Spotlight

A Cold Look at Odd Vertebrate Phylogenies

Philippe Janvier

URA12 du CNRS, Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, 8 rue Buffon, 75005 Paris, France

Since the dawn of molecular phylogenetics, morphologists concerned with phylogeny reconstructions have had many opportunities to be surprised, amused, or infuriated by what we now call "odd phylogenies," i.e., phylogenies which are strongly at odds with the current consensus. In this issue, A.-S. Rasmussen, A. Janke, and U. Arnason provide us with such an odd phylogeny of the craniates and vertebrates, with particular respect to the relationships among jawed vertebrates, or gnathostomes. Their results are based on the largest molecular data set used so far for resolving the phylogenetic relationships between vertebrate higher taxa, and they suggest that the amniotes diverged before all Recent bony fish, which thus appear as a clade. This also suggests that previous analyses of mitochondrial DNA (mtDNA) have led to the reconstruction of an "inverted" piscine tree. However odd this new vertebrate tree may be, my comments here should not be regarded as criticism of molecular phylogenetics, as some morphologists also happened to publish such odd (but reasonably so!) phylogenies since the nineteenth century, as exemplified by the heated debates about the lungfish–tetrapod or bird–mammal relationships in the 1980s and early 1990s.

In defense of their current vertebrate phylogenies, morphologists are prone to invoke the weight of century-long, detailed investigations on innumerable characters of Recent and fossil forms, but for a long time these morphological data have been used in widely different manners, often depending on the dominant philosophical backgrounds of the scientific communities. With the ad-

vent of Hennig's phylogenetic systematics, now known as cladistics, there appeared a broad consensus on the way data should be analyzed, even though debates remain heated about the nature, quality, and meaning of the characters. Fortunately molecular phylogeneticists have recognized the merits of cladistics and parsimony and can now have fruitful exchanges with morphologists, or even join their data into "total evidence" analyses. However, before the rise of cladistics, morphology-based theories of relationships sometimes displayed a wide range of diversity and "oddness."

Compared to previous studies of mitochondrial DNA, mtDNA, the topology discovered by Rasmussen et al. was reconstructed by rooting the craniate, or vertebrate, tree with an indisputable outgroup: three echinoderms. Rasmussen et al. show that extant cyclostomes (hagfishes and lampreys) are paraphyletic, with lampreys being the sister group of the gnathostomes. This could have been regarded as "odd" 20 years ago, before Løvtrup (1977) suggested this on the basis of morphological and physiological grounds, thereby raising controversies among morphologists. Now this theory has gained wide acceptance, although Stock and Whitt (1992) provided ambiguous results on the basis of 18S rRNA for these taxa. The situation is quite different from Rasmussen and co-workers' topology of the gnathostome tree, which suggests that the amniotes (let us extrapolate them to tetrapods, although they did not include any amphibian in their analysis) are the sister group of all extant piscine osteichthyans (i.e., the ray-finned fish, or actinopterygians, and lobe-finned fish, or sarcopterygians, with tetrapods classically included in the latter). In addition, Rasmussen et al. find that lungfish are the sister group of

Correspondence to: P. Janvier; e-mail: janvier@mnhn.fr

all other piscine osteichthyans and that the coelacanth falls among the actinopterygians; that is, the bichir is the sister group of the coelacanth and teleosts.

At first glance, the tree reconstructed by Rasmussen et al. leaves a present-day morphologist voiceless, and his/ her first reaction must be to leave it as absurd, without further deliberation. Nevertheless, a look at some old, morphology-based, theories of vertebrate relationships, now fallen into oblivion, reveals that such a strange position for the tetrapods was already suggested by Jaekel (1911), who considered tetrapods and fish as two sister groups ("Nebenstamm"). The famous anatomist E.S. Goodrich (1909) accepted tetrapods as osteichthyans but suggested a trichotomy for lungfish, tetrapods, and the teleostomes, the latter including the coelacanths, the bichir, and the other actinopterygians only. More recently, Jarvik (1980, 1981), although considering teleostomes (i.e., osteichthyans minus lungfish) as monophyletic, regarded the interrelationships among the coelacanths, bichirs, actinopterygians, urodeles, gymnophiones, and "eutetrapods" (i.e., anurans and amniotes) as being unresolved, yet he suggested some closer relationship between bichirs and coelacanths. He also clearly put lungfish among the "plagiostomes" (i.e., with chondrichthyans and, more particularly, holocephalans). Of course, such theories are now rejected by the majority of morphologists, be they neontologists or paleontologists, on the grounds that they neglect the principle of parsimony or are a mere remnant of idealistic morphology (i.e., the belief in "archetypes," wherefrom any character can arise convergently). The most parsimonious distribution of all available morphological and physiological characters now suggests the pattern for Recent gnathostome interrelationships (chondrichthyans (actinopterygians including bichirs (coelacanth (lungfish(tetrapods))))), yet some still remain "politically correct" in advocating (lungfish (coelacanth (tetrapods))) for the last three taxa (see review by Schultze 1994). As far as I am concerned, I generally feel satisfied with these theories (in particular, the first one), yet only 14 of the 34 characters supporting the monophyly of the sarcopterygians (i.e., coelacanths, lungfish, and tetrapods) are undisputably unique to this group. In contrast, the inclusion of bichirs in actinopterygians (as the sister group of all other recent actinopterygians) is supported by 10 characters, 8 of which are nonhomoplastic, yet disputed by Bjerring (1985). Now, when fossils are added to this phylogeny, a number of problems disappear, whereas others arise. The discovery of numerous 410 million- to 360-million-year-old "basal" sarcopterygians has contributed to settle the question of the relationships of coelacanths, lungfish, and tetrapods. A number of "intermediate forms," such as Ichthyostega, Acanthostega, Ventastega, Elginerpeton, and the elpistostegalians, link the tetrapods with an ensemble of fossil, piscine sarcopterygians, the osteolepiforms (Ahlberg and Milner 1994).

Other "intermediate forms" seem to link lungfish with a fossil group, the porolepiforms (Cloutier and Ahlberg 1996). Porolepiforms, osteolepiforms, elpistostegalians, and early tetrapods share a particular folded structure of the teeth, which never occurs in coelacanths—even in the earliest known ones—or in early actinopterygians. This, and some other characters, suggests that, among Recent sarcopterygians, lungfish are more closely related to tetrapods than to coelacanths. Now, the problem is perhaps with the meaning of the characters that we regard as sarcopterygian characters. The earliest known sarcopterygians, from the Late Silurian and Early devonian (about 410 Ma) of China, do not meet the prediction of the currently accepted sarcopterygian phylogeny, i.e., that coelacanths diverged earlier than lungfishes and tetrapods. None of these early forms show indications of coelacanth characters and the earliest known coelacanths, which are about 30 Ma younger, are morphologically very close to the extant Latimeria. Coelacanths share some characters with an extinct group of sarcopterygians, the onychodontiforms, which in turn share some characters with primitive actinopterygians (currently regarded as general osteichthyan characters). In contrast, the earliest known sarcopterygians seem to belong to the group of lungfish and porolepiforms, whereas others display an odd assemblage of sarcoptergyian characters and characters which occur only in some fossil, nonosteichthyan groups. This material is presently under study by Chinese colleagues and we must wait for detailed descriptions and analysis, but one must be aware that some of the characters currently considered as being sarcopterygian characters may possibly turn out to be general osteichthyan characters. I shall not go so far as to suggest that even osteichthyan characters may be general gnathostome characters, although this has once been suggested on the basis of placoderms, an extinct group of gnathostomes possessing large dermal bones, like osteichthyans, but now regarded as the sister group of all other gnathostomes. One of the most often cited characters of the sarcoptergyians is the monobasal articulation of paired fins (and limbs), and this character is assumed to be a consequence of the loss of the premetapterygial radials, leaving the metaptergyium as the only fin endoskeleton. Monobasal paired fins are known to occur, as homoplasies, in some fossil sharks and holocephalans, and these provide the only evidence that this condition is due to loss of premetapterygial radials. In no known sarcoptergyian, however, is there such evidence, be it palaeontological or ontogenetic. Nevertheless, one must keep in mind that the monobasal paired-fin skeleton of sarcopterygians is likely to be the result of a loss, and that the refutability of the homology of a loss is a fundamental question in phylogenetics.

However "odd" it may look, Rasmussen and coworkers' tree is a result based on the analysis of complete mtDNA molecules and I shall not comment here upon

the methods they use or the rooting they choose, as other workers in this field will certainly be prepared to do this. My aim is just to take their tree as an example of a strongly unconventional topology which, if repeated, will certainly mean something either at the level of the mtDNA structure or at the level of vertebrate phylogeny. In the latter case, it cannot be flatly discarded and should represent a challenge to morphology and paleontology. As for paleontology, such theories, however, unconventional they may be, may trigger new insights about puzzling fossil forms that are sometimes overlooked, in want of a better solution. Patterson (1981) once claimed that fossils never, or rarely, overturn phylogenies based on Recent taxa, thereby infuriating paleontologists. As for the morphology-based gnathostome phylogeny, this statement seems to hold, since the controversies about the position of lungfish within the sarcopterygians in current phylogenies involve neontologists as well as palaeontologists. Palaeontology, in this case, just gave more weight to the lungfish–tetrapod relationships by showing that lungfish are basically rhipidistians (sarcopterygians with folded teeth). With results such as Rasmussen and co-workers', the question becomes whether molecules can overturn phylogenies based on the morphology of either Recent forms or fossils or both. As for vertebrate morphologists, the debate about higher-taxon interrelationships hitherto bore on minor controversies, and practically all agreed on osteichthyan monophyly. Now, the controversy may occur between morphologists as a whole and molecular phylogeneticists, but the difference in the nature of the characters considered may well make the debate more heated than ever. Is mtDNA more reliable than morphological characters such as dermal bone pattern, fin rays, fin endoskeleton, or endochondral bone? Does paleontology provide a test of morphological homologies by showing their actual degree of generality among the "basal" taxa of each clade? My impression is that the morphology/molecule debate,

however heated it may be, will still address the same kinds of question as in the neontology/paleontology debate, that is, the relative weight or the number of characters versus that of their "quality." Now, what character "quality" means to morphologists varies from degree of complexity to low homoplasy or availability in the fossil record. Therefore, developmental genetics may soon become a fourth protagonist in the debate, by providing a possible test for the "quality" of morphological characters, through the knowledge of their genetic control. My only wish is that all three (or four) parties will take a cold look at the others' data and results, however "odd" they may look.

References

Ahlberg P, Milner AR (1994) The origin and early diversification of tetrapods. Nature 368:507–514

Bjerring H (1985) Facts and thoughts on piscine phylogeny. In: Foreman RE, Gorbman A, Dodd JM, Olsson R (eds) Evolutionary biology of primitive fishes. Plenum, New York, pp 31–57

Cloutier R, Ahlberg PE (1996) Morphology, characters and the interrelationships of basal sarcopterygians. In: Stiassny MLJ, Parenti LR, Johnson GD (eds) Interrelationships of fishes II. Academic Press, New York, pp 445–496

Goodrich ES (1909) Vertebrata craniata. First fascicle: cyclostomes and fishes. In: Lankester RE (ed) A treatise on zoology, Vol. 9. Black, London

Jaekel O (1911) Die Wirbeltiere, Bornträger, Berlin

Jarvik E (1980) Basic structure and evolution of vertebrates, Vol 1. Academic Press, London

Jarvik E (1981) Basic structure and evolution of vertebrates, Vol 2. Academic Press, London

Løvtrup S (1977) The phylogeny of vertebrata. Wiley, New York

Patterson C (1981) Significance of fossils in determining evolutionary relationships. Annu Rev Ecol Syst 12:195–223

Schultze H-P (1994) Comparison of hypotheses on the relationships of sarcopterygians. Syst Biol 43:155–173

Stock DW, Whitt GS (1992) Evidence from 18S ribosomal RNA that lampreys and hagfishes form a natural group. Science 257:787–789