

available within halite crystals, may affect the dynamics of the dislocation mode of deformation.

The findings go a long way towards explaining apparent inconsistencies (based on current ideas) in salt deformation at different depths and in different areas of some salt basins. They may also explain unusual phenomena such as the marked increase in flow rate during the wet season of the rock salt under normal temperature and pressure at the surface in the emergent Hormuz salt diapirs of Iran, and also the Joffé effect, in which a halite crystal exhibits a marked increase in ductility when deformed under fresh water⁶.

Plainly, the results obtained so far demand that attention is paid to the amount and distribution of inherent brine in the rock salt members of evaporite sequences in any basin, to make an effective analysis of the causes and results of plastic deformation. The message that low-stress conditions acting over long periods can produce significant plastic deformation in salt rock will have a considerable impact on our ideas about salt deformation in general. □

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Phylogeny

The German 'ostrich' and the molecular clock

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ONE of the major problems with molecular clocks is that they need to be located in an absolute time frame determined by the fossil record. Undoubtedly the best such clock available at the moment is the DNA-DNA hybridization clock of Sibley and Ahlquist¹, but Peter Houde on page 563 of this issue² argues that the DNA-DNA clock needs to be reset.

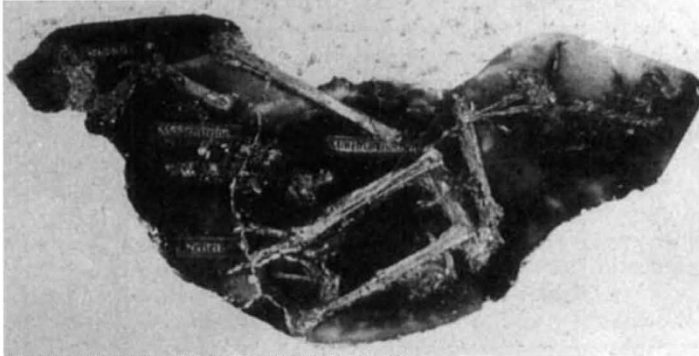
This molecular clock takes as one of its reference points the divergence of ostrich DNA from rhea DNA. This divergence has been timed from the break-up of the super-continent Gondwanaland which isolated the supposedly already ground-dwelling ratites (ostrich, rhea, emu, cassowaries and kiwi) on the different parts of the fragmenting supercontinent during the late Mesozoic. The palaeontological basis for such a reference point has always been weak as fossils ascribable to the modern genera of the ratites have not been

found in strata lower than the Miocene. So it is purely speculative that the ratites were grounded before the break-up of the Gondwanaland supercontinent.

The ratites are a rather odd assemblage of ground-dwelling birds confined to the southern continents and with a basic overall similarity due to their adoption of a flightless condition. What separates them from most other birds, even some which have become flightless, is the relatively primitive, reptilian (palaeognathous) structure of the palate and the presence of rhamphothecal grooves in the mandible. The ratite palatal structure, which is shared with the tinamous (themselves poor fliers) of South and Central

America, is intermediate between the palate of archosaurian reptiles and that seen in all other birds — the neognathous condition. This 'primitive' avian palate involves a characteristic arrangement of skull bones, with comparatively large vomers and palatines, the latter being firmly united to the pterygoids producing a less flexible skull than that observed in neognathous birds.

The current consensus of palaeontological and biochemical data indicates that



Boney issues: fossil *Palaeotis weigelti*, from the Geiseltal museum, Halle.

ratites and tinamous are a monophyletic assemblage, although whether they arose from a neognathous ancestor or are primitively palaeognathous is still a matter of contention. Olson³ outlines five possibilities to account for the palaeognathous condition of these birds: (1) that they are monophyletically derived from neognathous birds; (2) that such a derivation is due to neotony; (3) that their derivation is completely separate from the neognathous birds, with the different ratites evolving from a 'proto-tinamou'; (4) some living palaeognathes are derived from a primitively palaeognathous stock, whereas others are derived from one or more neognathous stocks; and (5) all living

palaeognathes are derived from different neognathous stocks.

Houde now suggests that an assemblage of palaeognathous birds with well-developed wings and pectoral girdles — the *Linorthis*-cohort — are the direct ancestors of all living ratites and evolved distinctive features of the ratite palate and bone histology during the Palaeocene and early Eocene in Europe and North America. This confirms the third of Olson's suggestions except that according to Houde the ratites diversified from a post-tinamous rather than a pre-tinamous condition. Houde further hypothesizes that a bird that retained the power of flight at this time must have flown to New Zealand to give rise to the extant kiwis, which retain some of the primitive characteristics of *Linorthis* that have been lost by other more derived ratites.

Meanwhile in Europe the *Linorthis*-cohort gave rise to an ostrich-grade palaeognath *Palaeotis weigelti* during the middle Eocene (see figure). Thus, ostriches appear to have evolved in Europe and subsequently emigrated overland to Africa at any time from the late Eocene onwards.

If the picture envisaged by Houde is correct and flying ratite ancestors inhabited North America and Europe during the Palaeocene and Lower Eocene and gave rise to an ostrich-grade descendant in the middle Eocene in Europe, long after the break-up of Gondwanaland, then the datum on which DNA-DNA hybridization data is tied in to the fossil record is out by tens of millions of years.

What may be true for ostriches may not apply to the other ratites, and although Houde does not mention it he must hypothesize an almost world-wide distribution for his *Linorthis*-cohort to explain the distribution of the ratites, and he does suggest they must have flown to New Zealand. The lack of fossil evidence for *Linorthis et al.* in the southern continents may only be Northern Hemisphere collecting bias and misidentification of the sort which plagues avian palaeontology. How else is one to explain the presence of the presumed flightless palaeognath *Diagenornis fragilis* from the Palaeocene of Brazil? The problem of the fossil record, however, does not conflict with his critique of the DNA-DNA clock; it is clear the calibration will require further scrutiny. □

1. Sibley, C.G. & Ahlquist, J.E. in *Evolution Today, Proc. Second Int. Congr. Syst. evol. Biol.* (eds Scudder, G.G.E. & Reveal, J.L.) 301-335 (Carnegie-Mellon Univ.).

2. Houde, P. *Nature* 324, 563-565 (1986).

3. Olson, S.L. in *Avian Biology* vol. 8, 80-238 (Academic, New York, 1985).

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