

Hanno Sandvik*

Department of Biology,
University of Tromsø, 9037
Tromsø, Norway; and Division
of Biology, Imperial College
London, Silwood Park, Ascot,
Berkshire SL5 7PY, UK

submitted March 2006

accepted June 2006

PERSPECTIVE

An inordinate fondness for Mecopteriformia

Abstract What is the Largest animal taxon? The most famous answer to this question has been given by Haldane who coined the phrase that ‘the Creator has an inordinate fondness for beetles’. Although much cited, this statement has never been tested. Other experts have suggested other candidates for the largest animal taxon, all of which included the beetles as a subordinate group. I here outline a novel phylogenetic-comparative method that can address the question in a testable way. The result of applying the algorithm to the Metazoa is astonishing: the largest animal taxon is neither beetles nor a taxon super- or subordinated to beetles, but the Mecopteriformia.

Key words Arthropoda, Coleoptera, largest animal taxon, Metazoa, phylogenetic-comparative method, species richness

What is the largest animal taxon? The persisting confusion surrounding this question has haunted zoology for decades. Generations after generations of zoological students have been left behind in befuddlement in view of the fact that even renowned experts continue to disagree on the answer of such a seemingly simple question. The most famous answer was given by J.B.S. Haldane (*cf.* Slater, 1951; Gould, 1993) who coined the phrase that ‘the Creator has an inordinate fondness for beetles’ (Coleoptera; approximately 360 000 described species). This statement has been much cited (e.g. Farrell, 1998; Ganeshiah, 1998; Grove & Stork, 2000; Mayhew, 2002) but never tested. On the other hand, R.M. May (1986) introduced another candidate by telling us that ‘to a good approximation, all species are insects’ (Hexapoda; 1.0 million species). Furthermore we find among the nominees for the largest animal taxon such groups as the holometabolous insects (Holometabola or Endopterygota; 800 000 species; nominated by N.P. Kristensen, 1999), and the arthropods (1.1 million species; Siewing, 1985). The corresponding group sizes as measured in species number diverge by more than 60%. How is it possible to reconcile these hypotheses?

Of course, the question raised – what is the largest animal taxon? – is entirely irrelevant to biology as a *science*. The ‘disagreement’ among the experts is not real, because they did not mean to make scientific statements in the first place. Arithmetically, it is straightforward to demonstrate that arthropods would be a better candidate than are insects than are

Holometabola than are beetles. The reason is simply that those taxa contain the remaining ones as their subordinated groups. Arguing along that line, the best candidate for the largest animal taxon would in fact be Metazoa, the entirety of multicellular animals (1.2 million species; Sandvik, 2001b). The latter solution at the same time answers the question and exposes its (scientific) meaninglessness. However, for some reason or another, the search for the largest animal subgroup seems to be *emotionally* quite relevant to many biologists – as well as some non-biologists. For that reason, I here outline a novel algorithm which hopefully will lay this long-lasting controversy (however [ir]relevant) to rest once and for all.

The disagreement between the experts does not lie in the size of taxa, but in how to ‘nominate’ taxa. The opening question can thus be reformulated as follows: which taxa should be nominated in the competition for the largest animal group? If insects are nominated, you cannot nominate beetles nor arthropods any more for the reasons mentioned above. There seems to be no trivial way of deciding whether, for example, insects or a sub- or a superordinated group in the taxonomic hierarchy ‘deserves’ nomination. Does this mean that the question is unsolvable in principle, that it belongs to the realms of metaphysics rather than being an empirically addressable problem? Luckily this conclusion does not follow. The solution lies in nominating only the smallest taxa that are still larger than other branches in the tree of life. The nomination procedure can thus be expressed as follows: a taxon is not nominated if one of its subclades is larger than all other competitors. Instead, such taxa are further subdivided. On the other hand, a taxon is not subdivided if this would make it smaller than any of the other competitor taxa (Fig. 1).

* Current address: Department of Biology, Norwegian University of Science and Technology, 7491 Trondheim, Norway
Email: hanno@evol.no

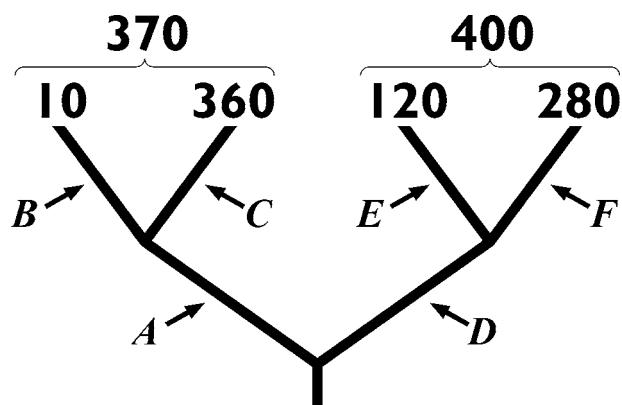


Figure 1 Example tree illustrating the nomination procedure in the search for the largest taxon. Numbers above the tree branches are numbers of species. Using the method outlined in the text, one can see that subdividing taxon *D* into taxa *E* and *F* would make each of them smaller than taxon *A*. Therefore, taxon *D* is not subdivided but nominated *in toto*. However, subdividing taxon *A* into taxa *B* and *C* does not affect the placement of taxon *C* or *A*, respectively, as the second largest taxon (after taxon *D*). Therefore, taxon *C* (or one of its subclades) rather than taxon *A* is nominated in the next round of the competition. If species numbers are multiplied by 1000, the taxa can be understood as: *A*, Neuropteriformia; *B*, Neuropteroidea; *C*, Coleopteroidea; *D*, Mecopteriformia; *E*, Hymenoptera; and *F*, Mecopteroidea (phylogeny and nomenclature follow Ax, 1995–2001).

The formal algorithm for discovering the largest taxon is as follows: (1) Start at the basal-most node of the phylogeny. (2) For each of the two branches at this node, estimate the number of species. (3) In the larger of the two branches, move one node upwards. (4) For each of the two branches at this node, estimate the number of species. (5) If at least one of the two branches contains more species than the largest of the other branches considered so far, go to step 3. (6) Otherwise, stop at the current node. If you wish to obtain not only the single largest taxon but a ranked list of the largest taxa, jump to the second largest taxon so far, and start again from step 4. Repeat this as often as is necessary.

The rationale of the algorithm is related to similar procedures that are used in identifying correlates of species diversification (e.g., Purvis, 1996; Barracough *et al.*, 1998; de Queiroz, 1998). A species-rich taxon may be so for different reasons: the entire taxon may have had an unusually high diversification rate (i.e. difference between speciation and extinction rate). Alternatively, most of the diversification occurred in one or several subclades contained in the taxon (Hennig, 1953; Mayhew, 2002). In that case, high species richness is more appropriately considered an attribute of those subgroups, not of the entire taxon. These two possibilities can only be separated if the phylogenetic, or sister-group, relationships within the taxon are known. Accordingly, and because sister groups have the same age, shared the same evolutionary history up to their splitting event, and evolved independently thereafter (Hennig, 1950; Felsenstein, 1985), knowledge of sister-group relationships is crucial.

The algorithm therefore presupposes a fully resolved (bifurcating) phylogenetic tree of the taxon of interest. A further decision that has to be made prior to applying the algorithm, is how to count species. Including all species would naturally be preferable. However, because of fuzzy species barriers (Hey, 2001) and incomplete knowledge it may be better to restrict counts to described extant species rather than using estimates of total numbers. This has at least the advantage of making the outcome directly testable. Guesstimates of the total diversity of many taxa diverge grossly (e.g. May, 1986), and would render impossible any direct comparison of their size.

The result of applying this algorithm to the Metazoa was staggering: the largest animal taxon was not even to be found among the set of taxa that had been considered nominees so far. The winning taxon was the Mecopteriformia. If you have not heard of this group before, you are definitely not alone. In fact it was not named until 1999 (Ax, 1995–2001, vol. 2). The reason for this fact is not that the group consists of only recently discovered species. To the contrary, it includes such well known animals as bees, butterflies, caddis flies, fleas, flies, scorpion flies, and their respective relatives (i.e. Diptera + Hymenoptera + Lepidoptera + Mecoptera + Siphonaptera + Trichoptera). With approximately 400 000 described species this group is larger than its sister taxon (or nearest relative), the Neuropteriformia, which include the beetles, lacewings and snakeflies (approximately 370 000 species, cf. Fig. 1).

The procedure described is scientific in the sense that its results are falsifiable by new evidence. If further species are described or our best estimate of the animal phylogeny changes, this may also affect the ranking of the largest taxa. Table 1 gives the best estimate currently available of the first ten places in the competition for the largest animal group. Beetle fans may find comfort in the fact that four subclades of beetles are among the top ten taxa, even though the clade itself did not qualify for the gold medal. Also, if current guesstimates of beetle diversity are close to the real numbers (e.g. Grove & Stork, 2000), coleopterists might easily change the ranking by describing a sufficient amount of new beetle species.

The reason that the Mecopteriformia have escaped attention thus far might simply be that this taxon has not got any Linnean category attached to it. In other words, it does not constitute what in traditional taxonomy is called an ‘order’ or ‘class’, but exists at a level sandwiched between those arbitrarily assigned labels. However, as far as the Creator is concerned, there seems to be no compelling reason to assume that She would let Her fondness be constrained by ordinal level.

In conclusion, the longstanding issue whether any specific animal taxon had attracted the Creator’s special fondness, and if so which, can finally be considered solved. This success reinforces the recognition of the fact that many biological problems can only be answered within a phylogenetic framework, i.e. against the background of our evolutionary knowledge about the groups concerned (Martins & Hansen, 1996). The reported finding may in fact be the greatest triumph of this so-called phylogenetic-comparative method ever

Rank	Taxon name	Groups included in the taxon	Approximate number of extant species described
1	Mecopteriformia	Holometabolous insects less Neuropteriformia: flies, moths, wasps etc.	400 000
2	Phytophaga	Chrysomeloidea + Curculionoidea: leaf beetles, longhorn beetles, weevils etc.	140 000
3	Lophotrochozoa	Protostomes less Ecdysozoa: earth worms, molluscs, ribbon worms etc.	120 000 ^a
4	Condylognatha	Hemiptera + Thysanoptera: bugs, leafhoppers, thrips etc.	90 000
5	Haplogastra	Scarabaeiformia + Staphyliniformia: rove beetles, scarabs, water scavengers etc.	80 000
6	Lipoctena	Arachnids less scorpions: harvest spiders, mites, spiders etc.	70 000
7	Cucujiformia s. str.	Cucujiform beetles less Phytophaga: fire-coloured, lady, ship-timber beetles etc.	60 000
8	Osteognathostomata	Actinopterygii + Diploï + <i>Latimeria</i> + Tetrapoda: bony fishes and terrestrial vertebrates	50 000
9	Carabidae	Ground beetles	30 000 ^a
10	Caridoida	Malacostracan crustaceans less Leptostraca and Stomatopoda: crabs, krill, shrimps etc.	20 000

Table 1 The top ten animal taxa. The algorithm outlined in the text helped to decide the competition for the largest animal group in favour of the Mecopteriformia. Phylogenetic relationships and species numbers were compiled from various sources (Ax, 1995–2001; Westheide & Rieger, 1996; Sandvik, 2001a; Beutel & Leschen, 2005; Grimaldi & Engel, 2005; and references therein).

^a The internal phylogeny for Carabidae and Lophotrochozoa is still insufficiently known. It may thus be that subclades of these taxa, rather than the entire groups, should be listed.

since it solved the puzzle whether chicken or egg came first (Shykoff & Widmer, 1998).

Acknowledgements

While finalising the manuscript, I very much enjoyed discussions with, and/or appreciated comments by Brian Rosen, Dick Vane-Wright, Quentin Wheeler and Roderick Page.

References

Ax, P. 1995–2001. *Das System der Metazoa. Ein Lehrbuch der phylogenetischen Systematik*, 3 volumes. Fischer, Stuttgart, and Spektrum, Heidelberg [English translation (1996–2003): *Multicellular Animals*. Springer, Berlin].

BARRACLOUGH, T.G., NEE, S. & HARVEY, P.H. 1998. Sister-group analysis in identifying correlates of diversification. *Evolutionary Ecology* **12**, 751–754.

BEUTEL, R.G. & LESCHEN, R.A.B., Eds. 2005. *Handbuch der Zoologie. Eine Naturgeschichte der Stämme des Tierreiches, Band IV Arthropoda: Insecta, Teilband 38 Coleoptera, beetles, Volume 1: morphology and systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim)*. De Gruyter, Berlin & New York.

DE QUEIROZ, A. 1998. Interpreting sister-group tests of key innovation hypotheses. *Systematic Biology* **47**, 710–718.

FARRELL, B.D. 1998. ‘Inordinate fondness’ explained: why are there so many beetles? *Science (Washington, D. C.)* **281**, 555–558.

FELSENSTEIN, J. 1985. Phylogenies and the comparative method. *American Naturalist* **125**, 1–15.

GANESHAIAH, K.N. 1998. Haldane’s God and the honoured beetles: the cost of a quip. *Current Science (Bangalore)* **74**, 656–660.

GOULD, S.J. 1993. A special fondness for beetles. *Natural History* **102**(1), 4, 6, 8, 10, 12.

GRIMALDI, D. & ENGEL, M.S. 2005. *Evolution of the Insects*. Cambridge University Press, Cambridge.

GROVE, S.J. & STORK, N.E. 2000. An inordinate fondness for beetles. *Invertebrate Taxonomy* **14**, 733–739.

HENNIG, W. 1950. *Grundzüge einer Theorie der Phylogenetischen Systematik*. Deutscher Zentralverlag, Berlin.

HENNIG, W. 1953. Kritische Bemerkungen zum phylogenetischen System der Insekten. *Beiträge zur Entomologie* **3** (Sonderheft), 1–85.

HEY, J. 2001. *Genes, Categories, and Species: the Evolutionary and Cognitive Causes of the Species Problem*. Oxford University Press, New York.

KRISTENSEN, N.P. 1999. Phylogeny of endopterygote insects, the most successful lineage of living organisms. *European Journal of Entomology* **96**, 237–253.

MARTINS, E.P. & HANSEN, T.F. 1996. The statistical analysis of interspecific data: a review and evaluation of phylogenetic comparative methods. In: MARTINS E.P. (Ed.), *Phylogenies and the Comparative Method in Animal Behavior*. Oxford University Press, New York & Oxford, pp. 22–75.

MAY, R.M. 1986. How many species are there? *Nature (London)* **324**, 514–515.

MAYHEW, P.J. 2002. Shifts in hexapod diversification and what Haldane could have said. *Proceedings of the Royal Society, Biological Sciences* **269**, 969–974.

PURVIS, A. 1996. Using interspecies phylogenies to test macroevolutionary hypotheses. In: HARVEY P.H., LEIGH BROWN A.J., MAYNARD SMITH J. & NEE, S. (Eds.), *New Uses for new Phylogenies*. Oxford University Press, Oxford, pp. 153–168.

SANDVIK, H. 2001a. *Dyrenes evolusjon – en innføring i systematisk zoologi og dyrenes stamtre*. Tapir, Trondheim.

SANDVIK, H. 2001b. Fylogeni Grand Prix: dyrenes topp 10. *Fauna* (Oslo) **54**, 132–139.

SHYKOFF, J.A. & WIDMER, A. 1998. Eggs first. *Trends in Ecology and Evolution* **13**, 158.

SIEWING, R., Ed. 1985. *Lehrbuch der Zoologie. Band 2: Systematik*. 3rd edition. Fischer, Stuttgart & New York.

SLATER, A.E. 1951. Biological problems of space flight: a report of professor Haldane's lecture to the Society on April 7, 1951. *Journal of the British Interplanetary Society* **10**, 154–158.

WESTHEIDE, W. & RIEGER, R., Eds. 1996. *Spezielle Zoologie. Teil 1: Einzeller und Wirbellose Tiere*. Fischer, Stuttgart.