

Phylogenetic Trees and the Unification of Systematic Biology

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EVOLUTIONARY TREES were a major focus of interest at a recent international meeting of 1500 systematists and evolutionary biologists, the Fourth International Congress of Systematic and Evolutionary Biology, held at the University of Maryland, USA in July. Since the previous Congress, held at the University of Sussex, UK in 1985, one of the most striking research trends seems to have been an increasing unification of the disparate wings of this broad field. The focus of interest is phylogenetic trees, and in particular the creation of such trees, the checking of their validity, and their use in testing hypotheses.

This seeming unanimity of purpose has not always been the norm. Indeed, there has often been a conflict between those branches of the subject that are more quantitative and experimental and those that appear to be purely descriptive. The connections between experimental genetics, molecular biochemistry, and systematics or palaeontology were not always clear.

Douglas Futuyma (State University of New York, Stony Brook) characterized the shift in attitudes in his plenary address. He found that in population genetic studies of coevolution between species, a major dimension that had been absent was time: proper account had often not been taken of the phylogeny of the groups under study. Independently derived cladograms of the organisms provide a base against which genetic, distributional, behavioural and physiological hypotheses could be tested. In particular, when a biologist wishes to compare two groups in a phylogenetic context, the only pairs that are appropriate are sister groups – the two equal branches that diverge from a common ancestor. The time of divergence of both groups is obviously identical, and both lineages started from a single gene pool.

The importance of phylogeny was borne out by the programme of symposia: nearly all 130 sessions involved historical aspects, whether implicitly or explicitly, and indeed there were 25 sessions devoted to the mechanics of phylogenetic tree reconstruction from both morphological and molecular data. In particular, contributors to these sessions were concerned with the questions of how to reconstruct trees, and how to test them. In other words, how confident can we be about the accuracy of the elaborate and seemingly precise cladograms that are now being published in increasing numbers?

Most sessions on tree reconstruc-

tion were devoted to cladistic approaches – those based on a search for clades, or monophyletic groups, which include all the descendants of a single common ancestor. Clades are identified by the possession of one or more unique characters, whether morphological or molecular. Most systematists favour cladistic methods because their principles and purpose are straightforward, and because they provide explicitly testable phylogenies. There are two current areas of difficulty, firstly in assessing the characters, and secondly in constructing the best tree from the data.

On the face of it, many phylogenetically useful characters are obvious: birds have feathers, and nothing else does, so 'possession of feathers' defines the clade Aves. In most cases, however, the relevant unique derived characters are not so clear-cut. It is hard to decide on the scale of a character. Should humans be defined by 'possession of a large brain', or by a hundred more precise subcharacters of that attribute, features of the architecture, neurology and function of the brain? Other problems in determining characters relate to non-heritable environmentally induced variation, sexual dimorphism, and developmental changes. The changes in form experienced by organisms during development may be complex. Paula Mabee (Dalhousie University, Halifax, Canada) showed how homologous adult conditions may arise from different developmental patterns, and Pere Alberch (Museo Nacional de Ciencias Naturales, Madrid) argued that many characters may show extensive convergence and parallelism as a result of the constraining properties of developmental processes. Daniel Faith and colleagues (CSIRO, Lyneham, Australia) described statistical techniques that could sort out certain environmentally dependent characters from those of more phylogenetic value¹.

The second controversial area of phylogenetic analysis – the techniques for converting patterns of character distributions into trees – received a great deal of attention. Most techniques focus on maximizing parsimony, that is, selecting the branching diagram (tree) that explains most of the character data in terms of the fewest character transformation steps. Problems arise when several different, but equally parsimonious, trees are produced

from one data set, or when different character sets produce different trees for the same taxa. S.J. Weller (Smithsonian Institution, Washington DC), D. Lipscomb and colleagues (George Washington University, Washington DC), and others, reviewed available techniques and introduced some new ones. Other contributors, such as N. Saitou (University of Tokyo), compared the various algorithms that are used to create order out of seemingly chaotic character data matrices. Some of these test out every possible tree, but most take short-cuts because of the sheer computing time involved: for three taxa, there are three different possible cladograms; for four taxa, nine; but for a more typical real example with 20 taxa, there are approximately 2×10^{20} possible cladograms, which would take hundreds of hours of computing time to test.

Most biologists are unable to cope with the complex algorithms required to generate and test trees, so they use the available computer packages. During one session, a virtuoso display of seven available packages was presented by their developers. All are cheap, operate on standard microcomputers, and most are extremely user-friendly. The computing power of some of the new versions also appears to be awesome, and their speed of operation was a major item during the sales pitches. A key development that became clear at the meeting was the focus in the new packages on testing the quality and the accuracy of the trees generated.

The quality of a tree may be assessed by several measures, the most popular of which is the consistency index (CI), the ratio between the minimum number of steps required to produce a fully homologous tree, and the actual number. It is inevitable, from this definition, that the CI declines as more taxa and more characters are added to an analysis, as James W. Archie (California State University, Long Beach) noted²⁻⁵. Indeed, George Klassen and colleagues (University of Toronto) showed how random data could be used to generate trees with respectable CIs. New measures of tree quality have been proposed that avoid the problems of scale.

The accuracy of a tree is harder to assess. What is required is some measure akin to a statistical confidence measure. Problems have arisen in the past because the accuracy

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of trees has not been assessed. For example, a molecular tree of all living things⁶ produced by K.G. Field (Oregon State University, Corvallis) proved highly controversial since the tree turned out to be supported at a confidence level of only about 50%. Additional data presented at the meeting raised the confidence level to 57% or 81%, depending on the tree-making algorithms used. One technique for confidence estimation that is gaining ground is bootstrapping, a non-parametric resampling method, entertainingly explained by Norman Gilinsky (Virginia Polytechnic Institute and State University, Blacksburg). Random samples of the whole data matrix are extracted, and trees are reconstructed on the basis of these subsets of data. The resampling may be repeated many times – 1000 times may be typical – and the

proportion of those bootstrapped trees that reproduces each branching point on the master tree may be noted. Values of over 95% are taken as representing an acceptable measure of confidence that any particular part of a tree, or a whole tree, is the most accurate tree available, *based on the existing data*.

It became clear at the meeting that evolutionary biologists should base their hypothesis testing on independently derived phylogenetic trees. It is also clear that the theory and technology of tree making are advancing rapidly, and that all biologists should appreciate the possibilities and the problems. As Stephen J. Gould (Harvard University) noted in his plenary address, phylogenetic trees are representations of contingencies, or sets of historical accidents, but should not therefore be eschewed as unscien-

tific. They are the keys to determining why life is as it is, so diverse in numbers and in activities. The crucial thing is to attempt to find which is the correct tree out of the many possible ones – the one that tells us what actually happened.

Acknowledgements

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Conservation of Biodiversity: A Southeast Asian Perspective

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THE TROPICAL RAIN FORESTS of Southeast Asia are among the greatest reservoirs of terrestrial biodiversity. For example, a 50 ha plot in Pasoh Forest Reserve in Malaysia is known to contain 820 species of trees. Within one particular area of just 100 m by 100 m, there are 210 species represented among the 500 trees. These data were presented by K.M. Kochummen and his associates (Forest Research Institute, Malaysia) at the International Conference on Conservation of Tropical Biodiversity, which was held in Kuala Lumpur in June. The meeting was organized by the Malayan Nature Society (MNS) and the Ministry of Science, Technology and Environment of the Government of Malaysia, and sponsored by, among others, the US National Science Foundation, to celebrate the 50th anniversary of MNS.

The purpose of the meeting was to review the conservation status of the unique biological resources of the

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region, particularly in relation to development and sustainable management. Ironically, in the still heavily forested countries of Malaysia and Indonesia, it is often forest management practices that pose a major threat to biodiversity. Often, for every log harvested, dozens of other trees, small and large, are destroyed (Illar Muul of Integrated Conservation Research, USA). Overharvesting is another problem (see Box 1). As D. Poore (Inverness-shire, UK) pointed out, a recent study by the International Timber Trade Organization (ITTO) suggests that in Sarawak a reduction in timber harvesting from the current 12 million m³ per year to 6 million m³ per year would be required for the forests to attain a level of sustained yield. The ITTO study could not identify any country in Southeast Asia that is sustainably managing its rain forest. According to Poore, the conditions for sustained management of tropical forests include long-term stability of logging concessions, control over logging practices, an appropriate financial environment to ensure reasonable profit, and adequate scientific information to establish management policies; yet these conditions exist for few, if any,

sites. Therefore, it is not surprising that the complex forests of the region are being degraded into secondary forests or being converted into monocultures of rubber, oil palm and other forest and agricultural crops, with a concomitant decline in biodiversity.

The squandering of biotic resources is not confined to forest products. Pisit na Patalung (Wildlife Fund Thailand, Bangkok) provided several examples from Thailand that epitomize the conflict between development and conservation, and among different branches of the government. Thailand earns approximately two million dollars annually from export of snakes, but spends many times more to control the rodent populations that are partially regulated by snake predators. Other speakers documented the decline in populations of beautiful montane rhododendrons, economically important rattans, vines, and the strange *Rafflesia* plants¹ that bear the world's largest flowers.

The highlight of the meeting, however, was not the pessimism about the decline in biodiversity or the misuse of forest resources, but the cautious optimism expressed by many speakers about the future of conservation in the area. Although the natural forests are being logged or converted for other land uses at an alarming rate, a relatively large area is being reserved as state or national parks.

In Thailand, where a complete ban on commercial logging was imposed