Recent Advances in the Origin and Early Radiation of Vertebrates
G. Arratia, M. V. H. Wilson & R. Cloutier (eds.): pp. 139-170, 11 figs.
 – ISBN 3-89937-052-X

Endocranial morphology in fossil and recent chondrichthyans

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Abstract

Craniate endocranial morphology has considerable phylogenetic potential, irrespective of how closely it corresponds to the anatomy of the brain and other cranial soft structures. Endocranial morphology may not be reflected by external features and can only be determined by direct observation; non-invasive CT-scanning is currently the preferred procedure. In this work, features of the principal endocranial and labyrinth cavities are described for the first time in several fossil elasmobranchs, based on high-resolution CT-scanning. Taxa investigated include *Tribodus*, *Egertonodus*, *Cladodoides*, *Cobelodus* and the early Devonian stem chondrichthyan *Pucapampella*. The comparison also includes CT-scan data from modern *Squalus* and *Notorynchus*, plus non-scan data from chimaeroids and the Paleozoic elasmobranchs *Orthacanthus* and *Tamiobatis*. Morphological variation in the telencephalic, hypophyseal and otic regions is described. Hybodonts and modern elasmobranchs share features in their skeletal labyrinth that are associated with semi-directional low-frequency phonoreception; these features are absent in chimaeroids, many Paleozoic elasmobranchs and *Pucapampella*. The Pennsylvanian shark *Cobelodus* represents the first known example of a chondrichthyan with a tropibasic braincase, and it shares many specialized cranial features with other tropibasic gnathostomes such as actinopterygians and certain placoderms.

Introduction

As more and more primitive gnathostome fossils have been discovered (especially in the late C20th), an impressive and previously unsuspected diversity has been revealed among the earliest forms, challenging earlier assumptions and even some of the most deeply entrenched views about basal gnathostome phylogeny. Recent fossil discoveries have highlighted the fact that at least some supposedly apomorphic osteichthyan and chondrichthyan characters have in fact been primitively conserved, and do not support monophyly of those groups as previously supposed. For example evidence of an eye-stalk (optic pedicel) has been found in Devonian actinopterygian and a sarcopterygian braincases (BASDEN et al 2000, ZHU et al. 2001); this feature known otherwise in modern elasmobranchs (but not chimaeroids) and a few placoderms. Conversely, some Devonian chondrichthyan braincases have a persistent ventral otic fissure (MAISEY 2001a, MAISEY & ANDERSON 2001), a feature which had previously been recognized only in primitive osteichthyans.

Most likely, future paleontological discoveries will continue this character whittling, perhaps even to the point where monophyly of one (or even both) the major gnathostome clades will become a real parsimony issue when fossils are included alongside the crown taxa. Such discoveries underscore how even a few relatively incomplete fossils can have a major impact at this deep phylogenetic level. We clearly need more fossils! However, as this paper will show, with modern technological improvements we can also retrieve considerably more data from existing fossils. High-resolution computed tomography (CT-scanning) now provides a non-invasive procedure which can (in conjunction with a variety of digital imaging protocols) reveal internal morphology in both modern and fossil material (ROWE et al. 1997), and offers many additional advantages because of its non-destructive nature.

Until recently there was a profound lack of empirical data concerning skeletal morphology in early shark-like fishes. As pointed out elsewhere (MAISEY 1986: 216), chondrichthyans have sometimes been

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