dence has been published in a different context by Muller (*13*), who argued for a very similar overall pattern of development in these three groups (and therefore probably in birds and reptiles in general), with differences explained by heterochrony (differences in the relative timing of developmental events) or by fusion of adjacent skeletogenic elements. But the present report gives the developmental evidence a sharp focus that makes it a timely contribution to current debate on bird origins. It represents a different methodology in ascertaining homology from that adopted by many paleontologists, who use multiple synapomorphies. However, increasingly, vertebrate morphologists are turning to development for information on the generation of diversity in evolution.

This convincing evidence of II-III-IV wing digit identity will not be to the liking of the cladistic supporters of a dinosaur origin of birds. For them, it introduces the possibility of convergence (rather than common origin) as an explanation of the similarities between the structure of the forelimb (and, indeed, of other structures) of theropods and the wing of *Archaeopteryx*.

Doubts about homology between theropod and bird digits remind us of some of the other problems in the "dinosaur-origin" hypothesis (*11*). These include the following: (i) The much smaller theropod forelimb (relative to body size) in comparison with the *Archaeopteryx* wing. Such small limbs are not convincing as proto-wings for a ground-up origin of flight in the relatively heavy dinosaurs. (ii) The rarity in theropods of the semilunate wrist bone, known in only four species (including *Deinonychus*). Most theropods have relatively large numbers of wrist elements, difficult to homologize with those of *Archaeopteryx*. (iii) The temporal paradox that most theropod dinosaurs and in particular the birdlike dromaeosaurs are all very much later in the fossil record than *Archaeopteryx*.

In reality, there is no easy solution to this question of bird origins, and for the moment the theropod dinosaur origin holds sway. Its supporters can point to some very striking theropod similarities with *Archaeopteryx*. But many of these could be due to convergence, with the birdlike dinosaurs appearing in the Cretaceous often some 75 million years after *Archaeopteryx*. Opponents of the orthodoxy are less united, but the thecodont origin still has support (*10, 11*). The problem for this view is the long evolutionary gap, with no convincing intermediates. What we need is a proto-*Archaeopteryx* find to complement the numerous post-*Archaeopteryx* finds that are now being made (*14*). But for the time being this important developmental evidence that birds have a II-III-IV digital formula, unlike the dinosaur I-II-III, is the most important barrier to belief in the dinosaur-origin orthodoxy.

References

1. D. E. Fastovsky and D. B. Weishampel, *The Evolution and Extinction of the Dinosaurs* (Cambridge Univ. Press, 1996).
2. J. Ostrom, *Biol. J. Linn. Soc.* **8**, 91 (1976).
3. ———, in *Origins of the Higher Groups of Taxa*, H.-P. Schultze and L. Trueb, Eds. (Cornell Univ. Press, Ithaca, NY, 1991), pp. 467–484.
4. A. C. Burke and A. Feduccia, *Science* **278**, 666 (1997).
5. T. H. Huxley, *Q. J. Geol. Soc. London* **26**, 12 (1870).
6. G. Heilmann, *The Origin of Birds* (Witherby, London, 1926).
7. J. A. Gauthier, *Mem. Calif. Acad. Sci.* **8**, 1 (1986).
8. L. Martin, in (*3*), pp. 485–540.
9. M. K. Hecht and B. M. Hecht, *Acta Palaeontol. Polo.* **38**, 329 (1994).
10. S. Tarsitano, in (*3*), pp. 541–576; ——— and M. K. Hecht, *Zool. J. Linn. Soc. London* **69**, 257 (1980).
11. A. Feduccia, *The Age of Birds* (Harvard Univ. Press, Cambridge, MA, 1980); *The Origin and Evolution of Birds* (Yale Univ. Press, New Haven, CT, 1996).
12. J. R. Hinchliffe, in *The Beginnings of Birds*, M. Hecht *et al.*, Eds. (Freunde des Jura-Museum, Eichstatt, 1984).
13. G. B. Muller, in *Developmental Patterning of the Vertebrate Limb*, J. R. Hinchliffe *et al.*, Eds. (Plenum, New York, 1991), pp. 395–405; J R Hinchliffe, *ibid.*, pp. 313–323.
14. L. M. Chiappe, *Nature* **378**, 349 (1995).

ECOLOGY

Mass Extinction and Evolution

Norman Myers

On pages 689 and 692 of this issue, two reports by Hughes and his colleagues (*1*) and by Nee and May (*2*) consider aspects of the mass extinction that is now overtaking the world's biodiversity. The new results indirectly throw light on an overlooked but significant angle of the biotic crisis: its grossly disruptive impact on the future course of evolution.

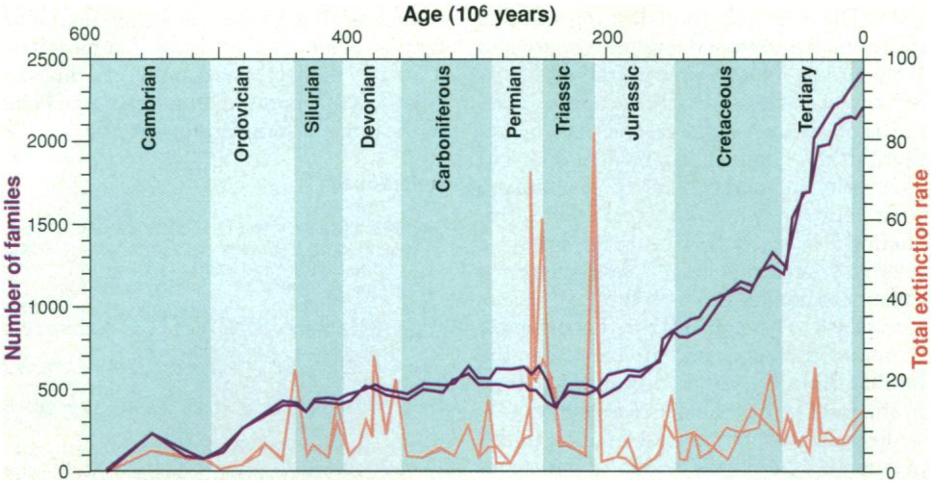
Hughes and her colleagues discuss the elimination of populations—the geographical or genetic subdivision of species—by human activity rather than the more commonly analyzed elimination of species. Indeed, populations are readily examined; whole species are not. The authors estimated global numbers of populations by evaluating diversity within species from the literature and calculated that, whereas a median estimate for the species total is 14 million, populations could well number over 3 billion. They find that in tropical forests alone, populations could be disappearing at a percentage rate three to eight times the rate for species extinctions (conservatively reckoned). This is a significant loss for the ecosystem services supplied to humankind by populations—for instance, soil generation, watershed functions, pest control, regulation of weather and climate—valued recently (*3*) at $33 trillion per year.

This raises critical questions for the foreseeable future. If we lose, say, half of all species plus 90% of the populations of surviving species, which will be more detrimental for the biggest service of all, environmental maintenance of the biosphere?

Equally significant, which will have the greater impact on future evolution? What counts is not only how many populations disappear, but also which populations disappear, with which functions. Do evolutionary processes such as speciation and origination stem largely from core populations within a species' range, or do they derive more from peripheral populations (which tend to be at greater risk through habitat loss)? In support of the second viewpoint is the notion that populations in border zones may contain greater genetic variability, because they have to adapt to environmental pressures that often arise in greatest measure among the semiforeign areas at the limit of a species' range. Or could it be that the richest resources for natural selection occur in the heartland zone, whereas natural selection pressures are greatest in the peripheries? These are vital questions (*4*) for a biosphere in extreme turmoil from human activities.

As an indication of how far a species can lose populations while still flourishing as a species, consider the case of wheat. The current crop with an expanse of more than 250 million hectares comprises at least 500 trillion individuals, probably a record. (For proportion, figure out how long a period of time is represented by 1 trillion seconds.) As a species, wheat is the opposite of endangered. But because of a protracted breeding trend toward genetic uniformity, the species has lost the great bulk of its populations and most of its genetic variability. This highlights the urgent need to conserve populations as well as species, in light of the many benefits supplied by populations but not by species.

The author is a consultant in environment and development headquartered at Upper Meadow, Old Road, Headington, Oxford OX3 8SZ, UK. E-mail: normanmyers@gn.apc.org



Extinctions in the past. Past major extinctions have produced transient dips in the proliferation of the number of families on Earth. The present human-generated mass extinction may have a more protracted outcome.

Nee and May focus on the entire tree of life in evolutionary terms, asserting that if 80% of the tree survives an extreme mass extinction like the Late Permian crash, there is little loss of "evolutionary history." True, the mass extinctions in the prehistoric past have pruned only 5 to 10% of the perhaps half billion species that have existed (see the figure). But these crash episodes can exert a strongly directional influence on subsequent evolution (*5*). Much depends of course on which species get the chop—whether clumps of species or species at random. For instance, the demise of the dinosaurs in the Late Cretaceous is a main reason why we are here to assess their fossilized remains.

The Nee and May report not only probes evolutionary history but prompts thoughts about the evolutionary future. Regrettably the latter remains a black hole of research, even though the next few decades seem set to impose a profoundly depletive hiatus on certain basic processes of evolution. A grand-scale fallout of species generally leaves homogenized biotas with generalist species in the ascendant, to the detriment of the more numerous specialist species. In contrast with the aftermath of prehistoric mass extinctions, human-dominated landscapes will encourage the generalist species to proliferate—all the more so as natural controls (predators, parasites) are preferentially eliminated. The upshot could well be a "pest and weed" ecology, with all that implies for evolutionary history.

At the same time, we are probably witnessing an end to the evolution of vertebrates larger than a few kilograms. More significant still, we are eliminating the evolutionary powerhouses of tropical forests and wetlands, these being regions that have supplied the majority of new species in the prehistoric past (*6*). This could well delay the biotic recovery by several million years beyond the "par" period of 5 million years for a postcrash phase. There is a host of such front-rank questions (*7*), yet they remain almost entirely unaddressed.

What does all this say for conservation planning? Should we continue with our overwhelming emphasis on saving as many species as we can, particularly the charismatic mega-vertebrates? Or perhaps we should try to limit future damage by safeguarding evolution's capacities for speciation, origination, and other forms of renewal. These two aims are far from congruent. The greatest evolutionary potential is manifested by invertebrates; their huge reproductive scope supplies abundant resources for natural selection to work on. Perhaps invertebrates should receive differential support from conservationists, in contrast to the whales, elephants, rhinoceroses, and the like, which, producing only a handful of offspring in a lifetime, are comparatively dead ends for speciation purposes.

Within a generation we may commit the biosphere to a grand-scale depletion that will disrupt evolution for at least 200,000 generations, or 20 times as long as humans have been a species. The number of people affected could be on the order of 500 trillion (on the basis of an average global population of 2.5 billion people), or 10,000 times more humans than have existed thus far. These are challenging times to be an evolutionary biologist. Although we are far from generating many definitive answers about future evolution, we should take a better crack at pinning down the right questions.

References

1. J. B. Hughes, G. C. Daily, P. R. Ehrlich, *Science* **278**, 689 (1997).
2. S. Nee and R. M. May, *ibid.*, p. 692.
3. R. Costanza *et al.*, *Nature* **387**, 253 (1997).
4. D. J. Futuyma, *Evolutionary Biology* (Sinauer, Sunderland, MA, 1986).
5. D. W. Jablonski, *Nature* **364**, 142 (1993).
6. ____ and D. J. Bottjer, *Science* **252**, 1831 (1991).
7. N. Myers, *Environmentalist* **16**, 37 (1996).

SEISMOLOGY

Tsunamigenic Sea-Floor Deformations

Costas Synolakis, Philip Liu, George Carrier, Harry Yeh

As important as it is for hazard mitigation, the calculation of three-dimensional tsunami inundation in real time remains a formidable undertaking. Recent advances in hydrodynamics (*1*) triggered by the availability of high-resolution field and laboratory data have demonstrated that—given reasonable initial data—the predictions of runup heights are correct to first-order, and therefore, attention has been focused on the effects of the seismic predictions of the fault parameters used for model initialization.

The National Science Foundation recently sponsored a workshop (*2*) to examine the state-of-the-art of interfacial seismology and its interface with tsunami hydrodynamics. One objective was to ascertain which quantitative features of the early sea-floor deformation can be inferred from teleseismic data, with what accuracy they are believed to be known, and the scientific basis of these inferences. Another objective was to discuss recent developments in the deployment of real-time bottom pressure recorders and seismic instrument arrays for real-time monitoring of tsunami generation, as well as the

---

C. Synolakis is in the Department of Civil and Environmental Engineering, University of Southern California, Los Angeles, CA 90089, USA. E-mail: costas@mizar.usc.edu. P. Liu is in the School of Civil and Environmental Engineering, Cornell University, Ithaca, NY 14853–3501, USA. E-mail: pll3@cornell.edu. G. Carrier is in the Department of Earth and Atmospheric Sciences, Harvard University, Cambridge, MA 20138, USA. H. Yeh is in the Department of Civil Engineering, University of Washington, Seattle, WA 98195, USA. E-mail: harryeh@u.washington.edu