# A Phylogenetic Supertree of the Hammerhead Sharks (Carcharhiniformes: Sphyrnidae)

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**Mauro José Cavalcanti (2007)** A phylogenetic supertree of the hammerhead sharks (Carcharhiniformes, Sphyrnidae). *Zoological Studies* **46**(1): 6-11. In this study, 5 hammerhead shark phylogenies (based on morphological, isozyme, and mtDNA sequence data) were combined to generate a complete, well-resolved composite phylogeny for the Sphyrnidae using matrix representation with parsimony. The resulting supertree contains all 8 known sphyrnid species and represents the best estimate of the combined relationships presented in the original 5 source trees. This supertree will provide a useful framework for further phylogenetic comparative studies of sphyrnid evolution, ecology, and biogeography. http://zoolstud.sinica.edu.tw/Journals/46.1/6.pdf

**Key words:** Composite trees, Matrix representation with parsimony, Phylogeny, *Sphyrna*, *Eusphyra*.

Hammerhead sharks (family Sphyrnidae) are recognized as a highly derived, monophyletic group in the order Carcharhiniformes, characterized by the presence of a dorsoventrally compressed and laterally expanded pre-branchial head, known as the cephalofoil (Gilbert 1967, Compagno 1988). The morphology of the cephalofoil differs greatly among species, from evenly rounded in the bonnethead shark (*Sphyrna tiburo*) to very wide and narrow in the winghead shark (*Eusphyra blochii*).

The evolution of the peculiar head shape of hammerhead sharks has been the subject of much debate, and several hypotheses have been advanced to explain the adaptive significance of this unusual head morphology. It has been suggested that the cephalofoil evolved from the slightly flattened head typical of many carcharhinid sharks (Compagno 1988), which acts as a bowplane that provides hydrodynamic lift and increases maneuverability (Nakaya 1995, Kajiura et al. 2003). Other hypotheses for the evolution of the cephalofoil (Kajiura 2001) invoke potential advantages of spacing sensory structures at the lateral ends of the head (eyes and nostrils) or across the surface of the head (lateral line and ampullae of Lorenzini). Only a few of these hypotheses have been empirically tested, and none of them has been placed within a phylogenetic framework. Clearly, what is needed to understand the evolution of the cephalofoil within the Sphyrnidae, and the diversification of the clade itself, is a comparative approach (Harvey and Pagel 1991). However, the lack of a complete and well-resolved phylogeny for the sphyrnids, based on all the available evidence afforded by morphological and molecular datasets, is a major obstacle to explaining what factors might have driven the evolution of the cephalofoil.

Morphological and molecular data have yielded very different phylogenetic trees for hammerhead sharks. The most complete phylogenetic hypothesis based on morphological characters and anatomical structures (Compagno 1988) indicates that evolution in this family has been characterized by a change from a plesiomorphic condition of small size, inshore dwelling, and bottom feeding, to a more-derived condition of large, pelagic piscivores. On the other hand, according to a hypothesis based on mtDNA sequence data

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(Martin 1993), the large pelagic species are more primitive than the small demersal species, and there is a trend towards the evolution of the cephalofoil along the evolution of the clade. This sequence of divergence is precisely the opposite from that suggested by the hypothesis based on morphological data.

Comparisons among phylogenies obtained by different techniques or based on different datasets can be performed by constructing consensus trees (Rohlf 1982). Consensus trees, introduced by Adams (1972), allow the combination of information from 2 (or more) phylogenetic trees into a single tree that represents the information in the set of trees being compared, but this procedure is only possible if the species sets present in the different phylogenies are the same.

Another possibility, developed more recently, is to construct a composite phylogeny or "supertree" from source trees derived from separate morphological and molecular datasets, based on the principle that the phylogenies can be converted in data matrices which, after combination, can be subjected to parsimony analysis (Sanderson et al. 1998, Bininda-Emonds et al. 2002). This procedure has the advantage of not requiring that all species be shared among the several studies being compared. As the method combines existing phylogenetic information in the form of trees, supertrees potentially resolve many of the problems associated with other character-based methods (e.g., the absence of homologous characters and incompatible data types). Supertree methods are capable of synthesizing the results of separate studies into more-comprehensive, larger-scale phylogenies that are useful for comparative and macroevolutionary studies and which represent major steps towards building the Tree of Life (Soltis and Soltis 2001, Bininda-Emonds et al. 2002, Page 2004). In addition to helping synthesize hypotheses of phylogenetic relationships among larger sets of taxa, supertrees can suggest optimal strategies for taxon sampling (either for future supertree construction or for experimental design issues such as the choice of outgroups for cladistic analyses) and can reveal emerging patterns in the large knowledge base of phylogenies currently in the literature (Sanderson et al. 1993).

Many supertrees have already been published for various groups of organisms, sometimes with associated comparative or macroevolutionary analysis (see Bininda-Emonds et al. 2002 for references on individual studies). However, many of the previous studies were concerned with mammalian supertrees and, to the author's knowledge, only 1 fish supertree has appeared before in the literature (Mank et al. 2005).

In this paper, all available published phylogenies of the Sphyrnidae were assembled to generate a composite phylogeny for hammerhead sharks using the technique of matrix representation with parsimony (Baum 1992, Ragan 1992). The resulting supertree will provide a useful framework for further phylogenetic comparative studies of sphyrnid evolution, ecology, and biogeography.

## MATERIALS AND METHODS

### Source trees

All phylogenetic source trees available for the Sphyrnidae (Fig. 1) were obtained from the literature (Gilbert 1967, Compagno 1988, Lavery 1992, Naylor 1992, Martin 1993), following the protocol proposed by Bininda-Emonds et al. (2004). The phylogenetic hypothesis of Gilbert (1967) was included as a "seed" tree, even though it was not built using a formal cladistic analysis, as recommended by Purvis (1995) and Bininda-Emonds and Sanderson (2001) to obtain complete taxonomic coverage and ensure sufficient overlap among the source trees, and therefore to improve the resolution of the composite phylogeny. When a given bibliographic source presented several phylogenetic trees for the same dataset, obtained with different methods, a strict consensus tree (Rohlf 1982) was initially computed among the trees, for inclusion in the procedure of supertree construction. The trees compiled from the literature were stored in the NEXUS format (Maddison et al. 1997) using the program, TreeView, vers. 1.6.6 (Page 1996) for further analysis.

### Data analysis

To construct the composite phylogeny, each source tree was recoded as a binary matrix using the Supertree program, vers. 0.85b (Salamin et al. 2002), after the procedure proposed by Baum (1992) and Ragan (1992). The Baum/Ragan method for constructing supertrees can be used whether the source trees are compatible or not. The minimum requirement for including a source tree in supertree construction is that it shares 2 or more taxa with at least 1 other source tree. These matrices are then combined and analyzed with

parsimony to generate the composite phylogeny or "supertree" (see Sanderson et al. 1998, Bininda-Emonds et al. 2002, Bininda-Emonds 2004, and Page 2004 for details on supertree construction using matrix representation with parsimony). The resulting MRP dataset had 8 taxa and 23 "characters". As all source trees were rooted, an all-zero hypothetical outgroup (the "MRP outgroup") was added to the data matrix to polarize the subsequent parsimony analysis, preserving the rooting information of the source trees (Bininda-Emonds et al. 2005).

Four separate analyses were performed, using different weighting schemes of the matrix elements and allowing or prohibiting reversals (Bininda-Emonds and Bryant 1998, Bininda-Emonds and Sanderson 2001). The matrix elements were weighted in proportion to their clade support on each source tree (Bininda-Emonds and Bryant 1998, Bininda-Emonds and Sanderson 2001).
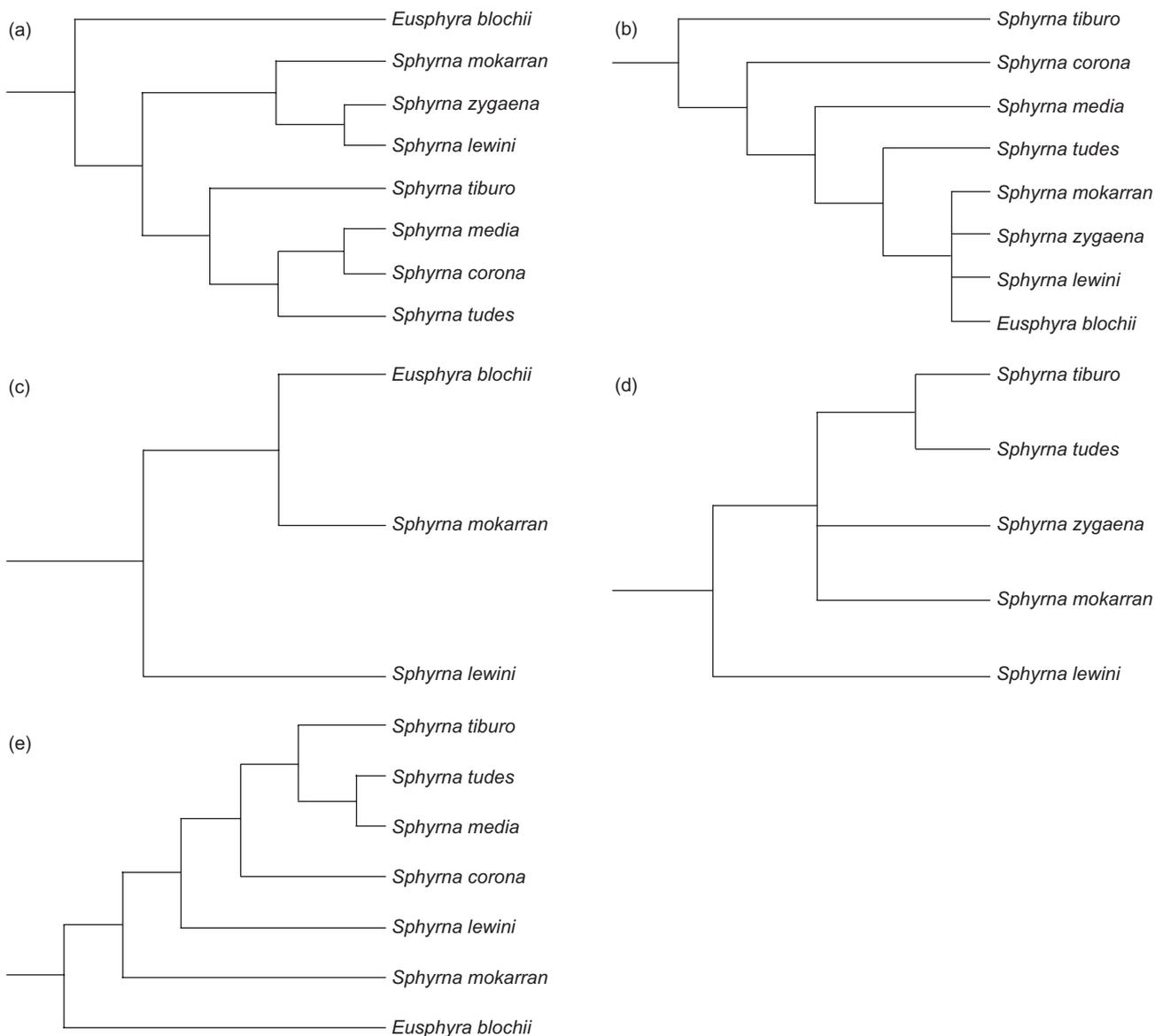
The degree of support of the composite phy-



**Fig. 1.** Topologies of the phylogenetic trees used to construct the composite phylogeny. (a) Gilbert (1967: fig. 4) based on morphology; (b) Compagno (1988: fig. 21.10c) based on morphology; (c) Lavery (1992: fig. 1) based on isozymes; (d) Naylor (1992: fig. 3c) based on isozymes; (e) Martin (1993: fig. 1) based on mitochondrial DNA sequences.

logeny was assessed by means of the qualitative support (QS) index of Bininda-Emonds (2003), using the program, QualiTree, vers, 1.1, written by O.R.P. Bininda-Emonds and available from http://141.40.125.5:8080/WWW/Homepages/Bininda-Emonds/ProgramsMain.html.  The value of the QS index varies between +1.0 (indicating a complete match among the source trees) and -1.0 (indicating total conflict among the source trees).

Parsimony analyses were performed using the program, PAUP*, vers. 4.0b10 (Swofford 2002).  The method of branch and bound (Hendy and Penny 1982) was used to search for the most parsimonious trees.

The resultant composite phylogeny and its associated MRP data matrix have been deposited in the TreeBASE database (www.treebase.org) under study accession number S1439 and matrix accession number M2590.

## RESULTS

Only 2 species (*S. lewini* and *S. mokarran*) were present in all 5 source trees used as input to build the supertree, and three of them (*S. zygaena*, *S. media*, and *S. corona*) appeared in just three of the original trees (Table 1).

Several most parsimonious trees were found, for the 4 analyses performed according to the different weighting schemas adopted and the possibility or exclusion of reversals.  Values of the QS index were negative for all of these analyses, which indicates that there was more conflict than agreement among the source trees as a whole. The degree of resolution varied among the different combinations of weighting/reversal schemes, from 100% for the weighted/irreversible tree to 71.4% for the unweighted/unordered tree (Table 2).  Differences between supertrees were due solely to differences in resolution and not to actual conflicting relationships.

The selected composite phylogeny (Fig. 2), including all of the 8 known species of the

Sphyrnidae, was based on the analysis (with weighted elements and irreversible transformations) that produced a single most parsimonious tree, with 178 steps in length, a consistency index of 0.6910, a retention index of 0.8736, and a QS index of -0.300.  This phylogeny is fully resolved and displays the highest QS index in comparison to all other trees; thus, it was selected to represent the best estimate of the phylogenetic relationships present in the 5 original source trees combined.

## DISCUSSION

The composite phylogeny presented in this study represents a combined summary of the available knowledge about the phylogenetic relationships of hammerhead sharks.  Thus, it can help to make novel statements about relationships of taxa that are not immediately apparent on any single source tree, while still retaining the hierarchical information from the original trees.

In the present study, the supertree approach sheds particular light on the relationships among *S. lewini*, *S. mokarran*, and *S. zygaena*, which have been rather controversial in the literature (Gilbert 1967, Compagno 1988).  These species

**Table 1.**  Frequency distribution of the taxa in the phylogenetic source trees used to build the composite phylogeny.  The frequency of ocurrency makes it possible to assess the relative representations of each taxon in the generated supertrees

| Taxon | Frequency |
|---|---|
| *Sphyrna zygaena* | 3 |
| *S. lewini* | 5 |
| *S. mokarran* | 5 |
| *S. media* | 3 |
| *S. corona* | 3 |
| *S. tudes* | 4 |
| *S. tiburo* | 4 |
| *Eusphyra blochii* | 4 |

**Table 2.**  Summary statistics for the 4 sphyrnid composite phylogenies

| Tree | No. of trees | Tree length | Consistency index | Retention index | Percent (%) resolution | QS index |
|---|---|---|---|---|---|---|
| Unweighted, unordered | 4 | 33 | 0.6970 | 0.6774 | 71.4 | -0.367 |
| Unweighted, irreversible | 2 | 34 | 0.6765 | 0.8608 | 85.7 | -0.340 |
| Weighted, unordered | 1 | 175 | 0.7029 | 0.7062 | 85.7 | -0.420 |
| Weighted, irreversible | 1 | 178 | 0.6910 | 0.8736 | 100.0 | -0.300 |

collapse as a polytomy (which also includes *E. blochii*) in the phylogenetic hypothesis of Compagno (1988), whereas the relationship between *S. mokarran* and *S. zygaena* was not resolved by the phylogenetic hypothesis of Naylor (1992). However, this group was recovered as a well-resolved clade in the composite phylogeny using weighted, irreversible characters (Fig. 2).

Compared to the source trees, the topology of the supertree is very similar to that of the tree proposed by Gilbert (1967), from which it differs only in the placement of *E. blochii* and *S. corona* (Fig. 1a). The topological structure of the composite phylogeny is also similar to that of the tree presented by Martin (1993), with regard to the relationship between *S. media* and *S. tudes* (Fig. 1e).

The supertree may also have broader taxonomic implications concerning the status of *Eusphyra* as a separate genus within the Sphyrnidae. Based on the topology of the composite tree, assigning *Eusphyra* to a separate genus would render the genus *Sphyrna* paraphyletic, since the winghead shark does occur among the other hammerheads in the tree. This has been a long-standing area of contention in the literature (Gilbert 1967, Dingerkus 1986, Compagno 1988, Nelson 1994, Shirai 1996), and because the composite tree represents a synthesis of a number of independent studies, it might be used to offer support for the proposals which place *Eusphyra* as a subgenus within *Sphyrna* (an arrangement previously advocated by Gilbert 1967, Dingerkus 1986, and Nelson 1994). However, direct evidence to support or refute any particular relationships suggested by the supertree should be sought from the original studies.

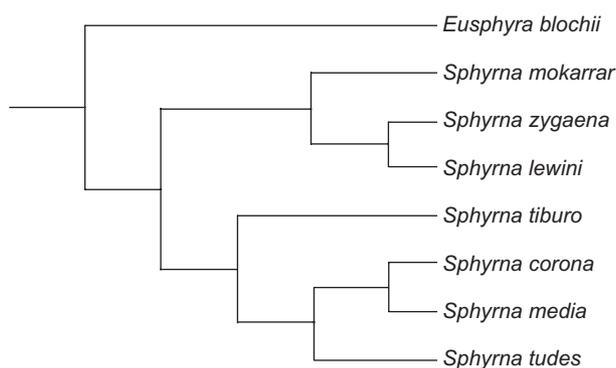The supertree will provide a more-complete framework for further studies of sphyrnid evolution and ecology by phylogenetic comparative methods (Harvey and Pagel 1991), especially in the context of the patterns and processes in the evolution of cephalofoil size (Cavalcanti 2004, Cavalcanti in prep.). It may also prove useful in studying the historical biogeography of hammerhead sharks, still a largely underexplored field (Gilbert 1967, Musick et al. 2004) using vicariance cladistics (Humphries and Parenti 1999).

Because it is not solely influenced by any of the individual studies used to build it (e.g., a source with more data which might be based on a single gene with rapid evolution), matrix representation with parsimony allows a more-complete estimate of the phylogeny of a given group than does a phylogenetic analysis based on just a single data source. Furthermore, the genetic and/or morphological datasets that can be assembled in a "super-matrix" approach are, as a matter of fact, less widely available than the published phylogenies which can be combined using the supertree approach (Sanderson et al. 1998, Kennedy and Page 2002).

As shown by this study, it seems clear that matrix representation with parsimony constitutes a potentially very promising technique for the integration of the growing flow of phylogenetic information on living and fossil species (Sanderson et al. 1993, Maddison et al. 2002, Bininda-Emonds 2004, Page 2004), thus contributing to a better understanding of the origin, diversity, and evolution of life on Earth.

**Fig. 2.** Species-level composite phylogeny of the Sphyrnidae, using matrix representation with parsimony (L = 178 steps; CI = 0.6910; RI = 0.8736; QS = -0.300).

## REFERENCES

Adams EN. 1972. Consensus techniques and the comparison of taxonomic trees. Syst. Zool. **21:** 390-397.

Baum BR. 1992. Combining trees as a way of combining data sets for phylogenetic inference, and the desirability of combining gene trees. Taxon **41:** 3-10.

Bininda-Emonds ORP. 2003. Novel versus unsupported clades: assessing the qualitative support for clades in MRP supertrees. Syst. Biol. **52:** 839-848.

Bininda-Emonds ORP. 2004. The evolution of supertrees. Trends Ecol. Evol. **19**: 315-322.

Bininda-Emonds ORP, RMD Beck, A Purvis. 2005. Getting to the roots of matrix representation. Syst. Biol. **54**: 668-672.

Bininda-Emonds ORP, HN Bryant. 1998. Properties of matrix representation with parsimony analyses. Syst. Biol. **47**: 497-508.

Bininda-Emonds ORP, JL Gittleman, MA Steel. 2002. The (super) Tree of Life: procedures, problems, and prospects. Annu. Rev. Ecol. Syst. **33**: 265-289.

Bininda-Emonds ORP, KE Jones, SA Price, M Cardillo, R Grenyer, A Purvis. 2004. Garbage in, garbage out: data issues in supertree construction. *In* ORP Bininda-Emonds, ed. Phylogenetic supertrees: combining information to reveal the tree of life. Dordrecht: Kluwer Academic Publishers, pp. 267-280.

Bininda-Emonds ORP, MJ Sanderson. 2001. Assessment of the accuracy of matrix representation with parsimony analysis supertree construction. Syst. Biol. **50**: 565-579.

Cavalcanti MJ. 2004. Geometric morphometric analysis of head shape variation in four species of hammerhead sharks (Carcharhiniformes: Sphyrnidae). *In* AMT Elewa, ed. Morphometrics - applications in biology and paleontology. Heidelberg: Springer-Verlag, pp. 97-113.

Compagno LJV. 1988. Sharks of the order Carcharhiniformes. Princeton, NJ: Princeton Univ. Press.

Dingerkus G. 1986. Interrelationships of orectolobiform sharks (Chondrichthyes: Selachii). *In* T Uyeno, R Arai, T Taniuchi, K Matsuura, eds. Indo-Pacific fish biology. Proceedings of the Second International Conference on Indo-Pacific Fishes. Tokyo: Ichthyological Society of Japan, pp. 227-245.

Gilbert CR. 1967. A revision of the hammerhead sharks (family Sphyrnidae). Proc. US Natl. Mus. **119**: 1-88.

Harvey PH, MD Pagel. 1991. The comparative method in evolutionary biology. Oxford, UK: Oxford Univ. Press.

Hendy MD, D Penny. 1982. Branch and bound algorithms to determine minimal evolutionary trees. Math. Biosci. **59**: 277-290.

Humphries CJ, LR Parenti. 1999. Cladistic biogeography, interpreting patterns of plant and animal distributions. Oxford, UK: Oxford Univ. Press.

Kajiura SM. 2001. Head morphology and electrosensory pore distribution of carcharhinid and sphyrnid sharks. Environ. Biol. Fish. **61**: 125-133.

Kajiura SM, JB Forni, AP Summers. 2003. Maneuvering in juvenile carcharhinid and sphyrnid sharks: the role of the hammerhead shark cephalofoil. Zoology **106**: 19-28.

Kennedy M, RDM Page. 2002. Seabird supertrees: combining partial estimates of procelariiform phylogeny. Auk **119**: 88-108.

Lavery S. 1992. Electrophoretic analysis of phylogenetic relationships among Australian carcharhinid sharks. Aust. J. Mar. Freshwater Res. **43**: 97-108.

Maddison DR, WP Maddison, J Frumkin, KS Schulz. 2002. The Tree of Life project: a multi-authored, distributed Internet project containing information about phylogeny and biodiversity. *In* H Saarenmaa, ES Nielsen, eds. Towards a global biological information infrastructure: challenges, opportunities, synergies, and the role of entomology. Copenhagen: European Environment Agency, pp. 5-14.

Maddison DR, DL Swofford, WP Maddison. 1997. NEXUS: an extensible file format for systematic information. Syst. Biol. **46**: 590-621.

Mank JE, DEL Promislow, JC Avise. 2005. Phylogenetic perspectives in the evolution of parental care in ray-finned fishes. Evolution **59**: 1570-1578.

Martin A. 1993. Hammerhead shark origins. Nature **364**: 494.

Musick JA, MM Harbin, LJV Compagno. 2004. Historical zoogeography of the Selachii. *In*: JC Carrier, JA Musick, MR Heithaus, eds. Biology of sharks and their relatives. Boca Raton: CRC Press, pp. 33-78.

Nakaya K. 1995. Hydrodynamic function of the head in the hammerhead sharks (Elasmobranchii: Sphyrnidae). Copeia **1995**: 330-336.

Naylor GJP. 1992. The phylogenetic relationships among requiem and hammerhead sharks: inferring phylogeny when thousands of equally most parsimonious trees result. Cladistics **8**: 295-318.

Nelson JS. 1994 Fishes of the world. 3rd ed. New York: John Wiley and Sons.

Page RDM. 1996. TREEVIEW: an application to display phylogenetic trees on personal computers. Comp. Appl. Biosci. **12**: 357-358.

Page RDM. 2004. Taxonomy, supertrees, and the Tree of Life. *In*: ORP Bininda-Emonds, ed. Phylogenetic supertrees: combining information to reveal the tree of life. Dordrecht: Kluwer Academic Publishers, pp. 247-265.

Ragan MA. 1992. Phylogenetic inference based on matrix representation of trees. Mol. Phylogenet. Evol. **1**: 53-58.

Rohlf FJ. 1982. Consensus indices for comparing classifications. Math. Biosci. **59**: 131-144.

Salamin N, TR Hodkinston, V Savolainen. 2002. Building supertrees: an empirical assessment using the grass family (Poaceae). Syst. Biol. **51**: 134-150.

Sanderson MJ, BG Baldwin, G Bharathan, CS Campbell, C Von Dohlen, D Ferguson, JM Porter, MF Wojciechowski, MJ Donoghue. 1993. The growth of phylogenetic information and the need for a phylogenetic data base. Syst. Biol. **42**: 562-568.

Sanderson MJ, A Purvis, C Henze. 1998. Phylogenetic supertrees: assembling the trees of life. Trends Ecol. Evol. **13**: 105-109.

Shirai S. 1996. Phylogenetic interrelationships of Neoselachian (Chondrichthyes: Euselachii). *In*: MLJ Stiassny, LR Parenti, GD Johnson, eds. Interrelationships of fishes. New York: Academic Press, pp. 9-32.

Soltis PS, DE Soltis. 2001. Molecular systematics: assembling and using the Tree of Life. Taxon **50**: 663-677.

Swofford DL. 2002. PAUP*: Phylogenetic Analysis Using Parsimony (*and other methods). Ver. 4.0. Sunderland: Sinauer Associates.