ON THE SPECIAL TREATMENT OF FOSSILS AND TAXONOMIC BURDEN: A RESPONSE TO LOCONTE

Arnold G. Kluge¹

¹ Museum of Zoology and Department of Biology, University of Michigan, Ann Arbor, MI 48109, U.S.A.

Loconte (1990) contends that extinct and extant organisms should be treated differently in cladistics, and he is not alone in this point of view (e.g., Crowson, 1970; Hennig, 1966, 1981; Løvtrup, 1977, 1985; Patterson, 1977, 1981a,b, 1982; Jefferies, 1979, 1986; Rieppel, 1979: 147; Rosen et al., 1981: 178; Fortey and Jefferies, 1982; Gardiner, 1982; Ax, 1985, 1987; Willmann, 1985; Forey, 1986; Craske and Jefferies, 1989). There are two interrelated issues in such a position: (a) fossils do not count as much as living terminal taxa in assessing sister group relationships, and (2) special taxonomic conventions, such as plesion (Patterson and Rosen, 1977), are required to be able to communicate accurately the position of fossils on a cladogram.

The importance attributed to different character bearers is usually reflected in the protocol recommended for cladogram construction. For example (Gardiner, 1982), clades of living organisms are individuated first, and the position of fossils, if they are considered at all, is examined in the context of those clades. In the jargon of Ax (1987: 201–231), fossils are added to the stem lineages connecting two monophyla that are adelphotaxa. Extant organisms are supposed to be more important than fossils because they are complete sources of information, are of the same age, and have had greater taxonomic stability (Patterson, 1981a,b; Craske and Jefferies, 1989: 73). The need for special taxonomic conventions is a consequence of the extra burden fossils place on the number of categorical ranks in the Linnaean system because extinct organisms tend to be plesiomorphic sister lineages (Gauthier et al., 1988).

Gauthier et al. (1988; see also Donoghue et al., 1989) addressed both of these issues. They demonstrated empirically that fossils can overturn a theory of relationships based only on Recent taxa, and concluded (p. 191) "that extant taxa may be even less informative, or for that matter unimportant in determining amniote phylogeny." Contrary to Loconte's claim (p. 187), Gauthier et al. did not "propose to distinguish stem lineages from their respective monophyla". In point of fact, Gauthier et al. analyzed a single set of all the relevant available evidence, one in which living and extinct forms were coequal as terminal taxa (Table 2, Fig. 3), and that operation is consistent with the maxim of total evidence (Kluge, 1989). Lastly, Loconte (p. 189) states that "if fossils are unambiguous members of a stem lineage, the fossil record can be utilized as a secondary criterion of character polarization that is capable of overturning a polarization by outgroup comparison between extant taxa, or resolving an equivocal polarization". These conclusions do not apply to fossils alone, and are therefore trivial, because "unambiguous" sister relationships of any kind of organism cannot be improved upon.

Gauthier et al. (1988) dealt with the burden fossils place on taxonomy by simply doing away with higher categorical ranks. They argued that the discovered cladogram serves

as the complete hierarchical system, and whatever clades are named must be monophyletic. Further, they noted that only the most detailed discussions of relationships may require a complete taxonomy. Loconte's alternative, the use of the plesion convention, is unacceptable because "a plesion is, in principle, a paraphyletic grouping since it contains part of the stem lineage and this will have been ancestral to non-members of the plesion" (Craske and Jefferies, 1989: 74; see also Hennig, 1981: 30).

Loconte, like Ax (1987), states that Reptilia is a paraphylum, and prefers Sauropsida for the (bird, crocodile, lepidosauromorph, turtle) clade because it is a monophylum. Paraphyly per se is not the issue here because Gauthier et al.'s (1988) Reptilia is consistent with how proper names are defined ostensively (Rowe, 1987). For example, Reptilla is defined on Gauthier et al.'s phylogenetic hypothesis (fig. 3) as the most recent common ancestor of Anapsida and Diapsida and all its descendants. As such, Reptilia is monophyletic, and the name denotes an entity which stands as a historical individual, and thus a product of evolution.

Indeed, the content of Reptilia has varied since its original definition. Subsequent authors (e.g., Romer, 1966) have even explicitly treated that taxon as a paraphyletic assemblage. Loconte objects to the burden of having to distinguish the different senses in which Reptilia has been used, and to him (p. 188) Reptilla "is an artificial grade of poikilothermic amniotes that lacks any evolutionary novelties" (my italics). Unfortunately, such complex and tainted taxonomic histories are not unusual. Even Loconte's preferred Sauropsida has had various meanings. For example, Pearse (1947: 18) included Synapsida and Reptilia (sensu Gauthier et al., 1988) in Sauropsida. In Pearse's sense, Sauropsida designates the level in the cladistic hierarchy where Amniota ordinarily appears. If the clades we recognize are matters of inference and change according to the evidence, and if we are to avoid intensional definitions and the appearance that taxa are classes, then we will be burdened to some extent. Proper names provide a certain degree of stability; however, just "as languages evolve, words change their meanings" (Hull, 1976: 179).

REFERENCES

Ax, P. 1985. Stem species and the stem lineage concept. Cladistics 1: 279-287.

Ax, P. 1987. The Phylogenetic System: the Systematization of Organisms on the Basis of their Phylogenesis. John Wiley, New York.

Craskse, A. J. and R. P. S. Jefferies, 1989. A new mitrate from the Upper Ordovician of Norway, and a new approach to subdividing a plesion. Palaeontology 32: 69–99.

Crowson, R. A. 1970. Classification and Biology. Aldine Publ. Co., Chicago.

Donoghue, M. J., J. A. Doyle, J. Gauthier, A. G. Kluge and T. Rowe. 1989. The importance of fossils in phylogeny reconstruction. Annu. Rev. Ecol. Syst. 20: 431–460.

Forey, P. L. 1986. Relationships of lungfishes. Jour. Morph. (Supplement) 1: 75-91.

FORTEY, R. A. AND R. P. S. JEFFERIES. 1982. Fossils and phylogeny—a compromise approach. *In* Joysey, K. A. and A. E. Friday (eds.), Problems of Phylogenetic Reconstruction. Syst. Assoc., London, pp. 197–234.

Gardiner, B. 1982. Tetrapod classification. Zool. Jour. Linnean Soc. 74: 207–232.

GAUTHIER, J., A. G. KLUGE AND T. Rowe. 1988. Amniote phylogeny and the importance of fossils. Cladistics 4: 105–209.

Hennig, W. 1966. Phylogenetic systematics. Univ. Illinois Press, Urbana.

HENNIG, W. 1981. Insect Phylogeny. John Wiley, New York.

Hull, D. L. 1976. Are species really individuals? Syst. Zool. 25: 174-191.

JEFFERIES, R. P. S. 1979. The origin of chordates—a methodological essay. In House, M. R. (ed.), The Origin of Major Invertebrate Groups. Syst. Assoc., London, pp. 443–447.

- JEFFERIES, R. P. S. 1986. Ancestry of the Vertebrates. Cambridge Univ. Press, New York.
- Kluge, A. G. 1989. A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). Syst. Zool. 37: 7-25.
- LOCONTE, H. 1990. Cladistic classification of Amniota: A response to Gauthier et al. Cladistics 6: 187–190.
- LØVTRUP, S. 1977. The phylogeny of Vertebrata. John Wiley, London.
- LØVTRUP, S. 1985. On the classification of the taxon Tetrapoda. Syst. Zool. 34: 463-470.
- Patterson, C. 1977. The contribution of paleontology to teleostean phylogeny. In Hecht, M. K., P. C. Goody and B. M. Hecht (eds.), Major Patterns in Vertebrate Evolution. Plenum Press, New York, pp. 579–643.
- Patterson, C. 1981a. Significance of fossils in determining evolutionary relationships. Annu. Rev. Ecol. Syst. 12: 195–223.
- Patterson, C. 1981b. Agassiz, Darwin, Huxley, and the fossil record of teleost fishes. Bull. Br. Mus. Nat. Hist. (Geol.) 35: 213-224.
- Patterson, C. 1982. Morphological characters and homology. *In Joysey*, K. A. and A. E. Friday (eds.). Problems of Phylogenetic Reconstruction. Syst. Assoc., London, pp. 21–74.
- Patterson, C. and D. E. Rosen. 1977. Review of ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. Bull. Am. Mus. Nat. Hist. 158: 81-172.
- Pearse, A. S. (ed.) 1947. Zoological Names: a List of Phyla, Classes, and Orders. Prepared for Section F, American Association for the Advancement of Science. Second edition. Durham, North Carolina, U.S.A., pp. 1–22.
- RIEPPEL 1979. A cladistic classification of primitive snakes based on skull structure. Z. Zool. Systematik Evolutionsforschung 17: 140–150.
- ROMER, A. S. 1966. Vertebrate Palaeontology. Third Edition. Univ. Chicago Press, Chicago.
- Rosen, D. E., P. L. Forey, B. G. Gardiner and C. Patterson. 1981. Lungfishes, tetrapods, palaeontology and plesiomorphy. Bull. Am. Mus. Nat. Hist. 167: 159–267.
- Rowe, T. 1987. Definition and diagnosis in the phylogenetic system. Syst. Zool. 36: 208-211.
- WILLMANN, R. 1985. Die Art in Raum und Zeit. Das Artkonzept in der Biologie und Palacontologie. Parey, Berlin and Hamburg.

(Received for publication 8 January 1990; accepted 29 January 1990)