

now presumably shifting to the predominance of ^{232}Th , the longest-lived of the sources. The other parameter of great importance in simple models is the temperature dependence of mantle viscosity, because this dictates the vigour of mantle convection and plate tectonics as the heat flow declines. In this approach, Earth's core has a heat flow that is strongly coupled to mantle evolution through the mantle's ability to cool and accept heat from the core.

Models of this kind are easy to construct and boringly monotonic. Furthermore, they cannot explain the widely accepted factor-of-two ratio for current Earth heat output to current radiogenic heat production. Our planet was more eventful than these simple models allow. Whereas Earth scientists have no desire to repeal the first law of thermodynamics, they are willing to challenge almost everything else. Recently, major disagreements have emerged in attempts to understand the energy budget of Earth's core, and there are still many uncertainties over how to incorporate the effects of plates, water, melting and layering into our picture of mantle circulation.

In the current debate about Earth's core, there is a contrast between low- and high-dissipation pictures of the dynamo responsible for the planet's magnetic field (P. Olson, Johns Hopkins Univ.). These respectively make different assumptions about the geometry of the magnetic fields and associated electrical currents in the core. There is much publication activity on this topic^{1–4}, but no consensus, because we don't know the full complexity of the field and currents involved. A new study⁵ invokes experimental dynamos as well as theoretical ideas, and suggests that dynamos may be less dissipative than some suppose, thereby making a dynamo easier to sustain. Uncertainties about the electrical and thermal conductivity of the core material, and its phase diagram, are also large enough to have a major effect on estimates of dissipation and convective vigour.

For decades, it has been popular to invoke Earth's solid inner core as one of the main contributors to the energy budget available to the dynamo. Latent heat and gravitational energy and buoyancy are released as the inner core grows and excludes some of the light-element components of the outer core (sulphur, oxygen and silicon, for example) from its crystalline structure. Standard evolutionary models have difficulty explaining how the inner core has existed for more than the past billion years or so, yet Earth's magnetic field has existed throughout most of geological time. There is no direct evidence on the age of the inner core, and the dynamo may operate without an inner core. Still, it would be surprising if it were a recent feature of Earth's structure. This is one of several reasons why some scientists wonder whether there is an additional energy source in the

core. A possible candidate is radioactive decay of ^{40}K . Although the amount of core radiogenic heating required may be modest compared with Earth's present total energy budget, that amount assumes increasing importance as one goes back in time because of ^{40}K 's relatively short half-life of around one billion years. It is not known whether even this modest amount of potassium in the core is assured by elemental partitioning between silicates and iron alloy at the time of core formation. Uranium is also a candidate, and additional non-radiogenic (gravitational) sources cannot be excluded.

Mantle convection driven by thermal buoyancy remains the agreed framework in which to understand plate tectonics and loss of Earth's heat. It is an unfortunate feature of simple models of convection that they can mimic many of the characteristics of plate tectonics, but cannot explain some essential features of plates. The danger of these simple pictures is that they may not provide an adequate predictive framework for how plate tectonics evolves through geological time. Some models^{6,7} suggest possible solutions, but the lack of agreement between these various approaches means that we are not close to a final resolution. Water may play a major role through its ability to lower the viscosity of the mantle and possibly the strength of plates. State-of-the-art approaches to elucidating mantle convection include ambitious attempts to describe mantle mixing and accommodate the geochemical constraints (L. Kellogg, Univ. California, Davis).

Partial melting of shallow mantle is the cause of oceanic crust formation, the relatively well-understood and dominant form of volcanism on Earth. But water and carbon dioxide have a major yet poorly understood effect on melting in the mantle (M. Hirschmann, Univ. Minnesota). We do not know the total amount of water in the mantle (although it is at least comparable to that in Earth's oceans), or the rate at which this reservoir is tapped and replenished. Nonetheless, the emergence of provocative ideas⁸ on the topic illustrate a growing willingness to tackle the central questions of Earth's interior ocean of water.

Remarkably, these seemingly disparate topics have a common thread. It seems likely that we will not understand the origin of Earth's magnetic field until we know how the mantle controls heat flow in the core. But we cannot understand the mantle side until we have a better understanding of plate tectonics. This may in turn depend on understanding Earth's water cycle. Could it be that magnetism, like life, depends on water? ■

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Entomology

Butterflies at that awkward age

Dick Vane-Wright

Beautifully preserved specimens of butterflies from the Caribbean, caught maybe in the act of egg-laying some 20 million years ago, provide welcome grist to the mill of debate about butterfly history.

Writing in *Proceedings of the Royal Society*, Hall and colleagues¹ describe a new fossil butterfly from examples preserved in amber from Dominica, on the island of Hispaniola. They have called the butterfly *Voltinia dramba*: about 20 million years old, it is the first adult butterfly to be formally described from Dominican or any other type of amber. Its discovery raises key issues about Caribbean biogeography, behavioural evolution (or lack of it), and the origin of butterflies.

The fossil is from the family Riodinidae (the metalmarks), and it belongs to a genus of nine living species now found only on the Latin American mainland (Fig. 1, overleaf). Over 1,000 species of riodinids are known from Central and South America, and in

some lowlands they form 20% of the local butterfly fauna. Yet of 300 butterfly species found in the West Indies today, only one is a riodinid, and that species is quite unrelated to the new fossil. So the first issue is how *V. dramba* reached Hispaniola.

With five known fossil examples, beautifully preserved, Hall *et al.*¹ are able to produce good evidence that one of the living species — *V. danforthi* from Mexico — is the closest relative of *V. dramba*. Given that the fossil specimens are 15–25 million years old, Hall *et al.* suggest that the best explanation for the butterfly's presence on Hispaniola is breakup of the 'proto-Greater-Antillean arc', which is postulated to have separated the Caribbean islands from Central America². They date this split, and that between *V. dramba* and

V. danforthi, at 40–50 million years ago. The implied survival time for the latter approaches an order of magnitude greater than the life-span³ of the average species, and Hall *et al.* suggest that *V. danforthi* qualifies as a ‘living fossil’. If this is correct, an implication is that the basic ecology of *Voltinia* has not changed over this huge time span.

The ecological context here is that the caterpillars of some butterfly species feed on a wide variety of flowering plants. Others are very restricted, as for example in the close relationship between white butterflies and cabbages. This suggests that groups can become locked together by accidents of history, their only option thereafter being to co-evolve⁴. Alternatively, caterpillars and their butterflies can be fickle, chopping and changing from host to host as opportunity arises or necessity dictates. In evolutionary biology we must be alert to mere story-telling, selecting suitable facts to support whatever view of events we favour. But in this case, the authors’ argument that the ecology of *Voltinia* has remained essentially the same for as long as 50 million years seems quite convincing.

Voltinia belongs to a small group of metalmarks in which the caterpillars have the unusual habit of feeding on bromeliads and orchids growing on tree trunks⁵. Both host-plant groups appear to have existed for at least 60 million years (R. Bateman, personal communication). Dominican amber is fossilized resin from an extinct leguminous tree, on which suitable host plants could have grown. Thus it does not seem surprising that a *Voltinia* would be the first adult butterfly found in amber. Moreover, all five known specimens of *V. dramba* are females. Hall *et al.*¹ make the obvious suggestion that they

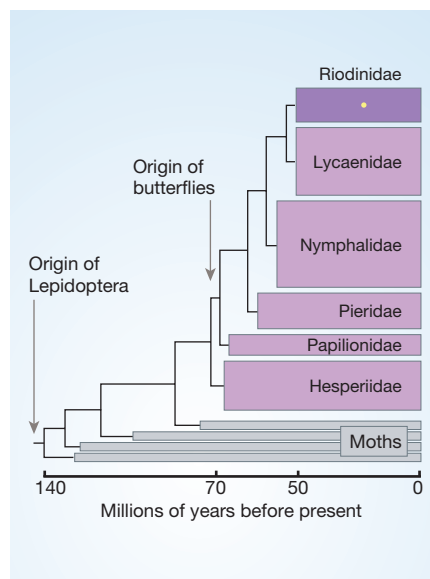


Figure 2 Relationships among the Lepidoptera — the butterflies (about 20,000 living species) and moths (ten times that number). Common names for the members of each butterfly family are metalmarks (Riodinidae); blues and coppers (Lycaenidae); admirals, heliconians, milkweeds and browns (Nymphalidae); whites and sulphurs (Pieridae); swallowtails (Papilionidae); skippers (Hesperidae). There are numerous separate lineages of moths. The *Voltinia dramba* fossils described by Hall *et al.*¹ are about 20 million years old (yellow dot). The oldest known butterfly fossil, thought to be a skipper, is 52 million years old; and the oldest known fossil of a lepidopteran associated with a flowering plant shows the track of a caterpillar that fed inside a leaf 97 million years ago. (Data from refs 1, 8, 9, 12, 13.)

became trapped in resin while laying their eggs. But given a 1:1 sex ratio, the odds against getting an all-female sample of five would seem to be only 32:1 against. As this is a single, unrepeatable sample, is this just story-telling?

Male butterflies are usually encountered more often than females, even though captive breeding⁶ almost invariably reveals a true sex ratio of 1:1. For the group of five genera to which *Voltinia* belongs⁵, the apparent sex ratio of these butterflies in The Natural History Museum collection is 1.65:1 — a seemingly small bias in favour of males. Using this figure to derive an encounter frequency of 0.375 for females, instead of 0.5, gives a probability of over 100:1 against getting a sample of five female *Voltinia* at random. Although this calculation is open to objections, it nonetheless suggests that Hall *et al.* are right

to seek a nonrandom explanation — and a remarkable 40–50-million-year behavioural stasis in egg-laying behaviour and host-plant choice seems the obvious conclusion.

Turning to butterfly origins, there are good reasons to believe that the major diversification of the Lepidoptera, the butterflies and moths, is linked to the evolution of flowering plants, currently dated at a minimum age of about 140 million years. Many modern Lepidoptera families were established by the early Tertiary⁷, 60–70 million years ago, and butterflies branch off high in the ‘crown’ of the lepidopteran evolutionary tree⁸ (Fig. 2). This suggests a possible date of about 70 million years ago for the origin of butterflies.

A persistent belief of some lepidopterists is that many higher groups of butterflies evolved in the great southern continent of Gondwana⁹. This landmass started to fragment during the middle–late Jurassic, some 175–160 million years ago, with final break-up being complete by the early Tertiary. If butterflies were much older than this, the Gondwana hypothesis would be plausible; if much younger, then it would be implausible. An age of about 70 million would be awkward for the hypothesis — neither fish nor fowl. Even so, Hall *et al.*¹ boldly state that their discovery of a 15–25-million-year-old riodinid “provides additional support for a Gondwanan origin for many of the butterfly tribes and subfamilies”. Is this really the case? And is there anything to suggest that butterflies are significantly older than 70 million years?

Within the true butterflies, the Papilionidae are the oldest group to diverge (Fig. 2). New molecular data seem to suggest that by far the largest genus in that group, *Papilio*, diverged about 55–65 million years ago¹⁰. Here again we have to beware of story-telling. Although this

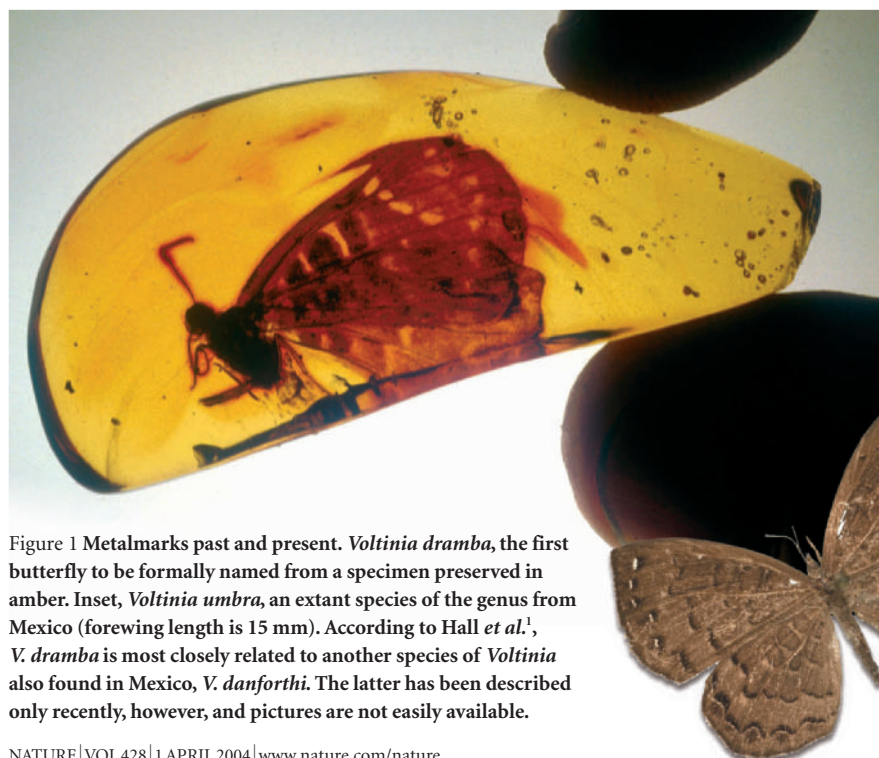


Figure 1 Metalmarks past and present. *Voltinia dramba*, the first butterfly to be formally named from a specimen preserved in amber. Inset, *Voltinia umbra*, an extant species of the genus from Mexico (forewing length is 15 mm). According to Hall *et al.*¹, *V. dramba* is most closely related to another species of *Voltinia* also found in Mexico, *V. danforthi*. The latter has been described only recently, however, and pictures are not easily available.

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figure fits well with the 70-million-year approximation, divergence times based on molecular data are usually presented as 'error-less numbers' — with proper statistical caveats added, and considered in a geological context, such estimates often appear meaningless¹¹.

Whether or not molecular data will ever give reliable dates is a moot point, but I see no existing evidence to suggest that butterflies are older than about 70 million years, and little to imply a key role for Gondwana in their diversification. Most of the higher groups are either very widespread, or restricted to a single biogeographic region or continent¹². As de Jong has wryly observed⁹: "We have no idea when the butterflies originated, although there is no shortage of wild guesses." Nonetheless, by applying their outstanding knowledge of riodinid systematics to the description of this remarkable find, Hall *et al.*¹ bring new life to the study of fossil butterflies. But their work also reminds us of many issues, both methodological and philosophical, that continue to dog the purely observational sciences. ■

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Evolutionary biology

Ferns reawakened

Torsten Eriksson

The principle of the evolutionary cul-de-sac is commonly invoked to explain the apparent lingering existence of once-diverse groups of organisms. Maybe that principle itself has had its day.

Some biological concepts keep popping up, even when they have been shown, time and again, not to be generally true. One well-known example is the 'biological species concept', the idea that only those organisms that can cross and produce fertile offspring belong to the same species. This can't generally be true for many reasons, the most obvious perhaps being that some organisms are not even sexual (such as bacteria and dandelions) and yet have species.

Schneider *et al.*¹ (page 553 of this issue) touch on another of these favourite concepts, the 'evolutionary cul-de-sac'. This is a common explanation for why some groups that show great diversity in the fossil record still exist but are greatly diminished in diversity, remaining largely unchanged — and supposedly unable to change. The new findings tell us that ferns, at least, do not belong in this category. Schneider *et al.* conclude that ferns (Fig. 1) have attained their current diversity much more recently than had been thought, and they probably did so as a response to the diversification of flowering plants.

During evolutionary history, many groups of organism have, of course, died out entirely. Plenty of others have persisted, however, even if much diminished compared with their apparent earlier diversity. Perhaps the best-known example among

land plants is the maidenhair tree (*Ginkgo*), which is the single living species of a lineage that is almost 300 million years old according to the fossil record. Horsetails (*Equisetum*) are another example: they now consist of only a handful of herbaceous species, but they belong to a lineage that was very diverse during the Carboniferous era (300 million years ago and older) and that included large



Figure 1 Ferns — diversified later than had been thought.

trees. The cycads are a further case: the 120 or so living species of palm-like seed plants are the meagre remnant of a much more diverse group that is at least 250 million years old.

There are many more examples, and in textbooks the extant members of such groups are invariably described as having remained virtually unchanged for several hundred million years. Even if it is not stated explicitly, the implication is that these poor plants were forced into an evolutionary cul-de-sac by more successful plants, or by becoming too specialized.

In this context, however, the ferns are a special case. The fossil record shows them to be an old group (one type, the leptosporangiate ferns, which contain the majority of extant ferns, is more than 250 million years old). But with more than 10,000 extant species they remain fairly numerous. It has been proposed that these species are not just an ancient remnant, but the consequence of a more recent expansion. Did the ferns diversify relatively recently? Or are they just dwindling more slowly than some other groups?

To resolve these questions, several methods and data have to be used in combination. Schneider *et al.*¹ make good use of them. First, there must be a sufficiently detailed evolutionary tree — that is, a cladogram with branch lengths — depicting relationships and distances between the relevant groups. Second, a method for estimating the age of branches in the tree has to be available. Third, appropriate fossils are necessary to calibrate the tree, and make it a 'chronogram'; that is, a direct timescale is needed. Fourth, to have confidence in the age estimates, the analysis should indicate the margin of error in the estimates. At the extremes, combining all these requirements would be expected to show the extant lineages as old (long terminal branches; Fig. 2a) or much more recently diverged (short terminal branches; Fig. 2b).

Before evolutionary trees were in use, it was hard to establish even the order of events in evolution. When 'traits', such as the occurrence of mitochondria or flowers, were placed in their most optimal position on the evolutionary trees, it became possible to determine on which branches the traits evolved (and sometimes their order). But correlation of other kinds of events, and in particular correlations between lineages, are much more difficult. Such correlations usually involve time comparisons, which are problematic because evolutionary rates are commonly different among different lineages, and a general molecular clock — that is, one based on molecular changes and ticking at a constant rate — cannot be applied. So the goal of putting absolute times on the branches of the tree of life has been hampered by the lack of methods that use a variable molecular clock. Such methods do now exist^{2–4}, and the one used by Schneider *et al.* allows both for variation in evolutionary rates and inference of the level of