

between metastable amorphous phases. The consequences extend further, as Mishima, Calvert and Whalley point out: other solids, which melt with a decrease of volume (like germanium, silicon and boron nitride), might exhibit several amorphous structures, some of them possibly resulting from 'melting' under pressure at low temperature.

Water vapour in the outer reaches of the Solar System that is condensed as amorphous ice and small bodies, like the particles in the rings of Saturn, the nuclei of comets and small icy satellites, may still contain a large proportion of (presumably) low-density amorphous ice (Smoluchowski, *R. Science* **222**, 161; 1983). Meteoritic impacts on the surface of icy bodies may also form amorphous ices by direct amorphization due to the shock, reversion of shock-produced high-pressure phases, or

recondensation of vapourized water. It has been suggested that the heat evolved during the transition from amorphous ice to cubic ice I at 153 K provides the supplement of energy needed to melt and resurface Saturn's satellites Enceladus and Dion (Klinger, *J. Nature* **299**, 41; 1982) and alters the heat and mass balance of comets (Klinger, *J. Science* **209**, 271; 1980). As pointed out by Mishima *et al.*, we now have to take into consideration the possibility that low-density amorphous ice might transform into dense amorphous ice during accretion of the larger icy satellites (like Ganymede, Callisto or Titan) and then retransform exothermally into a variety of amorphous structures as the temperature increases inside the planet. □

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Evolutionary biology

A new phylogeny for Darwin's Galapagos finches

from Paul H. Harvey

EVOLUTIONARY biologists owe it to the memory of Charles Darwin to produce a phylogeny of his famous Galápagos finches. Schluter has produced one such phylogeny in a recent paper¹; more importantly, he constructs it using a new method which assumes that natural selection alone has caused changes in morphology among the different finch species. Darwin might have appreciated that.

There have been two previous attempts to describe the relationships among the various finch species. The first, by Lack², was a qualitative assessment based on comparative morphology. The second, by Yang and Patton³, used electrophoretic variation of proteins. Differences between the two estimates may result both from the different databases used and the failure to base the analyses on suitable models of evolutionary change.

The justification for Schluter's new analysis comes from recent ecological studies on Darwin's finches by Grant and his colleagues^{4,5,6}. Their work leads to the conclusion that morphological variation among the finches is largely the result of differentiation by natural selection. But genetic constraints must also be taken into account if an evolutionary tree is to be derived on the assumption that differences between species are purely a result of natural selection. Genetic variances and covariances among the characters used in the analysis are the two relevant genetic constraints⁷. If genetic variances are high then characters are more susceptible to change by natural selection. If two characters covary positively then more selection is required to increase one and decrease the other than if the genetic

covariance were to be negative. Lande⁸ produced a quantitative genetic model that takes these factors into account and Schluter has adapted the model in order to estimate the total net force of natural selection that has led to differentiation among Darwin's finches. His analysis is based on phenotypic variances and covariances among eight measures of wing, tarsus and mandible size. The variances and covariances among the characters are similar within ground finches and within tree finches but differ between the two groups, so analyses were performed separately.

Phenotypic measures do not necessarily reflect underlying genetic trends but, fortunately, it appears that they do in the case of Darwin's finches. A recent genetic analysis of variation in the tree finch *Geospiza fortis*, which investigates five of the eight characters used by Schluter, shows that the five phenotypic and genetic variances correlate with a value of 0.98, while the ten covariances have a 0.99 correlation⁹. This allowed Schluter to substitute phenotypic estimates for the genetic variances and covariances.

Schluter includes the warbler finch *Certhidea olivacea* in both the ground finch and the tree

finch analyses because this species probably branches off prior to the division of the two groups; its omission from the calculations does not change either of the phylogenetic trees. Like Lack before him, Schluter incorporates data from Cocos Island's putative warbler finch *Pinaroloxias inornata*.

The new evolutionary trees, shown in the figure, are similar to Lack's, but there are some differences; the ground finches *Geospiza difficilis* and *G. scandens* appear more closely related than in Lack's analysis, while the tree finches *Camarhynchus pallidus* and *C. heliobates* come close to the ancestral condition according to Schluter, yet are highly modified forms according to Lack. Yang and Patton's electrophoretic analysis resulted in a tree similar to Schluter's, although it is based on only eleven of the fourteen species used by Schluter and Lack.

The new method differs from standard cladistic techniques¹⁰ in measuring branch lengths of the phylogenetic trees, while quantitative variation in the original characters is more effectively incorporated into the analysis. Equally important is the use of distance measures which are based on an explicit genetic model, many of the assumptions of which seem reasonable in the present case. □

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