parasites, predators and prey. This is knowledge gained largely the old-fashioned way, with muddy boots, muddy hands and dissecting microscopes. With the seductions of the impressive technological advances in biology, is there a danger that such fundamental skills could be lost [24]? As Glasse's apocryphal 1747 recipe for roasted hare begins, 'first, catch your hare' [25].

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References

1 Elton, C.S. (1958) *Ecology of Invasions by Animals and Plants.* Methuen & Co.
2 Odum, E.P. (1953) *Fundamentals of Ecology.* Saunders
3 McCann, K.S. (2000) The diversity–stability debate. *Nature* 405, 228–233
4 Price, P.W. (1980) Introduction. In *Evolutionary Biology of Parasites*, pp. 3–14, Princeton University Press
5 Cohen, J.E. *et al.* (1993) Improving food webs. *Ecology* 74, 252–258
6 Marcogliese, D.J. and Cone, D.K. (1997) Food webs: a plea for parasites. *Trends Ecol. Evol.* 12, 320–325
7 Huxham, M. and Raffaelli, D. (1995) Parasites and food-web patterns. *J. Anim. Ecol.* 64, 168–176
8 Memmott, J. *et al.* (2000) Predators, parasitoids and pathogens: species richness, trophic generality and body sizes in a natural food web. *J. Anim. Ecol.* 69, 1–15
9 Marcogliese, D.J. (2002) Food webs and the transmission of parasites to marine fish. *Parasitology* 124, S83–S99
10 Thompson, R.M. *et al.* (2005) Importance of parasites and their life cycle characteristics in determining the structure of a large marine food web. *J. Anim. Ecol.* 74, 77–85
11 Cohen, J.E. *et al.* (1990) Stochastic structure and nonlinear dynamics of food webs – qualitative stability in a Lotka–Volterra cascade model. *Proc. R. Soc. London B-Biol. Sci.* 240, 607–627
12 Polis, G.A. (1991) Complex trophic interactions in deserts – an empirical critique of food-web theory. *Am. Nat.* 138, 123–155
13 Lafferty, K.D. *et al.* (2006) Parasites dominate food web links. *Proc. Natl. Acad. Sci. U. S. A.* 103, 11211–11216
14 Lafferty, K.D. *et al.* (2006) Food webs and parasites in a salt marsh ecosystem. In *Disease Ecology: Community Structure and Pathogen Dynamics* (Collinge, S.K. and Ray, C., eds), pp. 119–134, Oxford University Press
15 Dunne, J.A. (2006) The network structure of food webs. In *Ecological Networks: Linking Structure to Dynamics in Food Webs* (Pascual, M. and Dunne, J.A., eds), pp. 27–86, Oxford University Press
16 Hudson, P.J. (2005) Parasites, diversity and the ecosystem. In *Parasitism and Ecosystems* (Thomas, F. *et al.*, eds), pp. 1–12, Oxford University Press
17 Moore, J. (2002) *Parasites and the Behavior of Animals.* Oxford University Press
18 Hudson, P.J. *et al.* (1998) Prevention of population cycles by parasite removal. *Science* 282, 2256–2258
19 Dobson, A.P. *et al.* (2006) Parasites and food webs. In *Ecological Networks: Linking Structure to Dynamics in Food Webs* (Pascual, M. and Dunne, J.A., eds), pp. 119–135, Oxford University Press
20 Hudson, P.J. *et al.* (2006) Is a healthy ecosystem one that is rich in parasites? *Trends Ecol. Evol.* 21, 381–385
21 Anderson, R.M. and May, R.M. (1978) Regulation and stability of host–parasite population interactions: 1. Regulatory processes. *J. Anim. Ecol.* 47, 219–247
22 May, R.M. and Anderson, R.M. (1978) Regulation and stability of host–parasite population interactions: 2. Destabilising processes. *J. Anim. Ecol.* 47, 249–267
23 Besansky, N.J. *et al.* (2003) DNA barcoding of parasites and invertebrate disease vectors: what you don't know can hurt you. *Trends Parasitol.* 19, 545–546
24 Barnish, G. *et al.* (2006) Parasitologists lost? *Trends Parasitol.* 22, 454–455
25 Glasse, H. (2004) *First Catch Your Hare: the Art of Cookery Made Plain and Easy.* Prospect Books
26 Kuris, A.M. (1990) Guild structure of larval trematodes in molluscan hosts: prevalence, dominance and significance of competition. In *Parasite Communities: Patterns and Processes* (Esch, G.W. *et al.*, eds), pp. 69–100, Chapman & Hall

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Letters

Evolution of parasitic life in the ocean

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Parasitism is one of the most successful modes of life [1]. In fact, the diversity of parasitic life in the oceans and on land exceeds that of non-parasitic life [2,3], and all organisms are susceptible to parasitic infection during at least one phase of their life [4].

The evolution of host–parasite diversity and the search for identifiable mechanisms responsible for patterns of infection are issues that are of considerable importance; they can help to interpret the exponential growth in the amount of information concerning parasite diversity, parasite and host phylogeny, and species interactions. Marine parasitology, however, has the additional complication that many systems, such as the central oceans and the deep sea, are difficult to access; hence, many marine organisms have never been studied for parasite infection. Particularly for heteroxenous parasites (those that use more than one host to complete their life cycle), researchers are still searching for model taxa in which larval and adult distribution patterns give insight into the evolutionary processes that are involved in species diversification. This letter focuses on the concept of cumulative evolution, which is the process by which parasites continuously diversify to inhabit a wider range of host species. Generalists (parasites with low host-specificity) are the driving force behind cumulative evolution, and Trypanorhynch cestodes, an ancient group of tapeworms, are used as an example in the case of parasites of marine fish.

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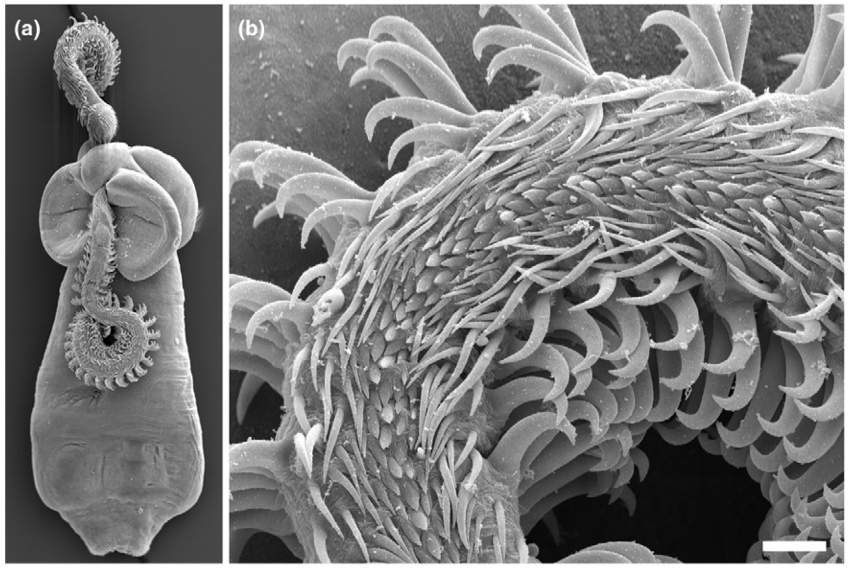

Figure 1. Images of the trypanorhynch *Grillotiella exile*. **(a)** Scolex of *G. exile* from Indonesia, with two bothria and armed tentacles (worm length = 0.8 mm). This species has been recorded from the tiger shark (*Galeocerdo cuvier*) and infests the gills of the narrow-barred Spanish mackerel (*Scomberomorus commerson*) as its intermediate host. **(b)** Tentacular armature of *G. exile* from Indonesia (scale bar = 10 μm). The arrangement of the tentacular hooks is species specific. Adults and larvae have the same armature patterns, which enables species identification.

With at least two or three species per host [2], parasites of fish are extremely diverse. Estimates indicate that there are ~100 000 species of protozoan and metazoan parasites of marine fish [5] in a total of 29 400 fish species (http://www.fishbase.org). Host–parasite infestation lists give more-detailed figures; for example, there are 3.1 metazoan parasites per fish species in German coastal waters [6], and a worldwide average of 1.5 metazoan parasites per fish species in the deep sea [7]. However, there is still a large number of free ecological niches that might be used by parasites, and these niches will enable more species of parasite to infect marine fish in the future [8]. The fundamental issue remains as to how this huge marine-parasite diversity is developing, and the search continues for the driving forces in marine-parasite evolution.

In theory, complex helminth-parasite life cycles evolved either by the addition of a new host after the existing definitive host, which would subsequently become an intermediate host (upward incorporation), or by the addition of a new host before the definitive host (downward incorporation) [9]. Because helminth life cycles often include three or, at most, four hosts, many incorporation events must have occurred a long time ago in evolutionary terms [9]. The involvement of further host species at a particular stage in the helminth life cycle (lateral incorporation [9]) depends on niche overlap between the existing and the new host (e.g. through the food web) and is supported by the presence of generalist parasites. A successful mutant that survives in an additional host can spread and become established. Although lateral incorporation does not extend the life cycle of helminths despite increasing the number of hosts, it is responsible for the wide variety of helminth life cycles. Consequently, it adds to the pool of helminth species that infect fish, thus contributing to the mixture of specific and nonspecific parasites.

Modelling is one way to identify possible reasons for generalism or specialism in parasites [10]; however, all models need to be verified using real host–parasite systems. Trypanorhynch cestodes (Figure 1) are an ancient group of marine tapeworms that have three or four hosts in their life cycle. Invertebrates and teleosts serve as intermediate hosts, and elasmobranchs serve as final hosts. Approximately 260 species have been identified from the 1000 elasmobranchs, and more species are discovered each year. A new classification of trypanorhynchs, which involved the analysis of 3945 host records worldwide, revealed that, although these cestodes are highly diverse, many seem to have a restricted phylogenetic and ecological specificity for the intermediate and final host [11]. It was suggested that generalism is advantageous for successful metazoan parasites of fish to explore new host species and habitats [11]. This idea supports the concept of lateral incorporation [9] but contradicts the assumption that other marine cestodes, especially those that infest the elasmobranchs (which have a long evolutionary lineage), are considered to be host specific and well adapted to their final host.

High parasite diversity in marine fish could be the result of a process of cumulative evolution of parasitic life forms [11]. Assuming that the ocean is a stable environment at an evolutionary scale, numbers of potential host species within a specific taxon are stable or can increase or decrease. All successful parasite taxa have diversified into groups that follow similar long (e.g. upward incorporation) but altered life cycles (see earlier). With successful infection after the discovery of a new suitable host, and assuming that the evolution of the parasite follows that of its host, the number of parasite species within each successful taxon will increase under stable, increased or decreased (shrinking but not becoming extinct) scenarios of host species number. This, therefore, results in a continual increase in total parasite species number and an increase in parasite:host ratio. Although upward and downward incorporation [11] led to different life cycles and parasitic taxa in the oceans, lateral incorporation by originally generalistic parasites, followed by further specialization [12] according to their principal life cycle, is responsible for the huge diversity of parasites of marine fish. This can also explain the coexistence of generalist and specialist parasites within the same taxon. The costs of generalism, in terms of infecting false hosts (one in which the parasite is unable to survive) or casual hosts (one in which the parasite is unable to complete its life cycle) [12], or being outcompeted by specialist parasites, are sufficiently small (even for larger taxa of parasites that infect marine fish) to maintain generalism over evolutionary time. Established generalists can be considered to be the driving force behind the evolution of parasite-species diversity.

An accurate estimate of the increasing number of parasite species will be difficult to determine because the ratio of generalists and specialists is different in each parasite taxon [11]. In addition, after the infection of a new host group, parasites might encounter certain problems that prevent further species radiation or development; for example, new invaders often face competition from established parasites. Various other factors influence the host–parasite relationship, such as the parasite causing disease or the host species facing extinction. However, negative effects are usually moderate and, in fact, most parasites do not cause severe pathology (with multiple infections being common), thus enabling both parasite and host to survive. This balanced relationship has enabled species of parasite that infect marine fish to diversify and increase in number, and these characteristics underlie the concept of cumulative parasite evolution.

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References

1 Poulin, R. and Morand, S. (2000) The diversity of parasites. *Q. Rev. Biol.* 75, 277–293
2 Hardy, A. (1959) *The Open Sea: its Natural History Pt II; Fish and Fisheries.* Houghton Mifflin
3 Price, P.W. (1980) *Evolutionary Biology of Parasites.* Princeton University Press
4 Marcogliese, D.J. and Price, J. (1997) The paradox of parasites. *Global Biodiversity* 7, 7–15
5 Rohde, K. (2002) Ecology and biogeography of marine parasites. *Adv. Mar. Biol.* 43, 1–86
6 Palm, H.W. *et al.* (1999) Checklist of metazoan fish parasites of German coastal waters. *Ber. Inst. Meereskd. Kiel* 307, 1–148
7 Klimpel, S. *et al.* (2001) *Deep-water Metazoan Fish Parasites of the World.* Logos-Verlag
8 Rohde, K. (1998) Is there a fixed number of niches for endoparasites of fish? *Int. J. Parasitol.* 28, 1861–1865
9 Parker, G.A. *et al.* (2003) Evolution of complex life cycle in helminth parasites. *Nature* 425, 480–484
10 Frank, S.A. (1993) Evolution of host–parasite diversity. *Evolution* 47, 1721–1732
11 Palm, H.W. (2004) *The Trypanorhyncha Diesing, 1863.* PKSPL-IPB Press
12 Odening, K. (1976) Conception and terminology of hosts in parasitology. *Adv. Parasitol.* 14, 1–93

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Implications of findings of bibliometric analyses in parasitology

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Although outweighed by chronic conditions such as heart disease, stroke, cancer and diabetes in developed countries, parasitic and tropical diseases remain a major burden of disease and overwhelm medical services and economic resources in developing nations. This is an ongoing problem, despite the success of some programs to reduce the incidence of parasitic diseases such as onchocerciasis [1] in Africa, dracunculosis [2] in Africa and Asia and the global effort for elimination of lymphatic filariasis.

Implications of findings of bibliometric studies in parasitology

Several bibliometric analyses in the fields of parasitology and tropical medicine have been published [3–6], including a study of the origin of 18 110 publications in parasitology between 1995 and 2003. Western Europe, USA, and Latin America and the Caribbean produced 34.8%, 19.9%, and 17.2% of the articles, respectively [3], and both Latin America and the Caribbean and Asia doubled their production of publications during the study period. Interestingly, Oceania ranked first in research productivity in parasitology when adjustments for both the gross national income per capita and population were made. It should be acknowledged that adjustments for spending on health-related research would be more satisfactory but accurate data on this important index are not available for many countries.

The most important finding of this analysis, however, is that both absolute (5.3%) and relative research productivity in parasitology in Africa is low, although it is higher

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