

ence of a male. The number of mounts attempted by a male was also scored and recorded. The results of all the experiments were converted to lordosis quotient (LQ), defined as a percentage of full lordosis response (perineum elevated, all four legs extended from the initial crouch position and the head at an angle of 45° from the floor) divided by the number of mounts. Each group consisted of six animals, and each female was tested for 10 min in the presence of a male. The animals were tested for lordosis response at 30 min and at 3 hours after injection of compounds. The effects of the compounds were not transient, because identical results were obtained at 30 min and at 3 hours after infusion.

29. Statistical analysis was done by either of two methods as appropriate: Kruskal-Wallis one-way ANOVA

on ranks followed by Dunn's method for comparison of all groups versus control group, or one-way ANOVA followed by Dunnett's method for comparison of all groups versus control group. Sigma Stat (Jandel Corporation) was used.

30. We thank K. Mayo for the sequence of the rat PR mRNA, J. Turcotte for assistance with the binding assays, the staff of the Center for Comparative Medicine at Baylor College of Medicine, and D. Scarff for help in the preparation of the figures. Supported in part by N.S. 19327 (NIH) and Research Scientist Development Award grant MH-00885 to J.D.B. and a NIH (National Institute of Child Health and Human Development) grant to B.W.O.

27 April 1994; accepted 8 July 1994

TECHNICAL COMMENTS

Accounting for Endothermy in Fishes

A basic premise of the recent article by B. A. Block *et al.* (1) is that a molecular phylogeny of scombroid fishes provides novel insight into the evolution of endothermy in fishes. Specifically, nucleotide sequence data from a portion of the mitochondrial *cytochrome b* gene were used to infer multiple origins of endothermy—in billfishes, butterfly mackerel and tunas—and to hypothesize selective, causative forces. Block *et al.* note that two recent hypotheses based on morphological data (2, 3) differ in the placement of the butterfly mackerel and billfishes, “taxa that are key to the study of the evolution of endothermy within the suborder” and state that “[i]n an attempt to resolve these relationships, we have produced a hypothesis of scombroid phylogeny based on molecular data” (1, p. 212).

We contend that the molecular phylogeny infers nothing new about the number of origins of endothermy in scombroid fishes. Despite their differences, both of the hypotheses based on morphology and that based on *cytochrome b* require three origins of endothermy (Fig. 1). The strategies for elevating body temperature in the three endothermic groups are strikingly different (4), and we perceive no arrangement of taxa in which a hypothesis of one (or two) origins of endothermy would be more parsimonious than one requiring three. For example, a single-origin hypothesis of endothermy in the form of a brain heater derived from the superior rectus muscle in the ancestor of billfishes and scombrids (Fig. 1A) not only requires the loss of the condition in “other scombrids” and “bonitos,” but the conversion of the lateral rectus eye muscle in the butterfly mackerel to a brain heater, and finally the evolution of a “whole body” form of endothermy in the tunas produced by countercurrent mechanisms (as opposed to thermogenic organ) in

the brain, muscle, and viscera. Block *et al.* (1) note that despite their derivation from different muscles, the thermogenic organs of billfishes and butterfly mackerel could be homologous, citing evidence of structural and biochemical similarity (5). But even in the absence of morphological and physiological data that suggest the three types of endothermy are nonhomologous, a hypothesis of independent origins requires the fewest evolutionary steps (three as opposed to a minimum of four, Fig. 1).

Hypothetically, it would be equally parsimonious to propose (i) a single origin of endothermy (in any of the three forms) with subsequent modifications and (ii) independent origins only if billfishes, tunas, and butterfly mackerel form a monophyletic group. Likewise, a sister-group relationship between any two of the endothermic taxa would render a double-origin hypothesis as likely as one requiring three events. None of those clades has been proposed, and thus the hypothesis of independent origins goes unchallenged. The cladograms based on morphology are derived mostly from characters independent of endothermy, and exclusion of the one endothermy character in each hypothesis does not affect the topology. In summary, the morphological data clearly suggest three origins of endothermy.

Block *et al.* (1) state that the molecular data are important because they provide information about the affinities of billfishes and butterfly mackerel. However, none of the six nodes that determine the placement of butterfly mackerel in their phylogeny [figure 2 in (1)] was supported in greater than 50% of 300 replications of the bootstrap calculation (1, p. 212). The molecular data also provide little evidence for the clade comprising endothermic tunas, the monophyly of which has not been questioned.

In a comparative review of recent studies

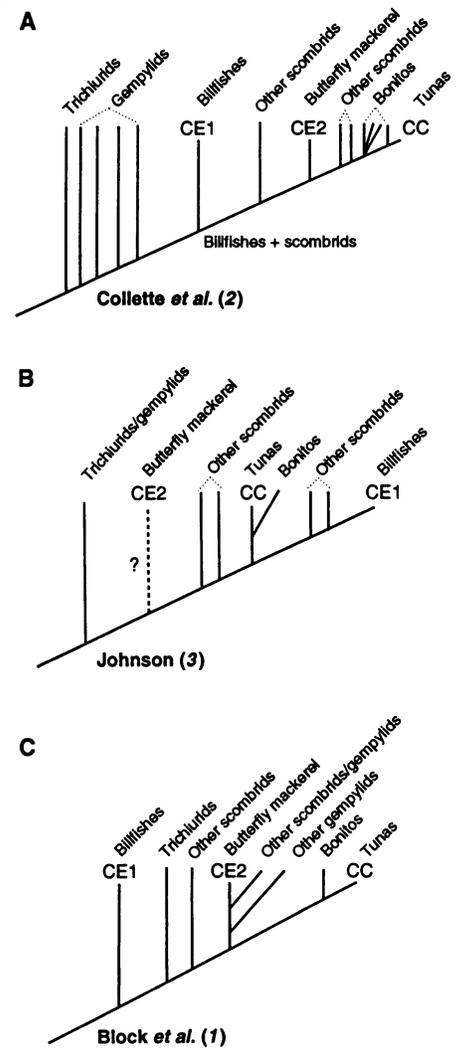


Fig. 1. Simplified versions of three recently proposed phylogenies of scombroid fishes. (A) and (B) are based on morphology (2 and 3, respectively) and (C) on sequences of a portion of the mitochondrial *cytochrome b* gene (1). CE1, cranial endothermy by a thermogenic organ derived from superior rectus eye muscle fibers; CE2, cranial endothermy by a thermogenic organ derived from lateral rectus eye muscle fibers; CC, whole body endothermy by counter-current heat exchangers in the brain, muscle, and viscera.

based on morphological or on molecular data, Patterson *et al.* (6, p. 179) found that “[c]ongruence between molecular phylogenies is as elusive as it is in morphology and as it is between molecules and morphology.” In the absence of additional hypotheses of scombroid phylogeny based on molecular data, it is premature to suggest the *cytochrome b* data have “resolved” scombroid relationships. One potential problem is that addition of taxa in molecular phylogenies often leads to decreased support for a previously preferred cladogram (6). The studies based on morphology included examination of all scombroid genera, whereas that based on molecular data (1) was limited to repre-

sentative taxa that included approximately one-third of the genera. For example, the wahoo, *Acanthocybium*, was not included in the molecular analysis (1), yet, as the sister group of the billfishes, it is a key taxon in one of the morphological phylogenies (2).

G. David Johnson
Carole C. Baldwin

Department of Vertebrate Zoology,
National Museum of Natural History,
Smithsonian Institution,
Washington, DC 20560, USA

REFERENCES

1. B. A. Block, J. R. Finnerty, A. F. R. Stewart, J. Kidd, *Science* **260**, 210 (1993).
2. B. B. Collette, W. J. Richards, S. Ueyanagi, J. L. Russo, Y. Nishikawa, in *Ontogeny and Systematics of Fishes*, H. G. Moser et al., Eds. (Spec. Publ. no. 1, Supplement to *Copeia*, American Society of Ichthyologists and Herpetologists, Lawrence, KS, 1984), pp. 591–620.
3. G. D. Johnson, *Bull. Mar. Sci.* **39**, 1 (1986).
4. I. Barrett and F. J. Hester, *Nature* **203**, 96 (1964); F. G. Carey and J. M. Teal, *Proc. Natl. Acad. Sci. U.S.A.* **56**, 1464 (1966); E. D. Stevens and F. E. J. Fry, *Comp. Biochem. Physiol.* **38A**, 203 (1971); F. G. Carey, *Sci. Am.* **238**, 36 (February 1973); J. B. Graham, *Proc. Natl. Acad. Sci. U.S.A.* **70**, 1964 (1973); R. M. Gooding, W. H. Neill, A. E. Dizon, *Fish. Bull. U.S.* **79**, 31 (1981); F. G. Carey, *Science* **216**, 1327 (1982); J. B. Graham and R. M. Laurs, *Mar. Biol.* **72**, 1 (1982); B. A. Block, *Am. Zool.* **23**, 936 (1983); *J. Morphol.* **190**, 169 (1986); R. W. Brill, *Fish. Bull. U.S.* **85**, 25 (1987); B. A. Block and C. Franzini-Armstrong, *J. Cell Biol.* **107**, 1099 (1988); B. A. Block, in *Biochemistry and Molecular Biology of Fishes*, P. Hochachka and T. Mommsen, Eds. (Elsevier, New York, 1991), pp. 269–311; B. A. Block, *Am. Zool.* **31**, 726 (1991).
5. A. Tullis et al., *J. Exp. Biol.* **161**, 383 (1991).
6. C. Patterson, D. M. Williams and C. J. Humphries, *Annu. Rev. Ecol. Syst.* **24**, 153 (1993).

1 October 1993; accepted 29 March 1994

Response: The morphological phylogenies of scombroid relationships leave major questions unanswered, particularly concerning the affinities of cranial endotherms, *Gasterochisma*, and billfishes. Our molecular phylogeny of scombroid fishes supports a single evolutionary origin of systemic endothermy (in the common ancestor of tunas) and dual origins of cranial endothermy in billfishes and the butterfly mackerel (*Gasterochisma*) lineage. *Cytochrome b* provides an answer to the question of the billfishes' relationship to other scombroids. Johnson and Baldwin contend that either of two existing morphology-based phylogenies could have been used to reconstruct the evolution of endothermy in the Scombroidei, but the morphological phylogenies differ significantly over the placement of billfishes. Johnson (1) published his "alternative hypothesis" of scombroid phylogeny in response to shortcomings that he said were presented in an earlier study by Collette et al. (2). Johnson did not place all of the endothermic taxa within an explicit phylogeny, and thus the point being raised here

by Johnson and Baldwin seems groundless. For example, the butterfly mackerel (*Gasterochisma melampus*) was not so placed because of a lack of ontogenetic data for this species, as the "precise affinities of *Gasterochisma* remain unresolved" (1, p. 32). Johnson called for additional data to help "resolve the placement of this enigmatic genus, which exhibits a perplexing combination of primitive and derived character states" (1, p. 38). In their redrawn version of the Johnson phylogeny (figure 1B of their comment) Johnson and Baldwin include *Gasterochisma* without reference to its uncertain affinities except for its connection to the tree by a dashed line.

Collette et al. (2) did place all of the

endothermic taxa within an explicit phylogenetic hypothesis for the suborder Scombroidei. However, they acknowledged uncertainty over the placement of billfishes because of homoplasious morphological evolution, raising the question of whether billfishes should be placed within the Scombroidei at all. Several morphology-based studies have argued that billfishes are distantly related to other scombroids and should not be placed within this suborder (4).

The existing morphological data have been used to argue for three competing hypotheses of billfish relationships (1, 2, 4). We have tried to complement, not displace, these phylogenies. *Cytochrome b* represents an important contribution to scom-

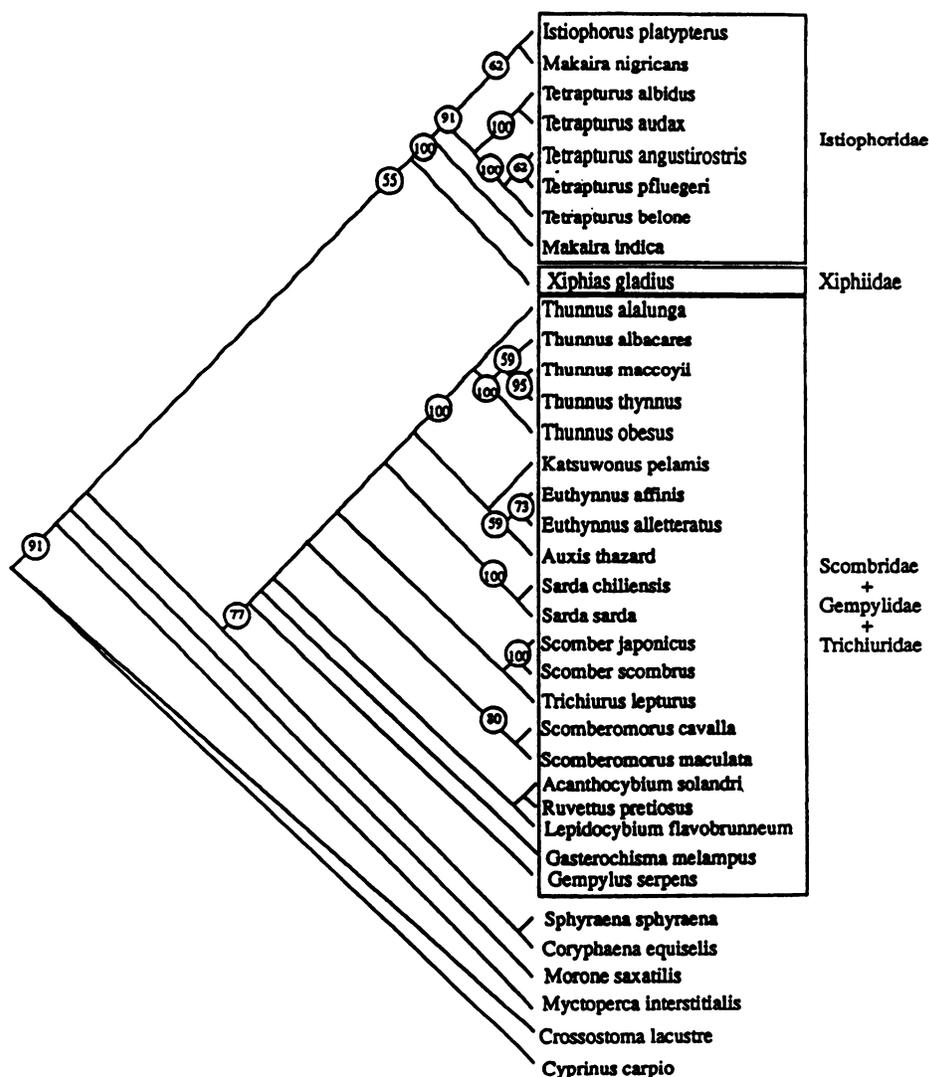


Fig. 1. Phylogeny of the Scombroidei based on a weighted, maximum parsimony analysis of informative nucleotide sites (10). The six types of nucleotide substitutions are weighted according to the ratio of their expected occurrence to their observed occurrence (11). Weights used for each substitution type are A to G = 1, C to T = 1, G to T = 13, G to C = 4, A to T = 2, and A to C = 2. *Crossostoma* and *Carpio* were specified as the outgroup. The tree depicted is the single most parsimonious topology identified in a heuristic search: TBR branch swapping was performed on 10 starting trees generated through random stepwise addition of taxa. Tree length is 2348 steps. Circled numbers at nodes indicated the percentage of trials in which a given partition between taxa is supported in 100 replications of the bootstrap calculation (5).

Accounting for Endothermy in Fishes

G. David Johnson and Carole C. Baldwin

Science **265** (5176), 1249-1250.
DOI: 10.1126/science.265.5176.1249

ARTICLE TOOLS

<http://science.sciencemag.org/content/265/5176/1249>

REFERENCES

This article cites 18 articles, 6 of which you can access for free
<http://science.sciencemag.org/content/265/5176/1249#BIBL>

PERMISSIONS

<http://www.sciencemag.org/help/reprints-and-permissions>

Use of this article is subject to the [Terms of Service](#)

Science (print ISSN 0036-8075; online ISSN 1095-9203) is published by the American Association for the Advancement of Science, 1200 New York Avenue NW, Washington, DC 20005. 2017 © The Authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original U.S. Government Works. The title *Science* is a registered trademark of AAAS.