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Accounting for Endothermy in Fishes

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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.

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## 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

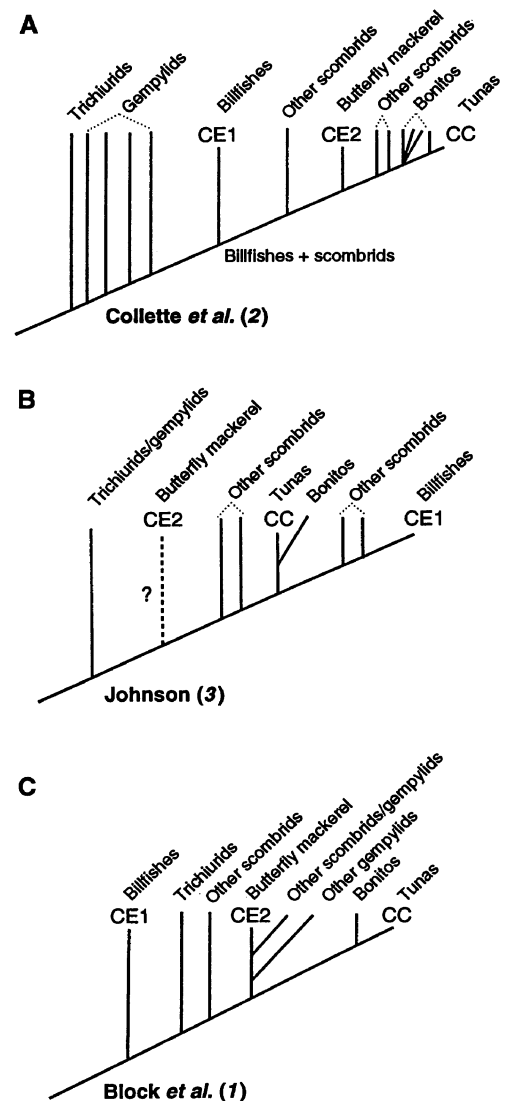


Fig. 1. Simplified versions of three recently proposed phylogenies of scombroid fishes. (A) and (B) are based on morphology (2 and 3, respectively) and (C) on sequences of a portion of the mitochondrial *cytochrome b* gene (1). CE1, cranial endothermy by a thermogenic organ derived from superior rectus 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).

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## 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).

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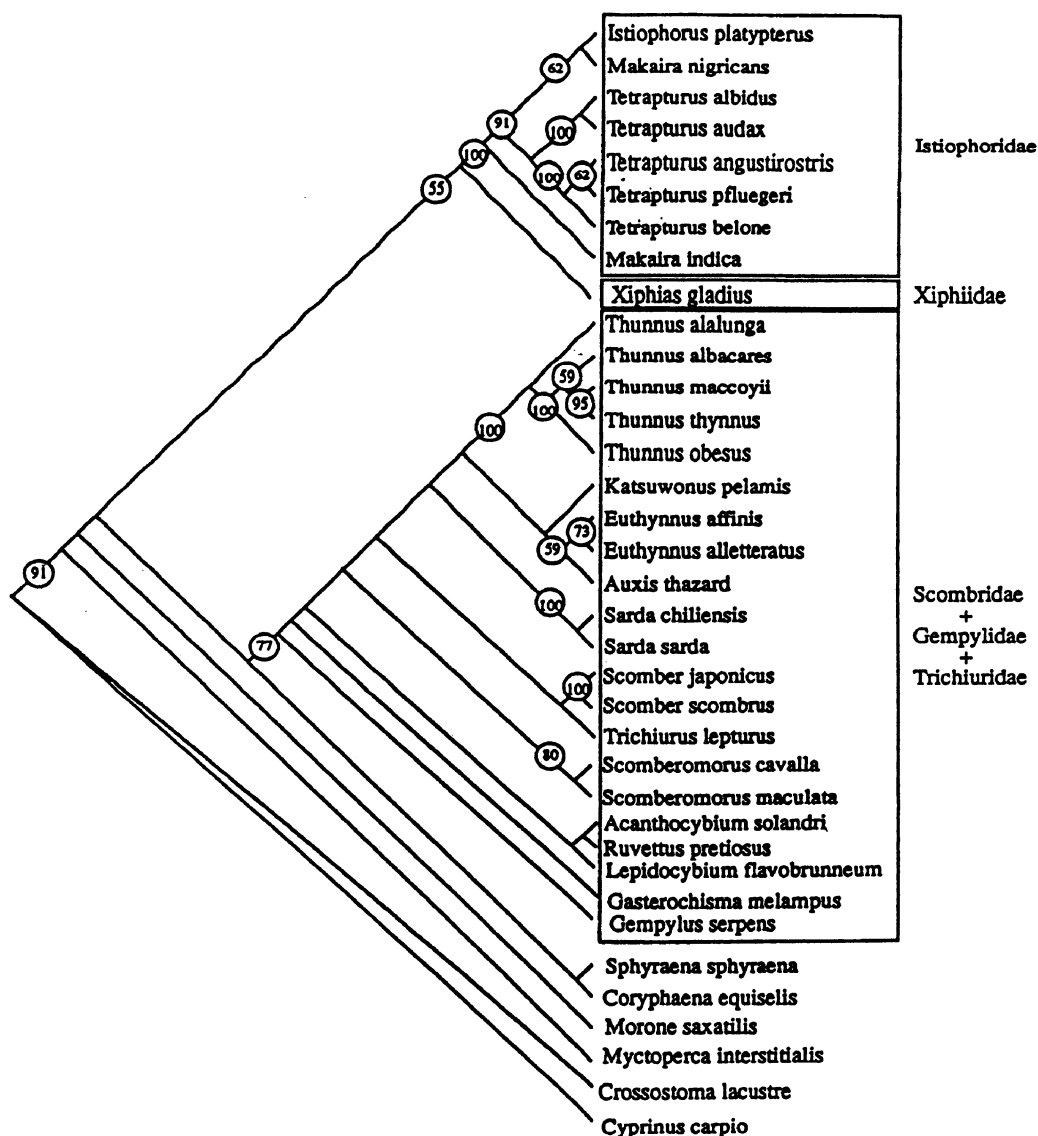
**Response:** The morphological phylogenies of scombroid relationships leave major questions unanswered, particularly concerning the affinities of cranial endotherms, *Gasterochisma*, and billfishes. Our molecular phylogeny of scombroid fishes supports a single evolutionary origin of systemic endothermy (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 (70). 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).

broid systematics because it provides a phylogenetic signal over an issue where morphology is equivocal due to homoplasy. In a maximum parsimony analysis of all informative nucleotide sites (1), billfishes composed one clade, and all other scombroids composed a separate clade. *Gasterochisma* was nested within the nonbillfish clade. In placing billfishes so distant from the scombrids, and thus the butterfly mackerel, our study provides strong evidence for two conclusions: cranial endothermy evolved two times, and it evolved independently in very distantly related lineages.

In 300 replications of the bootstrap procedure with the use of a heuristic search on all informative nucleotide sites (5), a grouping of all cranial endotherms (billfishes + *Gasterochisma*) did not occur. This finding (3) represents direct evidence against the monophyly of cranial endotherms (6). In a parsimony analysis of all informative amino acid sites (7), the strict consensus of 96 equally most parsimonious trees indicates separation of the billfish clade from *Gasterochisma*. Furthermore, a 10% increase in tree length is required to produce a topology that indicates monophyly of cranial endotherms (tree length increased from 111 to 122 amino acid substitutions). This difference in length represents highly significant statistical evidence against the monophyly of cranial endotherms according to the topology-dependent cladistic permutation test for nonmonophyly (8). Our phylogeny and that of Collette *et al.* (3) support the same conclusion about how many times these evolved but differ significantly from the morphological phylogeny of Johnson (2).

Beyond counting how many times endothermy has evolved we seek to understand the selective pressures that have favored the evolution of endothermy and the preadaptations that may have permitted its evolution in the Scombroidei. Thus, we must identify the ectothermic sister groups of the endothermic lineages.

The morphological hypotheses (1, 2) consider billfishes to be derived scombroids that share a most recent common ancestry with members of the family Scombridae. *Gasterochisma* resides within the Scombridae in one of these studies (2). The molecular data (3) indicate that billfishes lie outside of a clade composed of all other scombroids, suggesting that cranial endothermy evolved independently in two very distant lineages. The morphological data of Collette *et al.* (2) suggest that cranial endothermy evolved twice within a group of closely related fishes: the clade composed of billfishes plus Scombridae.

We have recently completed a second molecular analysis on scombroid relationships based on the nuclear gene *lactate dehydrogenase b* (9). The *LDH b* nucleotide

trees are similar to the *cytochrome b* trees and refute the monophyly of cranial endotherms with robust statistical support.

Johnson and Baldwin state that the addition of taxa could weaken the conclusions of our molecular phylogenetic analysis. This criticism could theoretically be leveled at any phylogenetic hypothesis. However, the addition (10) of taxa to the molecular phylogenetic analysis, including the wahoo, *Acanthocybium solandri*, a species which Johnson proposes is the sister group to billfishes, reinforces our conclusion (3) that the billfishes are distantly related to other scombroid fishes (Fig. 1). Furthermore, our analysis of this enlarged *cytochrome b* data set rejects the hypothesis by Johnson (1) that *Acanthocybium* is the sister-group of billfishes and is consistent with the placement of the wahoo made by Collette *et al.* (2). This conclusion is also strongly supported by the *LDH b* analysis.

Molecular data provide an important source of phylogenetic information for the Scombroidei, primarily because it complements existing morphological data and is informative in instances where morphological hypotheses conflict. We believe that historical patterns are best elucidated when a combination of different types of data, morphological and molecular, is used to corroborate and test phylogenetic hypotheses. We hope our study encourages such a synthesis.

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#### REFERENCES AND NOTES

1. G. D. Johnson, *Bull. Mar. Sci.* **39**, 1 (1986).
2. B. B. Collette, T. Potthoff, 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. B. A. Block, J. R. Finnerty, A. F. R. Stewart, J. Kidd, *Science* **260**, 210 (1993).
4. T. Potthoff, S. Kelley, S. Ueyanagi, *Bull. Mar. Sci.* **30**, 329 (1980); I. Nakamura, *Publ. Seto Mar. Biol. Lab.* **28**, 255 (1983); T. Potthoff and S. Kelley, *Fish. Bull. U.S.* **84**, 647 (1986).
5. J. Felsenstein, *Evolution* **39**, 783 (1985).
6. In the same way that a high bootstrap value for a particular node indicates support for the monophyly of a group of taxonomic units, a low value represents evidence that a group of taxonomic units is not monophyletic (D. P. Faith, personal communication).
7. The *cytochrome b* nucleotide sequences used to construct the phylogeny in our report [figure 1 of (1)] were translated into amino acid sequences. A heuristic search for the most parsimonious tree was performed on these data with the use of PAUP, version 3.0s [Phylogenetic Analysis Using Parsimony, Swoford, D. L., 1990; tree-bisection and reconnection (TBR) branch swapping were performed on ten starting trees generated through random addition of taxa]. Ninety-six equally most parsimonious trees identified in the search indicated that *Gasterochisma* is nested within a clade containing members of the scombroid families Scombridae and Gempylidae and that billfishes fall outside of this clade. The "enforce topological constraints" option of PAUP was used to identify the most parsimonious topology that supported the monophyly of cranial endotherms, *Gasterochisma*, and billfishes. This topological constraint resulted in an 11-step increase in tree length over the most parsimonious tree (122 over 111 steps).
8. D. P. Faith, *Syst. Zool.* **27**, 401 (1991). We conducted topology-dependent cladistic permutation (T-PTP) tests for non-monophyly of cranial endotherms with the use of the inferred amino acid sequences from the data of our report (1). Each data set was permuted 99 times such that the observed character states of each character were shuffled randomly among taxa. The permuted data sets were searched for the most parsimonious tree under two constraints: (i) include and (ii) do not include billfishes plus butterfly mackerel as a monophyletic group. The length difference between trees never equalled or exceeded the length difference from the unpermuted *cytochrome b* data (6) (T-PTP = 0.01).
9. Briefly, degenerate primers were designed to the *lactate dehydrogenase b* locus with the use of amino acid alignments of all isozymes of LDH sequenced in vertebrates. a subset of the taxa examined in the *cytochrome b* study (1) were used in the second molecular study. The consensus aligned sequence for the scombroid fishes that were examined, after the insertion of alignment gaps, is 628 base pairs long (Finnerty and Block, unpublished results).
10. J. R. Finnerty and B. A. Block, *Fish. Bull. U.S.*, in press.
11. A. Knight and D. P. Mindell, *Syst. Biol.* **42**, 18 (1993).

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## Earthquake Aftershocks: Update

Since 1989, the U.S. Geological Survey has provided public forecasts of expected aftershock activity following major earthquakes in California, based on a stochastic model (1). The model represents the rate of aftershocks of magnitude  $M$  or larger as

$$\lambda(t, M) = 10^{a + b(M_m - M)}(t + c)^{-p}$$

where  $t$  is time after the mainshock,  $M_m$  is the mainshock magnitude, and  $a$ ,  $b$ ,  $p$  and  $c$  are constant parameters. Forecasts based on

this model typically have been posed in probabilistic terms, such as, "There is a 50 percent chance of one or more magnitude 5 or larger earthquakes in the next 7 days." While such probabilistic statements may be clearly understood by scientists and emergency response officials, they often have created confusion and miscommunication among the press and general public. In an effort to more effectively communicate the aftershock hazard after the 17 January 1994