrrhine level of organization and as evidence that that grade was primitive for Anthropoidea. But such abstractions are always possible when comparing isolated attributes of closely related taxa. There is no reason to suspect that early catarrhines or protoanthropoids should especially resemble living platyrrhines in form or adaptation. New, anatomically unique, parapithecid pelves offer a cautionary caveat in this regard (FLEAGLE & SIMONS, 1979). The fossil record is revealing what comparative anatomy has always suggested: that we are dealing with transformation series of characters which are ultimately expressed as mosaics of primitive, derived and autapomorphous states in an assortment of taxa. In at least some respects protoanthropoids are likely to recall catarrhines more than platyrrhines. This appears to be the case in the occlusal anatomy of upper molars, for example. Fayum catarrhines retain paraconules and metaconules, widespread among Paleogene primates and certainly an ancestral condition of Anthropoidea, but these are essentially absent in all ceboids.

Given that platyrrhines will inevitably retain the primitive conditions of characters which became modified in catarrhines, and vice versa, it remains to be shown that any of those features portray qualitative differences in goodness of adaptation. That they do is another fundamental premise of the gradistic view at least in its early formulations ("...from the crown and summit of the animal creation down to creatures, from which there is but a step, as it seems, to the lowest, smallest, and least intelligent of the placental Mammalia"; HUXLEY 1863). Most of the morphological differences between these infraorders probably represent chance paradaptive differences (BOCK, 1969) rather than actual adaptive improvements. This contrasts with other cases in primate history where anagenetic advances are referable to certain features that distinguish higher taxa, such a the enhanced frugivorous capabilities of anthropoids versus tarsiiforms or the improved arboreal locomotor aptitude of euprimates versus plesiadapoids.

Grades of platyrrhines

The classical family divisions of Ceboidea, separating the clawed "callitrichids" from the nailed "cebids", reflects a classical segregation of supposed grades rather than a documentable cladistic distinction (ROSENBERGER, 1979 b). HERSHKOVITZ (1977) has elaborated this system by introducing a third intermediate "marmoset-like cebid" grade, composed of *Saimiri*, *Aotus* and *Callicebus*, and provided some four independent gradistic rankings for comparing each of the six marmoset (and tamarin) genera that he maintains (p. 406; Fig. VII.3). HERSHKOVITZ also recognized grade distinctions between the saki-uakari group and the "larger and prehensile-tailed cebids", *Cebus*, *Alouatta*, *Lagothrix*, *Ateles* and *Brachyteles*

Of these groupings, I fully endorse the associations of callitrichines, saki uakaris and atelines. These all appear to share specific, unique clusters of morphological and behavioral attributes which tie them genealogically and indicate a common, though internally diverse, ecological adaptation. HERSHKOVITZ' (1977 other assignments are far too heterogeneous. While *Cebus* is the largest nonatelin ceboid, it still weighs only half as much as an average ateline (BAUCHOT &

STEPHAN, 1969). Though it sports a powerful, manipulable tail, in craniodental morphology, body proportions, locomotor mode, behavior and general habitus, *Cebus* is quite unlike atelines (ERIKSON, 1963; HLADIK, 1975). The "marmosetlike cebid" assemblage unites three phenetically disparate genera and seems even more arbitrary. It includes species with diurnal and nocturnal activity rhythms, polygamous and monogamous social systems and dietary adaptations of fundamentally different sorts. In essence, HERSHKOVITZ' justification for defining and ranking these grades is based on similarities in body size, features correlated with it, and the morphological "stage of evolution" attained by parts of the brain, skull, dentition and postcranium of the various genera as they evolve along what he considers to be predictable, practically unswerving pathways. In principle, this seems highly unlikely. In practice, my own character analysis suggests that evolution is far more plastic. Finally, in view of the model of ceboid differentiation and diversification outlined below, I question the value of recognizing a "cebid" grade altogether.

As HERSHKOVITZ' (1977) recent historical review shows, opinions have long been divided on the interpretation of marmoset morphology and the marmoset "grade": do they represent a conservative or highly modified platyrrhine stock? Evidence supporting the hypothesis that they are essentially primitive is detailed by HERSHKOVITZ, who maintains this view. But a variety of studies contradict this rather emphatically in suggesting that some or all of the callitrichines are characterized by features that are uniquely derived for primates as well as ceboids. Among them are: the combination of twinning and simplex uterus; extended-family monogamy involving female-female reproductive inhibition; secondarily derived claws, not homologous with primitive eutherian claws; a clawed thumb; reduction or loss of M^3_3 and reduction of M^2_2; and in *Callithrix* – V-shaped modified incisal occlusion; hyperthrophied C_1 and P_2 in both sexes; extensive mandible; staggered incisor-canine emplacement; modified canine occlusion; increased I_{1-2} crown height; hypertrophy of buccal enamel and reduction or loss of lingual enamel on I_{1-2}. The emerging evolutionary interpretation of the callitrichines is that they are a rather specialized lineage which secondarily occupies a canopy-subcanopy spatial niche, thereby reducing competition with sympatric, larger bodied species of the canopy strata. They are probably secondarily small in size though selection has perhaps favored a subsequent increase in body size in some sublineages, e. g., *Leontopithecus*. Members of genus *Callithrix*, particularly the smallest, most derived species, *C. pygmaea* and *C. jacchus*, have become marvelously adapted to a highly gumivorous diet, which is quite an unusual strategem for a full-fledged anthropoid but may be an important feature of the callitrichine radiation.

Adaptive radiation and the fossil record

An ecological approach to evolutionary interpretations of the platyrrhines avoids the many assumptions inherent in the purely morphological, gradistic approach and provides testable hypothesis at various levels. Observational (HLADIK, 1975) and mechanical (KAY, 1975) studies of feeding and masticatory adaptations have shown that living ceboids are generally classifiable as frugivore-insectivores and frugivore-folivores with a minimal amount of taxonomic overlap between categories. These and other studies (e. g., ROSENBERGER & KINZEY, 1976) suggest that dietetic specializations of certain species are also discernible and with the inclusion of additional relevant data, e. g., other parts of the feeding mechanism, foraging modes, locomotor and manipulative behaviors, body size and social organization, adaptive inferences may be substantially refined. Following this rationale, I suggest that living ceboids, as a class of arboreal frugivores, occupy two semi-exclusive adaptive zones, a Frugivorous-Insectivorous Zone (FIZ) and a Frugivorous-Folivorous Zone (FFZ). This ecological division corresponds with a basal phyletic dichotomy and the family-group classification I employ. Initial zonal segregation centered on selection for efficient exploitation of alternative primary protein resources and is reflected in fundamentally contrasting organizations of the masticatory apparatus (ROSENBERGER, 1979 b). To generalize, cebids primitively inhabit the FIZ and display a light-weight feeding mechanism that deemphasizes molar processing; atelids primitively inhabit the FFZ and are characterized by a heavy-duty system designed for powerful molar occlusion.

Radiation within each zone, i. e., finer niche partitioning, is reflected in the derived morphologies of zone members. In FIZ, for example, an increase in body size and suspensory behaviors and a modification of occlusal morphology may have facilitated evolution of the impressive dietetic opportunism of *Cebus*, which genus may be justifiably regarded as an advanced omnivore. Callitrichines, as previously indicated, evolved a vertically ranging foraging mode and, in more derived lineages, a gum-harvesting dentition. *Saimiri*, by anthropoid standards, may prove to be a rather specialized insectivore, small in size, equipped with acutely designed puncture-crushing postcanines large premolars and highly convergent, frontated orbits.

Among FFZ constituents, *Aotus* altered its dyadic rhythm. Within the size range of frugivore-insectivores, yet removed from their competitive sphere of influence, the noctural *Aotus* partakes in a relatively large proportion of leaves (P. WRIGHT, pers. comm.), perhaps conditioned more by its heritage than anything else. *Callicebus, Pithecia, Chiropotes* and *Cacajao* commonly share a very modified ensemble of dental features, particularly evident in the harvesting incisors that appear to be specifically fruit-adapted, possibly to some highly exclusive resource. In postcranium and prehensile tail, atelines evince adaptations to a unique, though not fully understood, foraging mode. For *Ateles*, CANT (1977) suggests that rapid suspensory locomotion may be time-and-energy saving in traveling between widely dispersed patches of preferred fruit sources. *Ateles* and *Alouatta* also exhibit dental adaptations that are quite specific to fruits and leaves, respectively.

The fossil record of Cenozoic platyrrhines suggests that these dual radiations were already underway during the Oligocene-Miocene. The morphology of the early Oligocene *Branisella* is still poorly known but it does not appear to show the derived gnathic or molar features of FFZ atelids. There is very strong evidence of a close cladistic relationship between the late Oligocene *Dolichocebus* and *Saimiri*, whose crania bear several hallmarks of the light-weight FIZ feeding mechanism (ROSENBERGER, 1979 a). This implies that both *Cebus*, the closest living relative of *Saimiri*, and callitrichines, the sister-group of cebines, had already differentiated as lineages. The late Oligocene and early Miocene *Tremacebus* and *Homunculus*, collateral relatives of *Aotus* and the other pitheciines, respectively, document the roughly contemporaneous presence of atelids. *Tremacebus* appears to exhibit *Aotus*-like orbital expansion while *Homunculus* preserves indications of high-crowned, narrow-calibered incisors and stout canines, harvesting specializations of *Callicebus* and sakiuakaris. *Neosaimiri, Cebupithecia* and *Stirtonia*, known from middle Miocene material, each present dental features and adaptations that resemble their modern closest relatives, *Saimiri*, sakiuakaris, and *Alouatta*, in very fine details.

Thus, however meager the record may be, there are good indications that the four major sublineages of living ceboids, and several of the adaptive modalities they represent, were established quite early. It also shows that several generic lineages (i. e., *Dolichocebus-Neosaimiri-Saimiri; Tremacabus-Aotus; Stirtonia-Alouatta)* are particularly long-lived. The presence of such ancient generic lineages is suggestive of a common pattern of anagenetic advances, offsetting lineage extinction by increasingly fine habitat differentiation within relatively stable adaptive zones and heritage parameters. This may explain the surprising similarity of middle Miocene and modern species, the relatively large phenetic gaps between the modern genera, and, in part, their disproportionately large number of monospecific or narrowly varying genera.

This scenario is unlike the pattern inferred for catarrhines, which are even better sampled paleontologically. Their generic lineages do not extend anterior to the middle Miocene (E. DELSON, pers. comm.) and a large number of Neogene genera have differentiated, possibly developing into a series of successional adaptive replacements. One speculative explanation for these long range contrasts is that they reflect the greater endemicity of the South American island continent, its reduced surface area and environmental homogeneity placing a premium on directional selection and character divergence and minimizing dispersal possibilities.

Acknowledgements

I thank the organizers and hosts of the VII Congress of the International Primatological Society, Drs. P. D. GINGERICH, R. L. CIOCHON and B. CHIARELLI for their generosity and for making my participation possible. I am also grateful to the various museum officials who have allowed me access to their collections.

References

BAUCHOT, R. & STEPHAN, A.: Encephalization et niveau evolutif chez les simiens. — Mammalia 33, 225—275 (1969).

BOCK, W. J.: Comparative morphology in Systematics. — In: Systematic Biology, 411—447. Washington, D. C., National Academy of Sciences (1969).

CACHEL, S. M.: A functional analysis of the primate masticatory system and the origin of anthropoid post-orbital septum. — Amer. J. Phys. Anthrop. **50**, 1—17 (1978).

CANT, J. G. H.: Ecology, Locomotion, and Social Organization of Spider Monkeys *(Ateles geoffroyi)*. — Ph. D. Thesis, Univ. Microfilms, Ann Arbor (1977).

CLARK, W. E. LE GROS: The Antecedents of Man. — Harper Torchbooks ed., Harper and Row, N. Y. (1963).

CONROY, G.: Primate postcranial remains from the Oligocene of Egypt. — Contrib. Primatol. **8**, 1—134 (1976).

— Candidates for anthropoid ancestry: some morphological and paleozoological considerations. — In: CHIVERS & JOYSEY, Recent Advances in Primatology **3**, Evolution, 27—41. Academic Press, London (1978).

ERIKSON, G. E.: Brachiation in New World monkeys and in anthropoid apes. — Symp. Zool. Soc. London 10, 135—164 (1963).

FLEAGLE, J. G. & SIMONS, E. L.: Anatomy of the bony pelvis in parapithecid primates. — Folia primatol. **31**, 176—186 (1979).

HERSHKOVITZ, P.: Living New World Monkeys (Platyrrhini) With an Introduction to Primates, **1**. — Univ. of Chicago Press, Chicago (1977).

HLADIK, C. M.: Ecology, Diet and Social Patterning in Old and New World Primates. — In: TUTTLE, Socioecology and Psychology of Primates, 3—35. Mouton, The Hague (1975).

HUXLEY, T. H.: Man's Place in Nature. — Ann Arbor Paperback ed., Univ. Michigan Press, Ann Arbor (1863).

KAY, R. F.: The functional adaptations of primate molar teeth. — Amer. J. Phys. Anthrop. **43**, 195—216 (1975).

NAPIER, J. R. & NAPIER, P. H.: A Handbook of Living Primates. — Academic Press, N. Y. (1967).

ROSENBERGER, A. L.: Cranial anatomy and implications of *Dolichocebus*, a late Oligocene ceboid primate. — Nature 279, 416—418 (1979 a).

— Phylogeny, Evolution and Classification of New World Monkeys (Platyrrhini, Primates). — Ph. D. Thesis, City Univ. of New York (1979 b).

ROSENBERGER, A. L. & KINZEY, W. G.: Functional Patterns of Molar Occlusion in Platyrrhine Primates. — Amer. J. Phys. Anthrop. 45, 281—298 (1976).

SIMONS, E. L.: Primate Evolution. — Macmillan, New York (1972).

SZALAY, F. S. & DELSON, E.: Evolutionary History of the Primates. — Academic Press, N. Y. (1979).

Author's addresses:

Graduate Center, 33 W. 42 Street, New York, N. Y. 10036, U. S. A. — currently: University of Illinois at Chicago Circle, Dept. of Anthropology, Box 4348, Chicago, Illinois 60680, U. S. A.