League dreams of breeding players with titanium knees, they will have to make do with bones and ligaments for the foreseeable future. Constraints come in many forms, from those that limit the range of variation available for natural selection to act upon (elephants with titanium legs seem unlikely to appear) to the physical forces of fluid dynamics, gravity and the like. In 1995, Kurt Schwenk usefully divided constraints into two different classes. For one class, the constraint operates because organisms simply are unable to produce new variants, like titanium bones, that might be useful. Therefore, natural selection has no variation to use in sculpting new solutions. The second class of constraint is one where there is abundant variation, but various forces act through natural selection to limit the range of solutions. Schwenk pointed out that here constraint isn't even the right term — limitations are due to good old stabilizing selection.

Are there good examples? Take ichthyosaurs, these Triassic reptiles occupied a range of marine habitats, from estuaries and lagoons to the open ocean. The open ocean forms look for all the world like a tuna, until one gets up close and personal. This is because both ichthyosaurs and tuna played the same role in life: fast open ocean predators. The forces of fluid dynamics are the same in each case, and a narrow, streamlined body form with a powerful tail fin is the optimal engineering solution.

Do constraints only operate on form? Hardly. Biologists have documented constraints in morphology for years, but some of these may reflect the underlying potential of genetic and developmental regulatory systems. Arthropods, for instance, have segmented bodies, and this modular construction is thought to have played a major role in their success. But anatomical modularity reflects modularity in development, in this case of Hox genes and other developmental regulators.

Is a new theory of evolution in the offing? Almost certainly. Not a replacement for Darwin, nor a repudiation of the Modern Synthesis of the past 60 years; but an expansion that will include a more prominent role for the developmental genetics of evo-devo — in contrast to the transmission genetics of the Modern Synthesis. It will also include a greater appreciation for interesting biases in the generation of variation and possibly a role for a more hierarchical view of evolution as championed by Gould.

Are contingency and convergence opposing views of how evolution operates? One hopes not, as both have clearly been important in the history of life. As is so often the case in evolutionary biology, this is an issue of relative frequency, not absolute possibility. Chance can limit which groups are around to evolve, where they live, and even the range of future morphological possibilities. Convergence often reflects limited engineering solutions to particular problems, but does not predict that particular groups are likely to survive over the long-term. And convergence has little to do with many aspects of evolution where selection, genetic drift and chance are free to come up with the remarkable diversity of butterfly wing patterns, arthropod legs or the colors on seashells.

Where can I find out more?

Donley, J.M., Sepulveda, C.A., Konstantinidis, P., Gemballa, S., and Shadwick, R.E. (2004). Convergent evolution in mechanical design of lamnid sharks and tunas. Nature *429*, 61–65.

Gillespie, R. (2004). Community assembly through adaptive radiation in Hawaiian spiders. Science *303*, 356–359.

Losos, J.B., Jackman, T.R., Larson, A., de Queiroz, K., and Rodriguez-Schettino, L. (1998). Contingency and determinism in replicated adaptive radiations of island lizards. Science *279*, 21115–22118.

Schwenk, K. (1994/95). A utilitarian approach to evolutionary constraint. Zoology *98*, 251–262.

Wagner, P. W. and Erwin, D. H. (2006) Patterns of convergence in general shell form among Paleozoic gastropods. Paleobiology *32*, 315–336.

Department of Paleobiology, MRC-121, Smithsonian Institution, Washington, DC., 20013-7012, USA, and Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501, USA.
E-mail: erwind@si.edu

Evolutionary convergence

Simon Conway Morris

What is convergence? Consider your eye and that of an octopus. Both are built based on the camera principle, yet you are closely related to a starfish while the octopus is a near cousin of the oyster. The common ancestor of you and the octopus lived about 550 million years ago and at most possessed a simple eye-spot. Regarding the eyes, vertebrates and molluscs have arrived at the same solution, and in doing so have solved equally successfully problems such as how to correct spherical aberration. Camera-eyes are a brilliant evolutionary invention, and so it is less surprising that they convergently emerged in at least five other groups, including cubozoan jellyfish. And here is something else these groups have in common: with the exception of some snails that are 'landscape artists' (well, they are adept at spotting routes to safety on salt-marshes), all are fast-moving, predators and show an interesting tendency towards intelligence.

But aren't all camera-eyes built using the famous Pax-6 gene? Indeed, but so are compound eyes and they evolved independently at least four times. Pax-6 was almost certainly recruited from a more primitive role in the development of anterior sensory fields. That explains why this gene is also expressed in the nose and brain, as well as salivary glands. Remember also that nematodes lack eyes, but they possess Pax-6. To insist that a gene like Pax-6 'makes' an eye is an over-simplification: necessary but not sufficient.

Isn't convergence obvious? Tell that to the famous Victorian naturalist Henry Bates. In the Amazon, he was hunting hummingbirds and — extensive as his knowledge was — he routinely shot sphinx moths by mistake. Local people insisted that moth could transmute into bird; silly but understandable because the convergence is remarkable not only in terms of body shape and flight dynamics, but even in their similar energy budgets.

Did you say 'remarkable'? Odd isn't it, but almost invariably when biologists describe convergence the words they use are: 'striking', 'astonishing', 'stunning', 'uncanny', and, yes, 'surprising'. Why? Surely we all agree that the organisms must function, that physical laws apply, and that adaptation is real. Moreover, convergence is ubiquitous but it can be difficult to see the wood for the trees — oh yes, they are convergent, too. In these atomistic, reductionist and specialized times it is easy to forget that organisms — and cells — are functionally integrated. Look at the lamnid shark and tuna. Similar body shape, specialized muscle-tendon system and even warm bloodedness provide a wonderful example of convergence. The similarities are far more than skin-deep.

Do you ever see examples of molecular convergence? In principle, one shouldn't. Given the size of a typical protein and the 20 available amino acids the number of alternatives is more than astronomic. Nevertheless, molecular convergence is probably far more common than realized. Consider that chemically intractable molecule carbon dioxide, stable and with strong ionic bonds but the management of which is central to biological processes such as photosynthesis, biomineralization, and respiration. The key enzyme in CO_2 metabolism is a metalloprotein, carbonic anhydrase. Evolved once, twice? No — at least five times independently. And that is modest when compared to C4 photosynthesis, which has arisen at least 30 times.

Do extraterrestrials see with camera-eyes and breathe using carbonic anhydrase? Almost certainly; they are the obvious solutions. Evolutionary convergence allows us to predict what, one day, we might encounter. Not only in terms of eyes, but other sensory systems such as echolocation which has evolved independently at least three times — in bats, whales and birds. So too, in terms of social systems, think of the colossal convergence between elephants and sperm whales. Then there is eusociality, a system that has evolved repeatedly in insects and moreover in shrimps and even mammals, in the case of the naked mole rats. The mole rat is one of the very few examples in biology where a system was predicted before it was actually recognized. So, our planet may actually provide a very good guide to alien biospheres. Even if the planetary environment is very different, say a very dense atmosphere or giant oceans, we can still make a good estimate of what one day we may find. Not only that, but convergence tells us aliens will even think in much the same way.

Now you are joking! Neo-Darwinians typically assume human-like intelligence is an evolutionary fluke, a historical accident. If correct, then the Search for Extraterrestrial Intelligence (SETI) is a complete waste of time. But what we see on this planet tells us otherwise. All the evidence suggests the cognitive world of dolphins is remarkably similar to that of the the great apes. Certainly, both are mammals, but chimps don't live in oceans and the brain structures are markedly different. Even more remarkable is the cognitive architecture of birds, especially crows. Again it maps closely against the mind of the great apes but their brain is now known to be built to a completely different plan. When it comes to tool use the New Caledonian crows are well ahead of chimps. And the convergences don't stop there: warm-bloodedness and singing are convergent with mammals. So is social play. Did you know crows enjoy skiing? And what about the New Zealand parrot known as the kea? Watch out for those delinquent gangs of teenage birds as they roam around trashing cars.

Are we on the threshold of a general theory of evolution? Maybe.

Why does convergence matter? It shows adaptation is real, and not some Darwinian conspiracy. It insists that organisms are functionally integrated and not a heap of character states. Paradoxically, the very similarities seen in convergence are some of the best proofs of evolution. Next time you are cornered by a pair of creationists order them a stiff gin and tonic and then ask him why the position of the retina is opposite in our eye to that of octopus (clue: embryology), and ask her why the bacterial flagellar motor has evolved at least twice. Then when they are sobering up remind them that the way in which *Drosophila* reacts to ethanol is remarkably similar in terms of behaviour to the manner in which we get drunk. Please raise a glass to convergence.

Where can I find out more?

Bardy, S.L., Ng, S.Y.M., and Jarrell, K.F. (2003). Prokaryotic motility structures. Microbiol. *149*, 295–304.
Conway Morris, S. (2003). Life's solution: Inevitable humans in a lonely universe (Cambridge: Cambridge University Press).
Diamond, J., and Bond, A.S. (2003). A comparative analysis of social play in birds. Behav. *140*, 1091–1115.
Donley, J.M., Sepulveda, C.A., Konstantinidis, P., Gemballa, S., and Shadwick, R.E. (2004). Convergent evolution in mechanical design of lamnid sharks and tunas. Nature *429*, 61–65.
Emery, N.J., and Clayton, N.S. (2004). The mentality of crows: Convergent evolution of intelligence in corvids and apes. Science *306*, 1903–1907.
Jagger, W.S., and Sands, P.J. (1999). A wide-angle gradient index optical model of the crystalline lens and eye of octopus. Vision Res. *39*, 2841–2852.
Nilsson, D.E., Gislén, L., Coates, M.M., Skogh, C., and Garm, A. (2005). Advanced optics in a jellyfish eye. Nature *435*, 201–205.
So, A.K.-C., and Espie, G.S. (2005). Cyanobacterial carbonic anhydrases. Can. J. Bot. *83*, 721–734.
Weilgart, L., Whitehead, H., and Payne, K. (1996). A colossal convergence. Am. Sci. *84*, 278–287.
Weinreich, D.M., Delaney, N.F., DePristo, M.A., and Hartl, D.L. (2006). Darwinian evolution can follow only very few mutational paths to fitter proteins. Science *312*, 111–114.

Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge, CB2 3EQ, UK.
E-mail: sc113@esc.cam.ac.uk