Correlated Evolution and Dietary Change in Fossil Stickleback

Mark A. Purnell,[1]* Michael A. Bell,[2] David C. Baines,[1] Paul J. B. Hart,[3] Matthew P. Travis[2]

Models, experiments, and field studies provide evidence of the ecological controls on evolution, but extrapolating results over longer time scales is a perennial problem in evolutionary biology. Trophic ecology and competition for food, for example, are thought to drive speciation through niche differentiation, character displacement, and phenotypic divergence (*1*). Yet direct evidence that feeding controls evolution over extended time scales, available only from the fossil record, is difficult to obtain because it is rarely possible to directly analyze dietary change in long-dead animals. Functional changes must be inferred from changes in morphology, and attempts to determine whether morphological changes were caused by shifts in feeding can become circular.

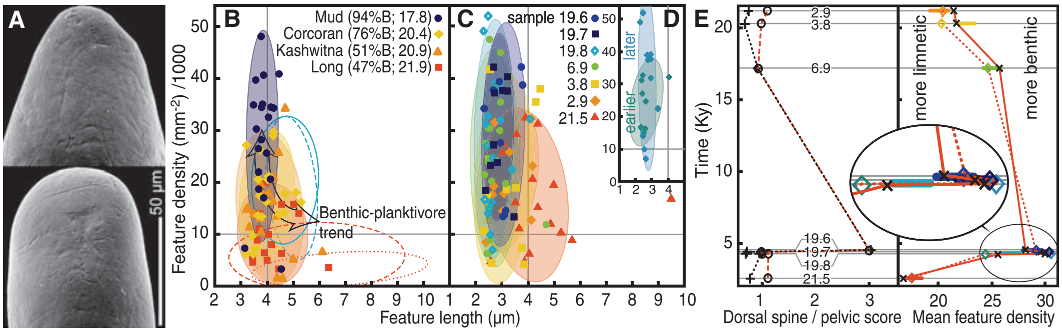

Fig. 1. Microwear in stickleback teeth and correlated evolutionary change. (**A**) Scanning electron micrographs showing tooth microwear in fossil (top) and extant benthic feeding (bottom) stickleback. For details, see fig. S1. (**B**) Microwear in wild-caught and lab-raised stickleback. Open ellipses indicate lab distributions (blue, benthic treatments; red, planktivore; solid, dashed, and dotted lines are course, medium, and no sand substrate, respectively). In wild fish, microwear tracks trophic ecology as indicated by % benthic stomach contents and mean gill raker count (Mud Lake, most benthic; Long Lake, least benthic). (**C**) Fossil stickleback microwear; inset (**D**) shows sample 19.8 divided into earlier (1746 to 1753 years) and later (1757 to 1771 years) subsamples with shift toward more benthic trophic ecology in later interval. Ky, thousand years. (**E**) Trophic niche and morphology in fossil stickleback through time [○ dorsal armor; + pelvic armor; ◊ mean feature density; × DF scores (minimum of 0.38 and maximum of 2.51)]. Colored horizontal bars show niche scores reflecting the position of the samples in the benthic-planktivore microwear spectrum (C). Time scale follows (*3*).

Here, we report an investigation of trophic resource use in a fossil sequence preserving an evolving lineage of threespine stickleback (*Gasterosteus*). We focus on stickleback for two reasons. First, perhaps the best-known work on speciation in fishes concerns stickleback in postglacial coastal lakes in Canada, where planktivores and benthic feeders coexist as two reproductively isolated and phenotypically distinct trophic forms. The differences between these forms result from competition for food (*1*, *2*). Second, fossil stickleback from the Miocene Truckee Formation (Nevada) provide a detailed, high-resolution record of evolutionary change within a lineage spanning tens of thousands of years (*3*).

We investigated the relationship between trophic resource use and evolutionary change through quantitative analysis of dental microwear (*4*). Laboratory feeding experiments and analyses of wild stickleback populations show that microwear exhibits a progressive shift from planktivores to benthic feeders (Fig. 1, A and B) (*5*). Discriminant analysis using feature length and density indicates that scores for the first discriminant function (DF) are a good predictor of trophic ecology. For wild fish populations (n = 4), mean scores were significantly correlated with diet ($r = 0.95$, $P = 0.05$) and gill raker number ($r = –0.996$, $P = 0.004$).

Analysis of fossil stickleback teeth revealed an overall range and pattern of feature densities and lengths similar to that of extant fish (Fig. 1C), suggesting that the fossil microwear records a similar benthic-planktonic feeding spectrum. This was supported by application of the DF derived from wild fish to the fossils: DF scores vary significantly between samples (F = 10.8, df of 7 and 87, P = 0.0001), and a Tukey-Kramer procedure revealed significant pairwise differences. This procedure also grouped some fossil samples with benthic-feeding wild populations (samples 19.6, 19.7, 19.6, and 6.9), others with planktivore populations (21.5), with some placed between (2.9 and 3.8).

These changes in inferred trophic ecology are significantly correlated with evolutionary changes in armor phenotype through time (*3*) (Fig. 1E). DF scores are correlated with dorsal [nonparametric Spearman rank correlation (r_s) = 0.23, P = 0.03, n = 89 fish] and pelvic armor (r_s = 0.21, P = 0.05), feature density with dorsal armor (r_s = 0.24, P = 0.02). Interestingly, the shift to a more benthic ecology within sample 19.8 (Fig. 1, D and E) precedes the increase in mean armor scores in 19.6 (a time lag of circa 100 years). This evidence of an ecological shift preceding phenotypic change suggests that this part of the sequence may record rapid evolution driven by shifts in trophic ecology and adaptation to benthic niches. If this hypothesis is correct, however, the low number of specimens displaying intermediate phenotypes is puzzling, and the scenario of replacement of one lineage by another (*3*) cannot be ruled out. The gradual shift to less benthic ecology over the next 17,000 years supports the interpretation that a return to low-armor phenotypes reflects directional natural selection (*3*).

Our analysis shows that dental microwear analysis can provide direct evidence for changes in trophic niche and resource exploitation in fossil fishes. That changes in feeding can be detected independently of morphological change highlights the potential of this approach to provide important insights into trophic ecology during adaptive radiations of fishes and other evolutionary events.

References and Notes

1. D. Schluter, *The Ecology of Adaptive Radiations* (Oxford Univ. Press, Oxford, 2000).
2. D. Schluter, J. D. McPhail, *Am. Nat.* **140**, 85 (1992).
3. M. A. Bell, M. P. Travis, D. M. Blouw, *Paleobiology* **32**, 562 (2006).
4. Materials and methods are available as supporting material on *Science* Online.
5. M. A. Purnell, P. J. B. Hart, D. C. Baines, M. A. Bell, *J. Anim. Ecol.* **75**, 967 (2006).
6. Funded by Natural Environment Research Council (NERC) grants NER/B/S/2000/00338 and NE/B000125/1 to M.A.P. and P.J.B.H.; M.A.P. also supported by NERC Advanced Fellowship NER/J/S/2002/00673. Fossil stickleback collected and prepared under NSF grants EAR9870337 and DEB0322818 to M.A.B. and F. J. Rohlf.

Supporting Online Material

www.sciencemag.org/cgi/content/full/317/5846/1887/DC1
Materials and Methods
Fig. S1

3 July 2007; accepted 15 August 2007
10.1126/science.1147337

---

[1] Department of Geology, University of Leicester, Leicester LE1 7RH, UK. [2] Department of Ecology and Evolution, Stony Brook University, Stony Brook, NY 11794–5245, USA. [3] Department of Biology, University of Leicester, Leicester LE1 7RH, UK.

*To whom correspondence should be addressed. E-mail: mark.purnell@leicester.ac.uk