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Morphology of the Braincase in the Broadnose Sevengill Shark *Notorynchus* (Elasmobranchii, Hexanchiformes), Based on CT Scanning

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ABSTRACT

A detailed description is presented of the neurocranium in the hexanchiform shark *Notorynchus cepedianus*, a primitive modern elasmobranch (neoselachian). The study is based on high-resolution CT scanning and digital imaging, which revealed both the external and internal morphology of a wax-impregnated braincase. Besides providing new data concerning *Notorynchus* and neoselachians generally, the investigation also provides a control for establishing the reliability of morphological observations of fossil elasmobranch braincases based on CT scans. Many of the features described here have considerable phylogenetic potential, although comparative CT scan data are still unavailable for most modern and extinct elasmobranchs.

INTRODUCTION

This work describes the morphology of a shark braincase, based almost entirely on digital imaging and analysis of high-resolution computerized tomography (CT) scanning. Scanning provides a reliable, nondestructive procedure for repeated observation of structures in original (and often unique) specimens (Rowe et al., 1997). Digital imaging allows the three-dimensional reconstruction of internal and external morphological features in ways that are difficult or impossible with conventional serial sectioning or grinding techniques.

The principal goals of this work are twofold: (1) To provide a description of the braincase in *Notorynchus*, a primitive modern elasmobranch (neoselachian), including its external morphology and major internal features, together with an account of topographic relationships between these struc-

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tures within designated regions of the cranial walls. (2) To establish the reliability of CT scanning and digital imaging in morphological description of cranial morphology in a modern elasmobranch, thereby providing a control for the interpretation of CT scans when digitally reconstructing neurocranial features in fossil elasmobranchs whose morphology may differ from that of extant forms.

Most external features of the braincase seen in the CT scans are well documented in many modern elasmobranchs (e.g., Allis, 1923; Daniel, 1934; Iselstöger, 1937; Holmgren, 1941, Devillers, 1958), and are therefore easily verified. Unfortunately, the same cannot be said for internal features, since available descriptions differ widely in their level of detail and reliability (especially in the earlier literature), and internal morphology of the braincase has only been described in a few extant neoselachians (nevertheless, these encompass a wide systematic range of taxa, including squaloids, galeomorphs, batoids, hexanchiforms, *Heterodontus*, and *Chlamydoselachus*). As might be expected, the most extensively studied form is *Squalus*, including descriptions of its internal cranial morphology and skeletal labyrinth (Wells, 1917; Devillers, 1958; Schaeffer, 1981), the relationship of the brain and other internal structures to the braincase (Marinelli and Strenger, 1959), and cranial development (De Beer, 1931; Holmgren, 1940; El-Toubi, 1949; Jollie, 1971). In general, however, ontogenetic studies of the braincase in neoselachians have focused on cladistically derived taxa (e.g., *Squalus*, *Etmopterus*, *Scyliorhinus*, *Raja*, *Torpedo*, *Urolophus*), and there is still no description of its development in primitive neoselachians such as hexanchiforms and *Chlamydoselachus* although later developmental stages have been investigated in *Heterodontus* (De Beer, 1924; Holmgren, 1940), a putative sister taxon to modern galeomorphs (Shirai 1992, 1996; Carvalho, 1996).

The present study represents a direct extension of J. Frank Daniel's seminal early 20th-century work on elasmobranchs, because the *Notorynchus* braincase scanned for this investigation (fig. 1) is supposedly one of two wax-impregnated specimens originally described (under the name *Heptanchus*) in his classic volume *The Elasmobranch Fishes* (first published in 1922; the 1934 second edition was used in the present work). Unfortunately, his illustrations cannot be matched precisely with either of these specimens, suggesting either that his figures were based on another specimen or that they are composites based on more than one example. It nevertheless seems appropriate that the present investigation involves one of these historically well-documented specimens, and that modern technology permits new observations to be tied to those made by J. Frank Daniel more than 80 years previously.

The broadnose sevengill shark *Notorynchus cepedianus* is unusual among modern hexanchiforms in favoring relatively shallow waters of the continental shelves, whereas sixgill and sharpnose sevengill sharks (*Hexanchus*, *Heptranchias*) generally occur in deeper water (up to 1900 m) on outer shelves and upper continental slopes. The preferred habitat of *Notorynchus* is clearly more accessible to ichthyologists, perhaps explaining why this form has become the best investigated member of the Order Hexanchiformes.

From a historical perspective, Daniel's choice of a hexanchiform as a paradigm for elasmobranch anatomy was logical, because these sharks have long been considered extremely primitive and have even been compared with some of the earliest known extinct sharks such as *Cladoselache* and *Cladododoides* from the Devonian (Holmgren, 1941; Romer, 1966; Jarvik, 1980). However, the hexanchiform fossil record can be reliably traced only to the Lower Jurassic, although some isolated shark teeth of lower and middle Devonian age (Emsian-Eifelian) from Australia have been tentatively referred to the Hexanchiformes (*McMurdodus*; Turner and Young, 1987). The presence of a postorbital palatoquadrate articulation, more than five gill slits, and an unconstricted notochord have all been cited as primitive elasmobranch features retained by modern hexanchiforms (Young, 1962), although these supposedly ancient and conserved evolutionary attributes do not withstand critical appraisal. The Jurassic hexanchiform *Notidanoides* has a well-developed vertebral column, with centra constricting the notochord as in other

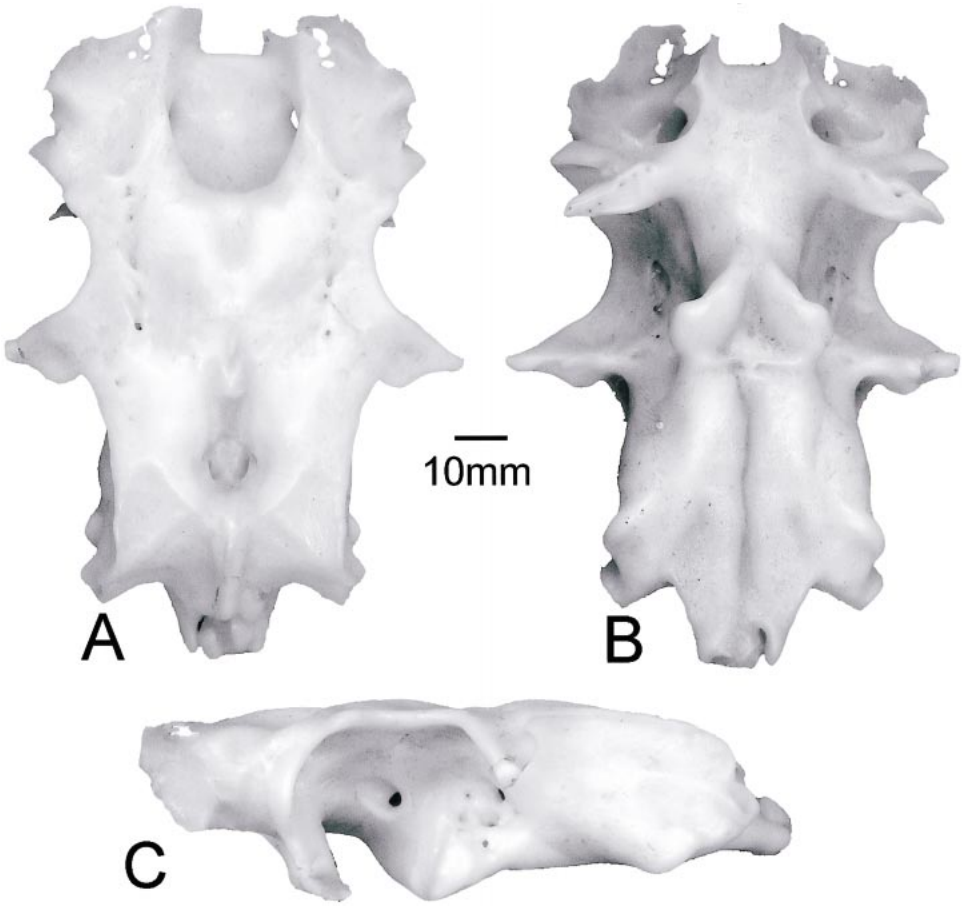


Fig. 1. *Notorynchus cepedianus* braincase photographed in dorsal (**A**), ventral (**B**), and left lateral (**C**) views. This illustration is included for comparison with digital images from CT scans in the remaining illustrations. Scale bar = 10 mm.

''modern-level'' or crown-group (neoselachian) elasmobranchs, and both the absence of vertebral calcification and corresponding notochordal constrictions may be apomorphic features of Recent hexanchiforms (Maisey, 1986). The persistent notion that elasmobranchs primitively had more than five gill slits is unsubstantiated by fossil evidence, although ironically it appears to have arisen from Dean's (1909) pioneer observations of the Devonian shark *Cladoselache*. He identified only five branchial arches in this form, but surmised that there may have been a sixth and even a seventh. Subsequently, however, the presence of only five gill arches in *Cladoselache* has become widely accepted (e.g., Blot, 1969; Moy-Thomas and Miles, 1971), and there are clearly only five gill clefts in a three-dimensional cladoselachian fossil described more recently (Maisey, 1989). Furthermore, there is no evidence of more than five branchial arches in hybodonts (Maisey, 1982), the putative sister group to neoselachians (Maisey et al., in press), and modern phylogenetic analyses of neoselachians based on morphology consistently resolve the higher number of gill clefts in modern hexanchiforms as a derived condition (Shirai, 1992, 1996; Carvalho, 1996; Carvalho and Maisey, 1996). Finally, the number of gill arches has never been determined in any fossil hexanchiform, and while it is

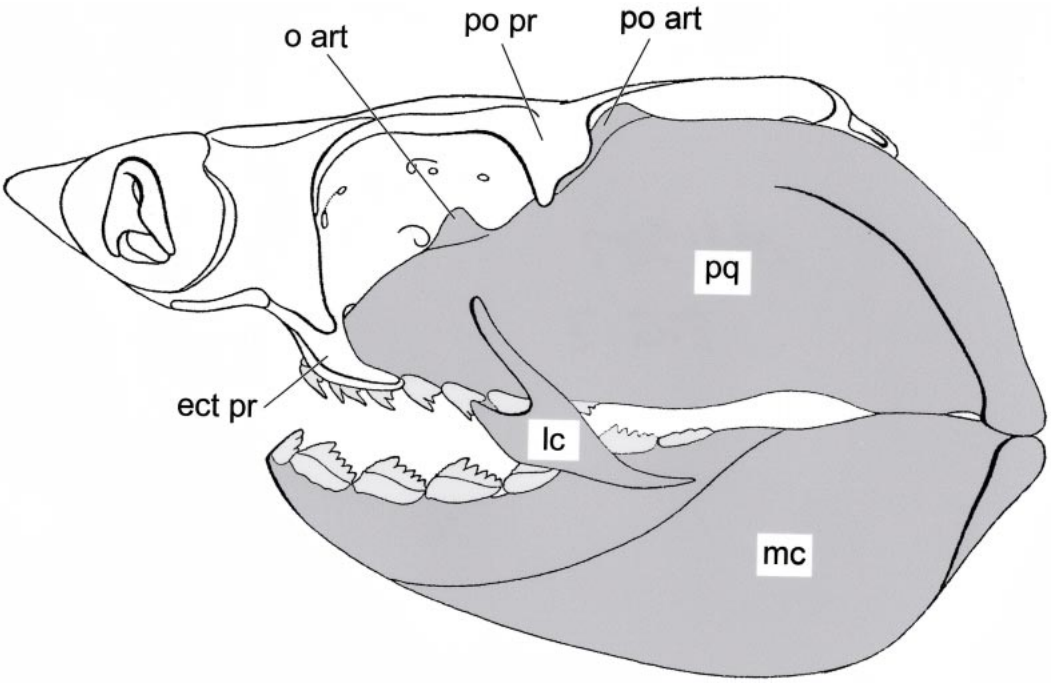


Fig. 2. *Notorynchus* braincase and jaws in lateral view, showing their articular relationships (after Daniel). No scale.

widely assumed that they all had more than five this may not necessarily have been the case.

The postorbital articulation (fig. 2) remains one of the most controversial aspects of hexanchiform anatomy, because it closely resembles the joint found in many extinct sharks (especially Paleozoic taxa). A postorbital articulation is also present in some basal neoselachians and primitive extinct galeomorphs such as *Synechodus*; Maisey, 1985), so its presence in hexanchiforms does not necessarily support a more remote placement deeper in chondrichthyan phylogeny than at the neoselachian level. In modern morphologically based phylogenetic analyses, hexanchiforms have been resolved in a basal position among neoselachians, within a large hypnosqualean clade that also includes squaloids, squatinoids, pristiophoroids, and batoids. However, in an alternative molecular phylogeny based on the RAG-1 nuclear gene (Maisey et al., in press) hexanchiforms fall at the base of a clade comprising ''orbitostylic'' sharks (sensu Maisey, 1980; essentially the hypnosqualeans minus batoids). Despite this fundamental disagreement between modern morphological and molecular analyses regarding the placement of batoids, they nevertheless agree in placing hexanchiforms firmly within the neoselachian clade (furthermore, they also agree that the frilled shark *Chlamydoselachus* is the closest living relative of hexanchiforms). Under these circumstances, the postorbital articulation in hexanchiforms could represent a conserved, plesiomorphic neoselachian condition. Among hybodonts, however, a postorbital articulation is typically absent, suggesting that this feature was either lost independently in hybodonts and various neoselachian lineages, or that it was lost once in the common ancestors of hybodonts and neoselachians and was reacquired in some neoselachians (see remarks below).

Thus, while hexanchiforms such as *Notorynchus* can be considered very primitive living neoselachians, perhaps they do not deserve the icon status of basal elasmobranchs (in the sense of a taxonomically much broader group, including all crown-group elasmobranchs plus many additional extinct selachi-

an lineages such as hybodonts, cladoselachians, etc.). Hexanchiforms are nevertheless of considerable phylogenetic importance, as one of the most primitive and geologically earliest appearing groups of crown-group elasmobranchs (even if *McMurdodus* is excluded), and they may indeed have retained many primitive features of early neoselachians. Given the interest historically shown in hexanchiforms, and the fact that these sharks are comparatively well known, *Notorynchus* certainly provides a useful starting point for morphological comparisons of cranial morphology in modern and fossil elasmobranchs.

MATERIALS AND METHODS

Notorynchus maculatus Ayres. Recent, provenance unknown, but probably from San Francisco Bay. Uncataloged specimen; wax-impregnated braincase, preserved length ca. 120 mm, reportedly one of two specimens used as a basis of J. Frank Daniel's original early 20th-century studies on elasmobranch morphology and now housed in the Museum of Vertebrate Paleontology at the University of California, Berkeley (fig. 1). Wax impregnation has preserved the braincase essentially intact, with only minor damage to external features, while CT scanning reveals minimal internal damage and complete impregnation of internal structures (a remarkable testament to preparation skills of the early 20th-century). The braincase was scanned normal to its *z* (long) axis by R. Ketcham and M. Colbert (University of Texas at Austin, 3 Dec., 1999). RLS, 420 kV, 1.8 mA, no filter, air wedge, 130% offset, gain 8, integration time 32 ms, slice thickness 0.25 mm, S.O.D. 730 mm, 1000 views, 2 rays averaged per view, 1 sample per view, interslice spacing 0.25 mm, field of reconstruction 95 mm, reconstruction offset 400, reconstruction scale 1450. 8-bit export parameters: level 2047, width 4095. Original imaging by M. Colbert using Voxblast was adapted by the author for publication here. Additional images of the vestibular region were rendered by the author using Imaris/Surpass software. The CT slices used in this investigation are available online at http://research.amnh.org/vertpaleo/maisey/ct.html

ABBREVIATIONS

aa	anterior ampulla
acv	passage for anterior cerebral vein
asc	anterior semicircular canal
atfr	acustico-trigemino-facialis recess (internal)
ba	basal angle
cer	cerebellar chamber
ds	dorsum sellae
ea	external ampulla
ect ch	ectethmoid chamber
ect pr	ectethmoid process
end f	endolymphatic foramen
eps	passage for efferent pseudobranchial artery
esc	external (horizontal) semicircular canal
fm	foramen magnum
hc?	hypophyseal canal
hl	hypotic lamina
hm art	hyomandibular articulation
hyp	hypophyseal chamber
ic	passage for internal carotid artery
inp	internasal plate
ioc	infraorbital canal
lag	lagenar chamber
lc	labial cartilage
lr	foramen for lateral ramule of buccal + maxillary ramus (= classical ''buccal branch of facial nerve'')
mc	Meckel's cartilage (lower jaw)
mcw	median capsular wall
med	medullary chamber
mes	mesencephalic chamber
myc	myencephalic chamber
not	notochordal canal
o	foramen for otic lateral line nerve (= classical ''otic ramus of trigeminal nerve'')
o art	orbital articulation for palatoquadrate
oc cot	occipital cotylus
oc cr	occipital crest
olf can	olfactory canal
olf cap	olfactory capsule (position of)
onc	orbitonasal canal
or	orbit
ora	passage for orbital artery
ot cap	otic capsule
pa	posterior ampulla
pac	ascending pre-ampullary part of posterior semicircular canal
p can	perilymphatic canal
ped	attachment area for optic pedicel
pff	prefrontal fontanelle
p fen	perilymphatic fenestra
p fos	parietal (endolymphatic) fossa

pnw	postnasal wall
po art	postorbital articulation for palatoquadrate
po pr	postorbital process
pot pr	post-otic process
p pr	preorbital process
pq	palatoquadrate
prcf	precerebral fontanelle
prof	passage for profundal nerve above olfactory capsule (= classical ''profundus branch of trigeminal nerve'')
psc	posterior semicircular canal
sac	saccular chamber
soc	passages for spino-occipital nerves
soph	passages for superficial ophthalmic ramus of anterodorsal lateral line nerve (= classical ''superficial ophthalmic branch of facial nerve'')
sor	subocular ridge
st	supratemporal lateral line nerve (= classical ''dorsal ramus of vagus'')
sup cr	supraorbital crest
tel	telencephalic chamber
t med	taenia medialis
tpf	trigemino-pituitary fossa (external)
ur	utricular recess
vlc	vestibulolateral (auricular) chambers
v pr	vestibular process
II	optic nerve
III	oculomotor nerve
IV	trochlear nerve
V	trigeminal nerve
VII	facial nerve
VII h	hyomandibular trunk of facial nerve
VIII octaval	(acousticovestibular) nerve
IX	glossopharyngeal nerve
X	vagal nerve

NOTE: Terminology for cranial nerves follows Northcutt and Bemis (1993); see text for details.

EXTERNAL MORPHOLOGY

As Daniel (1934) observed, the braincase of *Notorynchus* is a single-unit chondrocranium, like that of all modern chondrichthyans (figs. 1–6). It has been suggested that such a continuous single-unit cartilaginous chondrocranium is primitive for gnathostomes (Goodrich, 1930: 231), but there is mounting evidence that the modern elasmobranch braincase is specialized rather than primitive (particularly in the otic and occipital regions; Maisey, 2001b and in press) and that the braincase in early chondrichthyans consisted of more than one component (Maisey and Anderson, 2001). The braincase of *Notorynchus* can be characterized as platybasic, with a centrally located cranial cavity in contact with the basicranium and separating the orbital cartilages. There is no appreciable deepening of the prehypophyseal (trabecular) part of the basicranium although it is certainly narrow in places (e.g., in the posterior part of the orbit; Holmgren, 1942). As in other modern elasmobranchs, the brain in *Notorynchus* contacts the basicranium for most of its length, an arrangement which Northcutt (1978) suggested may be primitive for craniates and gnathostomes.

In *Notorynchus* there is very little calcification of the braincase or the rest of the chondral skeleton (typical for modern hexanchiforms, but unusual for neoselachians generally). An optic pedicel is present in *Notorynchus*, although it is not preserved in the CT scanned braincase. Its former position is marked by a low expansion of the orbital wall near the anterior edge of the trigeminopituitary fossa. The braincase consists of a relatively thin-walled box to which the olfactory and otic capsules are fused, and it bears articular surfaces for the palatoquadrate and epihyal (hyomandibular) cartilage laterally and for the vertebral column posteriorly (fig. 1). In dorsal view, the braincase is remarkably similar to that of *Chlamydoselachus* and *Hexanchus* (Allis, 1923; Holmgren, 1941). It is broadly pointed anteriorly and almost square posteriorly, although the occipital region projects for some distance behind the otic capsules (fig. 3). *Heptranchias* differs from *Notorynchus*, *Hexanchus* and *Chlamydoselachus* in having a much narrower braincase and a shorter postorbital process.

In *Notorynchus* the cranial roof is slightly convex anteriorly, and extends above the internal cranial cavity as far as the large dorsally located opening of the anterior or precerebral fontanelle (cavum praecerebrale of Allis, 1913). As in other modern sharks, there is no posterior fontanelle in the cranial roof (unlike in batoids, where there is often a large posterior fontanelle). There is a thin, delicate cartilaginous roof above the olfactory capsules, penetrated by a short canal for the profundal nerve, behind which there are one or two openings on each side for the distal part of the superficial ophthalmic ramus of the anterodorsal lateral line nerve. A series

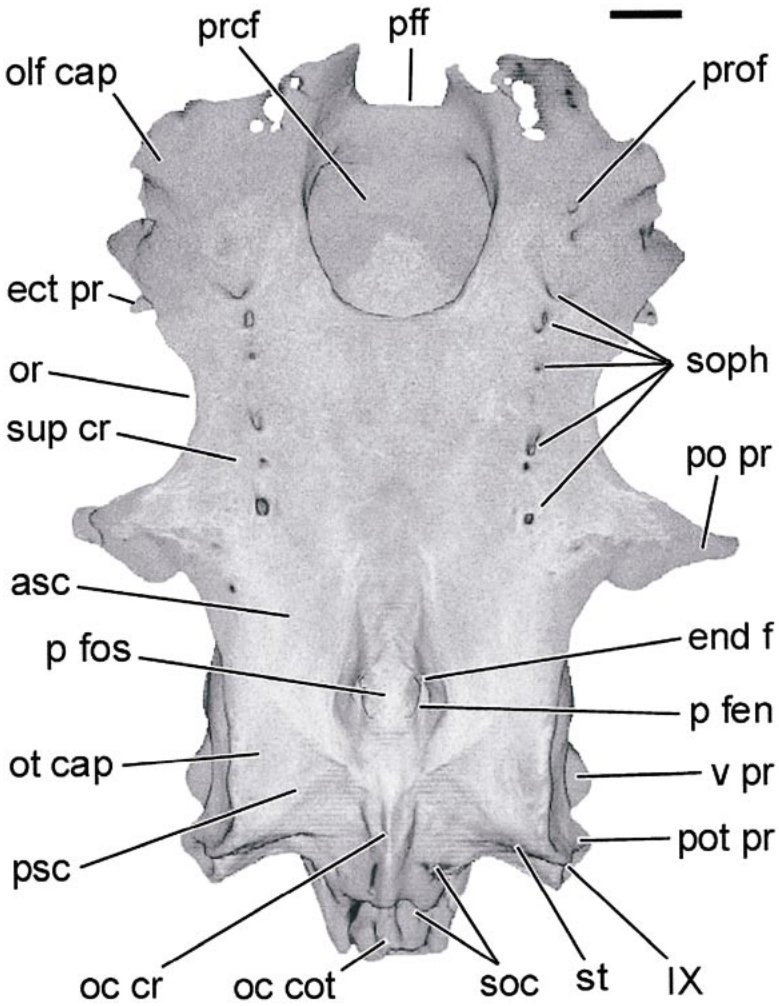


Fig. 3. Dorsal view of *Notorynchus cepedianus* braincase; external virtual image rendered from CT scans. Anterior to top of page. Scale bar = 10 mm.

of smaller foramina for ramules of the same nerve are arrayed along the wide supraorbital shelf farther posteriorly. The junction of the orbital and otic regions is marked laterally by the postorbital process (figs. 3–6). In the otic region there is a broad median dorsal depression (the parietal or endolymphatic fossa) containing the paired perilymphatic fenestrae and endolymphatic foramina (figs. 3, 6B). The positions of the anterior and posterior semicircular canals are marked by faint V-shaped ridges on the cranial roof on each side of the parietal fossa. Behind the fossa is a short occipital region with a medial crest.

As in other modern hexanchiforms, the ventral surface of the braincase in *Notorynchus* is angular, with a large, ventrally directed process beneath the orbits (figs. 4, 5B; curiously, a ventral view was never figured in any editions of Daniel's *Elasmobranch Fishes*). This process is formed within a thickened area of the basicranium termed the basal angle, which has been extensively studied in *Squalus* (El-Toubi, 1949; Jollie, 1971). A basal angle is found in modern squaloids and hexanchiforms, but not in other adult extant elasmobranchs (Holmgren, 1942). The cartilage forming the lateral part of the basal

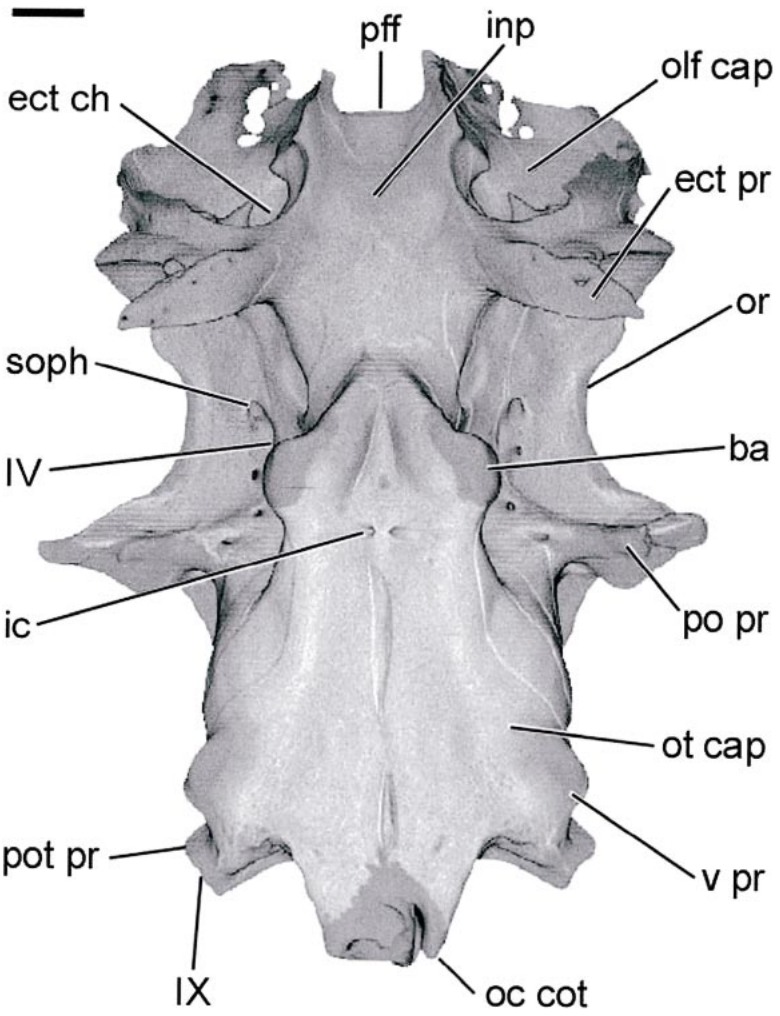


Fig. 4. Ventral view of *Notorynchus cepedianus* braincase; external virtual image rendered from CT scans. Anterior to top of page. Scale bar = 10 mm.

angle in *Notorynchus* is very thick and forms a prominent articular surface for the orbital process of the palatoquadrate.

Like other modern hexanchiforms, *Notorynchus* has a postorbital articulation for the palatoquadrate, located on the chondrified upper part of the postorbital process. However, a postorbital articulation is absent in *Chlamydoselachus*, the immediate sister taxon to hexanchiforms, according to Shirai (1992, 1996) and Carvalho (1996). Furthermore, in the Upper Jurassic hexanchiform *Notidanoides* the quadrate flange of the palatoquadrate is low and elongated (as in *Chlamydoselachus*) and there is no evidence of any articular surface for the palatoquadrate on the postorbital process (Maisey, 1986: 100). It is therefore possible that a postorbital articulation was primitively absent in hexanchiforms, and may represent a synapomorphy only of more derived members of this lineage (including the crown group). The postorbital articulation in *Notorynchus* is discussed further below.

ROSTRAL AND ETHMOIDAL REGIONS

GENERAL: The neurocranium of *Notorynchus* is broad and somewhat blunt anteriorly, with a short rostrum beneath the precerebral

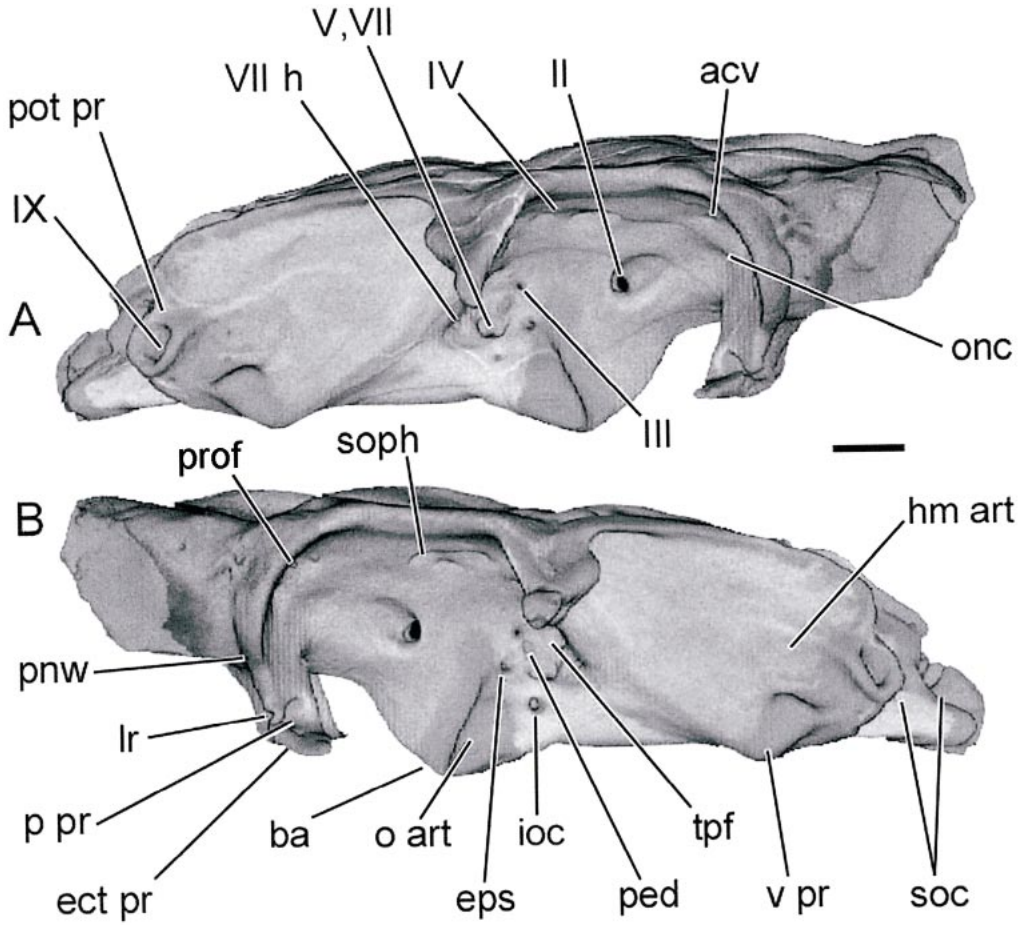


Fig. 5. Lateral views of *Notorynchus cepedianus* braincase; external virtual images rendered from CT scans. Right side (**A**); left side (**B**). Scale bar = 10 mm.

fontanelle. There is a short, broad rostral plate, which encloses a small median opening (the prefrontal fontanelle of Holmgren, 1941). The anterior margin of this fontanelle is broken in the scanned specimen, but was shown intact in the braincase illustrated by Daniel (1934: fig. 45). In other modern hexanchiforms (e.g., *Hexanchus*, *Heptranchias*) and in *Chlamydoselachus* the anterior margin of the rostral cartilage is smooth and rounded. The prefrontal fontanelle is therefore unique to *Notorynchus* among crown group hexanchiforms, but there is some evidence that one was also present in the Jurassic hexanchiform *Notidanoides* (Maisey, 1986).

ROSTRAL CARTILAGE AND PRECEREBRAL FONTANELLE: In *Notorynchus* the cartilage between the rostral plate and nasal capsules is extremely thin and is perforated by several small irregular openings (sometimes conjoined; figs. 1, 3). In *Chlamydoselachus* there is a distinct notch on either side of the rostrum, housing an anterior extension of the infraorbital sensory canal (Allis, 1923: pls. IV, VI—VIII). In the scanned specimen of *Notorynchus* no such notch is evident, although one was suggested by Holmgren (1941: fig. 5) and there is also a small notch between the rostral plate and olfactory capsule in the *Hexanchus* braincase figured by Shirai (1992: pl. 2). A similar notch for the infraorbital canal seems to have been present in *Notidanoides* (Maisey, 1986).

The dorsal opening of the precerebral fon-

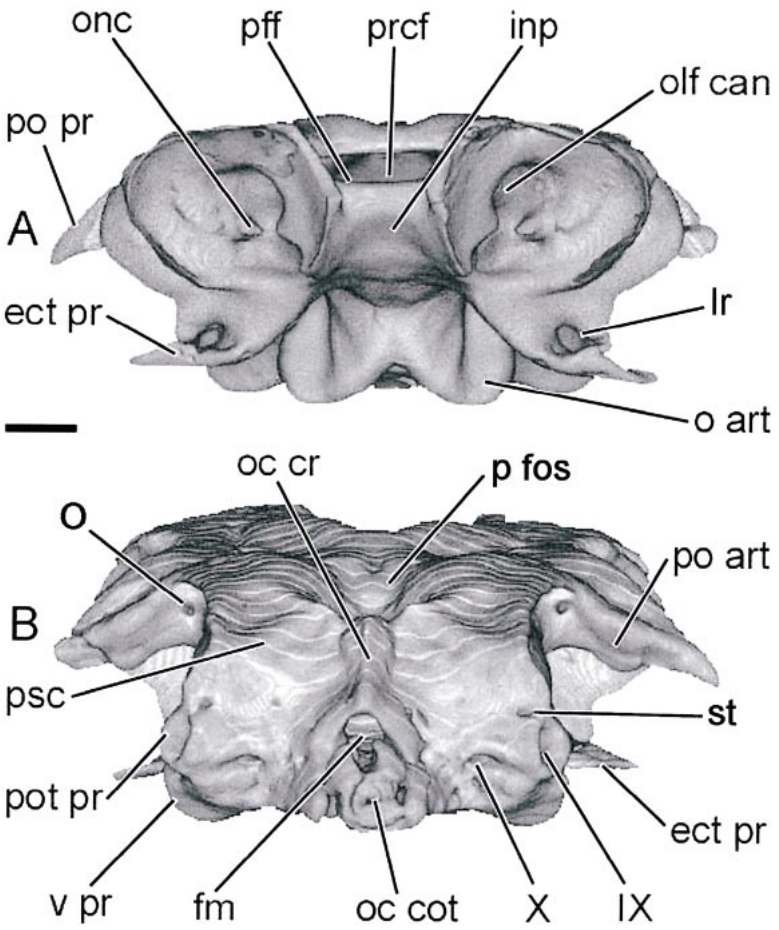


Fig. 6. Anterior (**A**) and posterior (**B**) views of *Notorynchus cepedianus* braincase; external virtual images rendered from CT scans. Scale bar = 10 mm.

tanelle in *Notorynchus* is smooth and has an almost oval outline, apart from a slight bulge posteriorly. This opening lacks a small, medially-directed processes like that found in *Chlamydoselachus* (Allis, 1923: fig. 9). According to Allis (1923), the cartilage forming the floor of the fontanelle in *Chlamydoselachus* probably corresponds to the rostral plate of Sewertzoff (1899), and the same may be true in *Notorynchus*, although the earliest stages of cranial development have still not been described in any of these taxa. The rostral plate in these forms may represent an anterior extension of the trabeculae as in *Squalus*, rather than a separate rostral cartilage as in galeomorphs (De Beer, 1937; El-Toubi, 1949; Devillers, 1958).

The floor of the fontanelle in the scanned *Notorynchus* braincase is confluent with the floor of the cranial cavity farther posteriorly (fig. 3). Although the precerebral and cranial spaces would have been separated in life by the membranous dura mater surrounding the brain, no obvious skeletal feature marks the former position of this membrane (a common situation in elasmobranchs). Instead, the cartilage flooring the cranial cavity and the precerebral area farther anteriorly is smoothly continuous, suggesting that the morphology of the anterior basicranium was not greatly affected by the anterior extent of the forebrain or the position of the dura mater. Similarly, the posterior limit of the precerebral fontanelle located in the roof of the braincase

does not correspond to the anterior limit of the cranial cavity in *Notorynchus*, because the pineal organ (which is located within the upper anterior part of the cranial cavity) is not enclosed by cartilage and lies instead within the fontanelle (as in *Chlamydoselachus*). In many other elasmobranchs there is a separate pineal opening in the roof of the braincase, marking the position of the pineal organ behind the fontanelle (e.g., *Hexanchus*, *Squalus*). Thus, the extent to which the fontanelle is truly precerebral in elasmobranchs is variable and not easily determined from inspection of the braincase alone. When ''soft'' tissues are unavailable (as in fossils), the absence of noteworthy morphological landmarks tends to obscure the original boundary of internal cranial and extracranial spaces in the ethmoid region.

In *Notorynchus* the ventral surface of the cartilage flooring the precerebral fontanelle is concave from side to side, and there is no cartilaginous keel in the ventral midline of the nasal or ethmoid region (fig. 4). In life the precerebral fontanelle is separated from the olfactory capsules by the ectethmoid chamber (an extracranial space behind and medial to the capsules), but the olfactory capsule is missing in the scanned braincase and the precerebral fontanelle therefore appears to be confluent with the olfactory chamber. In elasmobranchs generally, the nasal septum is formed by fusion and upgrowth of the anterior part of the trabeculae (Goodrich, 1930: 232). In *Notorynchus* this area is slightly narrower than in *Chlamydoselachus* or *Hexanchus*, but is still much wider than in *Heptranchias*.

NASAL REGION: There appears to be a correlation between the width of the rostral plate/nasal septum and the lateral spacing of the olfactory capsules and ectethmoid chambers. The rostral plate and nasal septum are both broad in *Chlamydoselachus* and *Notidanoides*, and their olfactory capsules and ectethmoid chambers are widely separated. In *Hexanchus* and *Notorynchus* the rostral plate and nasal septum are slightly narrower, but still separate the capsules and ectethmoid chambers quite widely. However, in *Heptranchias* (and some squaloids), the rostral plate and nasal septum are both very narrow, and the olfactory capsules and ectethmoid chambers are located close to the ventral midline.

The olfactory capsules are missing in the CT scanned *Notorynchus* braincase, but their original position is clearly marked by large chambers (the cavum nasi of Gaupp, 1906) formed in the cartilage of the nasal septum. The posterior wall of the cavum nasi (antorbital process of Goodrich, 1930) forms the postnasal or antorbital wall (= planum orbitale or planum orbitonasalis) and separates the cavum nasi from the orbital opening.

In *Notorynchus* a large olfactory canal extends posteromedially, and in life the nasal apertures are directed ventrally (and to some extent laterally; Holmgren, 1941). According to Goodrich (1930), the olfactory canal is first defined by cartilage forming the antorbital process, which represents an outgrowth of the trabecular cartilage around the olfactory tract that then rejoins the nasal septum. In *Notorynchus* a small orbitonasal canal runs through the postnasal wall from the orbit and opens anteriorly into the ectethmoid chamber below the opening of the olfactory canal (fig. 6A). In hexanchiforms and many squaloids, the ectethmoid chamber is filled in life with diffuse connective tissue (Holmgren, 1941), but in *Chlamydoselachus* the chamber is covered by a tough, glistening membrane (Allis, 1923). In *Notorynchus* the roof of the ectethmoid chamber contains paired openings into the precerebral region. Whether these opened into the fontanelle or the cranial cavity behind the dura mater cannot be determined from the preserved braincase alone, although they are tucked within the olfactory canals and are not exposed in dorsal view like the paired subnasal or rostral fenestrae (''basal communicating canals'') of other taxa such as *Squalus*, which do not contain blood vessels or nerves and are filled with connective tissue in life. In many squaloids, the subnasal fenestrae open directly into the floor of the precerebral fontanelle.

ECTETHMOID AND PREORBITAL PROCESSES: Daniel (1934) identified two processes of the postnasal wall of *Notorynchus*: a preorbital process located on the posterolateral margin of the postnasal wall, and an antorbital (ectethmoid) process farther ventrally (fig. 5B). There is some evidence that both these processes were also present in the Jurassic hex-

anchiform *Notidanoides* (Maisey, 1986: fig. 5).

The ectethmoid process of *Notorynchus* clearly differs from the ''antorbital process'' discussed by Goodrich (1930), which is an embryonic precursor of the entire postnasal wall. An ectethmoid process is well developed in all hexanchiforms, as well as in *Chlamydoselachus*, squaloids, and some galeomorphs (Allis, 1923; Holmgren, 1941; Schaeffer, 1981), and has been defined as forming from cartilage located lateral to the orbitonasal canal (De Beer, 1931). Unfortunately, this topographic/ontogenetic criterion can only be established reliably using an ontogenetic series, and since cranial development has never been adequately investigated in a modern hexanchiform the true identity of the supposed ectethmoid process in these forms remains untested (although it continues to be regarded as such here). Similar problems surround the supposed ectethmoid process in certain extinct elasmobranchs (e.g., in hybodonts: Maisey, 1983; Coates and Sequeira, 1998; Maisey et al., in press).

In *Notorynchus* the ectethmoid process clearly arises from the posteroventral margin of the postnasal wall, as in *Chlamydoselachus* and *Hexanchus*. In all these taxa the process is very large, extending posterolaterally behind the olfactory capsules and lateral to the ectethmoid chamber. By contrast, in *Heptranchias* the ectethmoid process is much smaller, oriented more posteriorly and medially, and does not extend lateral to the ectethmoid chamber. In all modern hexanchiforms, the ectethmoid process is separated from the ectethmoid chamber by a narrow cartilaginous band, whereas in *Chlamydoselachus* the anterior margin of the process overhangs the posterior margin of the ectethmoid chamber without any intervening cartilage. In modern squaloids the ectethmoid process and chamber are usually separated by a broad cartilaginous area of the postnasal wall (= antorbital shelf of Wells, 1917), and the process is usually positioned some distance behind the chamber (e.g., *Squalus*; Devillers, 1958: fig. 349). Overlap of the ectethmoid chamber by the ectethmoid process in *Chlamydoselachus* is therefore an unusual condition, apparently representing an autapomorphy of the genus.

The ectethmoid process in *Notorynchus* is unusual in having a canal passing through it anteroposteriorly (fig. 6A). According to Holmgren (1941: fig. 5) this canal houses the buccal branch of the facial nerve (= buccal ramus of the anterodorsal lateral line nerve; Northcutt and Bemis, 1993). The canal is absent in other hexanchiforms and *Chlamydoselachus*. In *Chlamydoselachus* the buccal ramus of the anterodorsal lateral line nerve passes dorsal to the ectethmoid process, along with the maxillary artery, the facial vein, and the maxillary ramus of the trigeminal nerve (Allis, 1923; Jarvik, 1942). The cartilage forming this process presumably extends slightly farther dorsally in *Notorynchus* than in *Chlamydoselachus*.

The elasmobranch preorbital process seems to lack any precise topographic definition, although according to Daniel (1934) it is located even farther laterally on the postnasal wall than the ectethmoid process. Since it is difficult to define, its systematic distribution is problematic to determine. A preorbital process is supposedly present in *Notorynchus* and *Hexanchus* but seems to be absent in *Heptranchias* and weakly developed in *Chlamydoselachus* (Holmgren, 1941). There is apparently no equivalent process in *Squalus*.

ETHMOIDAL ''ARTICULATION'': According to Wolfram (1984), in *Notorynchus* the anterior ends of the palatoquadrates are strongly bound to each other by ligaments; this symphsis is held in place against the floor of the braincase by additional strong, ligamentous tissue which arises just anterior to the articulation (located near at the midline between the antorbital processes) and extends above the tooth-bearing part of the palatoquadrate, eventually merging with a tendon associated with the adductor musculature. Unfortunately, there is no indication of where these ligaments arose on the cleaned braincase, and no articular surface for an ethmoidal articulation can be identified in the *Notorynchus* braincases examined here, nor in other hexanchiforms or *Chlamydoselachus*.

In *Orthacanthus* (and apparently in many other Paleozoic sharks), the anterior part of the palatoquadrate has a well-developed process anteriorly, which articulated with the

ethmoid region of the basicranium just below or behind the olfactory capsules (Hotton, 1952; Schaeffer, 1981). Wolfram (1984) noted that the anterior ends of the palatoquadrates in *Orthacanthus* do not meet at the midline and lack a symphyseal surface, and instead are rounded as in *Notorynchus*, suggesting a loose symphyseal connection that would permit a degree of lateral eversion of the palatoquadrate. Furthermore, she noted that the anterior process in *Orthacanthus* is strongly angled inwards in the orbit, unlike the more vertical orbital articulation of *Notorynchus* and other hexanchiforms. Although the ethmoidal articulation in extinct sharks such as *Orthacanthus* differs from the orbital articulation of neoselachians in its topographic position within the orbit, its relationship to the efferent pseudobranchial foramen and polar cartilage are similar and the articulations could be homologous.

ORBITAL REGION

GENERAL: As in other modern elasmobranchs, in *Notorynchus* the entire orbital wall is chondrified except for various foramina for nerves and vessels (fig. 5). The most prominent opening in the orbital wall is for the optic nerve, which is located more or less centrally in the orbit. Some distance behind this, at approximately the same height in the orbit, is a smaller opening for the oculomotor nerve. According to Sewertzoff (1899), the optic and oculomotor foramina provide important developmental landmarks, marking the approximate line of fusion between the embryonic trabecular and orbital cartilages. The superficial ophthalmic branch of the anterodorsal lateral line nerve leaves the orbit anteriorly via the preorbital canal, near to which is a small foramen for a deep branch of the trigeminal nerve. Closer to the roof of the orbit (behind the superficial ophthalmic foramen) is a small trochlear foramen, providing innervation to the superior oblique eye muscle. In the front of the orbit, above the orbitonasal canal, the foramen for the profundal nerve leads into a short, anterodorsally directed passage which opens on the braincase roof behind the ectethmoid chamber (figs. 3, 5B). A foramen for the anterior cerebral vein is also situated here (fig. 3A), just above the profundal foramen.

TRIGEMINO-PITUITARY FOSSA: In gnathostomes, the main branches of the trigeminal and facial nerves leave the braincase via foramina situated low down in the back of the orbit, just in front of the otic capsule and postorbital process. In *Notorynchus* and many other modern elasmobranchs, the openings for these nerves are located in the posteroventral part of the orbit, within an external embayment or recess (the orbital fissure of Daniel, 1934; in part the trigeminopituitary fossa of Allis, 1914; trigemino-facialis recess of Schaeffer, 1981). The anteroventral margin of the trigemino-pituitary fossa also contains foramina for the abducens nerve and pituitary vein (fig. 5). This recess is distinct from the acustico-trigemino-facialis recess of Allis (1914), which is a related but internal feature of the endocranial wall that contains the exits not only of the trigeminal and facial nerves, but also the passage of the acoustic nerve leading into the otic capsule (discussed below).

Within the trigemino-pituitary fossa in *Notorynchus* there is a narrow prefacial commissure (an upgrowth of the embryonic basal plate extending to the otic capsule; Goodrich, 1930). The commissure separates the palatine ramus and hyomandibular trunk of the facial nerve from what used to be regarded as its ophthalmic and buccal branches (corresponding to the anterodorsal lateral line nerve of Northcutt and Bemis, 1993), as well as separating the facial and trigeminal nerves. The prefacial commissure therefore takes on heightened morphological significance according to this interpretation, because it more clearly separates distinct nerves (the facial, and the anterodorsal lateral line + trigeminal), rather than merely dividing the ''facial'' components.

SUBORBITAL REGION: In *Notorynchus* (as in other modern hexanchiforms and squaloids), a suborbital shelf is absent, although there is an inflated area of cartilage forming the medial surface of the orbital articulation on either side of the basal angle. In the Upper Jurassic hexanchiform *Notidanoides*, the basicranium is broader than in *Notorynchus*, but a suborbital shelf still seems to be absent (Maisey, 1986: fig. 6). In *Squatina*, a sub-

orbital shelf is present behind the orbital articulation, which is unusual in (1) extending obliquely across much of the orbit, and (2) not forming a well-defined articular surface as in other orbitostylic sharks (Iselstöger, 1937; Holmgren, 1941). Unfortunately, ontogenetic data for *Squatina* are mostly lacking, and consequently it is not possible to determine whether its suborbital shelf is homologous with that of galeomorphs.

BASAL ANGLE AND ORBITAL ARTICULATION: In *Notorynchus*, the basal angle forms a prominent projection on the ventral surface of the braincase. Its topographic relationships to surrounding features are complex; it is positioned below and slightly anterior to the trigemino-pituitary fossa, and behind the level of the optic foramen but anterior to the optic pedicel, rectus musculature, and efferent pseudobranchial foramen (figs. 4, 5). The lateral surface of the basal angle includes a smooth, almost vertical groove forming an articular surface for the orbital process of the palatoquadrate (= ''ethmopalatine groove'' of Wilga, 2002). The dorsal part of this groove extends onto the orbital wall and is positioned approximately midway between the optic foramen and trigemino-pituitary fossa, but most of the groove lies entirely below the level of these features. The margins of the articular groove are formed in life by fibrous connective tissue connecting it to the orbital process of the palatoquadrate (fig. 2), and these are loosely held together by a ligamentous sheet forming a sac which encloses the entire joint (Wolfram, 1984).

HYPOPHYSEAL REGION: There is no hypophyseal opening in the basicranium of *Notorynchus*, although there is evidence of a vestigial hypophyseal duct within the thickness of the basicranial cartilage (discussed below). The internal carotid foramina (which lie more or less between the postorbital processes in *Notorynchus*) nevertheless provide an important topographic and developmental landmark, since the internal carotids enter the braincase between the embryonic trabeculae and parachordals. During ontogeny, the paired trabeculae fuse to each other anteriorly, and also to the basal (parachordal) plate posteriorly, leaving an anterior basicranial fenestra containing the hypophysis and internal carotids (Goodrich, 1930: 234). Fusion between the trabecular and parachordal cartilages may also involve a separate polar cartilage (e.g., *Squalus*; van Wijhe, 1922), but it is unknown whether such a cartilage is present in *Notorynchus*. The polar cartilage has a widespread occurrence in many gnathostomes, and may even surround the internal carotids (e.g., in birds; Goodrich, 1930).

POSTORBITAL PROCESS

GENERAL: In *Notorynchus* the postorbital process is a prominent feature of the braincase defining the posterior limit of the orbit, extending laterally from its midregion above the lateral head vein and the hyomandibular ramus of the facial nerve (figs. 1–6). The postorbital process is an important developmental landmark in gnathostomes because it arises from the anterolateral margin of the basal plate within the blastemic lateral commissure, level with or just behind the embryonic trabecular–parachordal junction. The lateral commissure develops secondarily as an upward extension of the basal plate that eventually fuses with the prootic region of the otic capsule (De Beer, 1937; Schaeffer, 1981). According to Holmgren (1940, 1941), in hexanchiforms the lateral commissure does not persist and only the primary postorbital process (extending from the embryonic supraorbital cartilage) is chondrified (fig. 5). Thus, the postorbital articulation (discussed below) is confined to the primary postorbital process and does not include cartilage derived from the lateral commissure (an important difference from extinct amphistylic sharks).

INNERVATION: In *Notorynchus* the dorsal surface of the postorbital process is flat or slightly concave, and bears a few small openings for branches of the buccal ramus of the anterodorsal lateral line nerve, innervating the overlying sensory canal (figs. 1A, 3). Similar openings occur in *Chlamydoselachus*, but are far more numerous (Allis, 1923). There is a single opening near the base of the posterior surface of the postorbital process in *Notorynchus*, corresponding to the foramen for the otic lateral line nerve in *Chlamydoselachus* (fig. 6B).

POSTORBITAL ARTICULATION: One of the most important features of the postorbital

process in hexanchoids is the presence of an articular surface for the otic process of the palatoquadrate (figs. 1–6). In *Notorynchus*, the surface extends transversely across part of the posterior surface of the process. No comparable articulation is present in *Chlamydoselachus*, nor has one been described in any other modern elasmobranch. It has been claimed that a postorbital articulation is present in the crocodile shark *Pseudocarcharias* (Compagno, 1977), but its structure has never been described and the connection is apparently lost during jaw protraction.

Curiously, the structure of the postorbital articulation in hexanchiforms has not been described in detail, despite its obvious phylogenetic interest (although it has been investigated in *Notorynchus*, as part of an unpublished Master's thesis; Wolfram, 1984). In *Notorynchus*, the articular surface of the postorbital process is little more than a flat surface extending posteroventrally (fig. 4). This surface contacted a corresponding anterodorsally directed surface on the palatoquadrate. According to Wolfram (1984), these articulating surfaces are covered with fibrous connective tissue and are surrounded by a tough connective tissue which forms a bursa around the articulation. Garman (1913) noted that the postorbital articulation in *Heptranchias* is stronger than in *Notorynchus* or *Hexanchus*; Holmgren (1941) also noted that the articular surface for the palatoquadrate (''articular disc'') on the postorbital process of *Heptranchias* was ''well delimited''.

Wolfram (1984) concluded that, given the ligamentous connections and articular surfaces she observed in the postorbital articulation of *Notorynchus*, only one pattern of palatoquadrate movement was possible, involving lateral eversion of the posterior end of the palatoquadrate as well as slight medial rotation of the anterior margin about its long axis. She found that such movement produced (1) rotation of the palatoquadrate at the postorbital articulation about an axis running parallel to its long axis; (2) translation along the groove forming the orbital articulation, and (3) posterior translation of the upper jaw symphysis along the ventral surface of the braincase. Luther (1908) and Wolfram (1984) both concluded that no anterior translating or shifting of the jaws is possible in the hexanchoids they examined.

The postorbital articulation in extinct amphistylic sharks such as *Orthacanthus*, *Tamiobatis*, and *Cladodoides* is more complex than in hexanchiforms. The articular surface is about twice as wide as deep (i.e., much wider than in *Notorynchus*), and is usually curved into a complex saddle shape, convex transversely and concave dorsoventrally. Also, the articular surface typically has a pronounced anhedral angle, so its distal extremity is somewhat lower than its proximal part. Furthermore the articular surface is located farther laterally on the postorbital process than in *Notorynchus* and other hexanchiforms, and it clearly extends onto the lateral commissure unlike in modern hexanchiforms. Thus, the postorbital articulation of hexanchiforms differs significantly from that of extinct amphistylic sharks both in its topographic extent and its relationship to the lateral commissure, although they are similar in their presumed relationship to the lateral head vein/jugular canal and involve identical skeletal components (e.g., postorbital process, otic flange of palatoquadrate). A postorbital articulation is supposedly present in the extinct neoselachian *Synechodus*, but its lateral commissure was unchondrified and presumably the articular surface was confined to the primary postorbital process as in hexanchiforms (Maisey, 1985).

PARACHORDAL PLATE AND OTIC CAPSULES

GENERAL: In craniates generally, the otic capsules develop above the basal (parachordal) plate as independent structures dorsal to the hyoidean and first branchial arches, first appearing as invaginations (otic placodes) which subsequently undergo an unequal growth pattern to produce all the major structural parts of the inner ear (Maisey, 2001a). Chondrification of the otic capsule supposedly begins at two different centers, one associated with the anterior and horizontal ampullae, the other with the posterior ampulla (*Squalus*; van Wijhe, 1922). The fact that the anterior and horizontal ampullae share a single chondrification center undoubtedly reflects an underlying developmental relation-

ship between them, since gene expression patterns of the anterior and horizontal cristae are similar (Morsli et al., 1998), and the anterior and horizontal ampullae are both supplied by the anterior branch of the octaval (acousticovestibular) nerve whereas the posterior ampulla is not (Maisey, 2001a).

In elasmobranchs, a separate floor (the hypotic lamina or lamina basiotica) develops from the parachordal cartilage beneath the capsule (Goodrich, 1930). The otic capsule eventually fuses with the hypotic lamina, although parts of the capsule floor may remain unchondrified (especially above the passage for the glossopharyngeal and middle lateral line nerves, as discussed below). Space between the lamina and capsule (i.e., the embryonic metotic or basicapsular fissure) is progressively obliterated by this fusion, leaving only the glossopharyngeal canal (Goodrich, 1930; Schaeffer, 1981). The metotic fissure is also closed by the occipital pila, which grows up and fuses with the wall of the otic capsule above the vagal nerve. The posterior semicircular canal is ultimately sandwiched between the glossopharyngeal canal medially and vagal canal laterally.

PARIETAL (ENDOLYMPHATIC) FOSSA: In *Notorynchus*, the mid-dorsal surface of the otic region includes the parietal fossa (figs. 1, 3, 6B), a shallow depression located between the otic capsules. A parietal fossa is well developed in most modern elasmobranchs, although its extent and depth differ considerably. In *Notorynchus*, the fossa is well defined laterally, but merges smoothly with the cranial roof anteriorly and posteriorly. By contrast, in *Chlamydoselachus* the posterior wall of the fossa is steep although its anterior margin is smooth (Allis, 1923), and in *Squalus* the fossa lacks a well-defined border except posteriorly (Devillers, 1958: fig. 345). During ontogeny, the anteroposterior extent of the elasmobranch parietal fossa is defined by two transverse bridges between the otic capsules, the synotic tectum anteriorly and posterior tectum posteriorly (although the distinction between them is not absolute; Gaupp, 1906; Goodrich, 1930).

The parietal fossa contains large paired perilymphatic fenestrae and smaller paired endolymphatic foramina. The perilymphatic fenestrae are covered by a membrane in life, below which the perilymphatic canals are connected (via a posterior canal duct) to the perilymphatic space surrounding the posterior semicircular canal (Corwin, 1989). Developmentally, the perilymphatic fenestra represents an unchondrified region in the medial wall of the otic capsule, where it meets the posterior semicircular canal (De Beer, 1931, 1937; Holmgren, 1940). The inner ear of modern elasmobranchs is highly specialized toward semidirectional low-frequency phonoreception (Maisey, 2001a), but the perilymphatic fenestrae represent the only external feature of the braincase that is associated with this ability (many internal skeletal features are also associated with it; see discussion below). The perilymphatic fenestrae lie medially and posteriorly to the paired endolymphatic foramina, which are connected with the saccular region of the inner ear via the endolymphatic ducts.

LATERAL SURFACE OF OTIC REGION: In *Notorynchus* this region is relatively featureless except posteriorly. The dorsal margin of the lateral surface forms a distinct ridge as in *Chlamydoselachus*, which Allis (1923) regarded as corresponding to the spheno-pterotic ridge of actinopterygians (although such putative homologies seem dubious given the lack of any ossification centers in elasmobranchs comparable to those of osteichthyans). A similar ridge extends posteriorly from the postorbital process in many modern elasmobranchs. In *Notorynchus*, the ridge is relatively straight, whereas in *Chlamydoselachus* and *Squalus* it bears a short process (pterotic process; Wells, 1917: fig. 1; Allis, 1923: figs. 8–10; Devillers, 1958: fig. 345).

In *Notorynchus*, the head of the hyomandibula makes contact with the posterior part of the capsular wall at a weakly defined articular fossa (fig. 5B), unlike in *Chlamydoselachus* where the dorsal margin of the fossa forms a distinct ridge on the lateral capsular wall. According to Gegenbaur (1872) and Gadow (1888), this connection between the hyomandibula and braincase in sharks is merely ligamentous rather than a true articulation; Gadow (1888) even suggested that in *Hexanchus* there is no absolute contact between the hyomandibula and cranium because of intervening ligaments. However, Wolfram (1984) found that in *Notorynchus*

the hyomandibula is held securely in the articular fossa by ligaments, and it contacts the medial capsular wall. She found only a limited range of motion was permitted by these ligaments, including some rotation except anteriorly, with the greatest range of movement about an axis parallel to the long axis of the fossa (allowing the distal end of the hyomandibula to swing laterally).

The hyomandibular fossa in *Notorynchus* forms a deep embayment between two processes: ventrally there is a rather short, square vestibular process (Gadow, 1888) and dorsally there is a longer postotic process containing the glossopharyngeal foramen (Holmgren, 1941), just above which is a small foramen housing what is classically regarded as a dorsal branch of the vagal nerve, but now identified as the supratemporal lateral line nerve (figs. 3, 6B). According to Holmgren (1941: figs. 6,8), the corresponding foramen in *Chlamydoselachus* houses the same nerve, although this was not noted by Allis (1923).

Postotic and vestibular processes are both present in other modern hexanchiforms and at least the postotic process is present in *Notidanoides* (= ''lateral otic process'' of Maisey, 1986). Both processes are also present in *Squatina* (''Dorsalrand'' and ''Basalrand des Hyoidgelenkes'' of Iselstöger, 1937: pl. 6). In many other modern elasmobranchs the glossopharyngeal canal is contained within a postotic process, but the vestibular process is highly variable in its occurrence and is weak or absent in some taxa.

In *Notorynchus*, the vestibular process is not associated with any foramen. By contrast, in *Hexanchus* the vestibular process contains an opening (the ''vacuity below hyomandibular fossa'' of Shirai, 1992), and Gegenbaur (1872) illustrated a corresponding foramen in *Heptranchias*. A vestibular process is present in *Chlamydoselachus*, but it does not have a foramen.

The postotic process has been compared with the lateral otic process in other extinct sharks (e.g., *Orthacanthus*, *Tamiobatis*; Schaeffer, 1981), but that process is positioned farther dorsolaterally (relative to the inferred position of the glossopharyngeal nerve) than the postotic process, and the lateral otic process in these fossils does not contain the glossopharyngeal canal.

VENTRAL SURFACE OF OTIC REGION: The region behind the internal carotid foramina mostly represents cartilage of parachordal derivation. In *Notorynchus*, it is relatively featureless, apart from a median sulcus (perhaps emphasized by slight shrinkage of the cartilage), corresponding approximately to the former line of contact between the paired parachordals. Posteriorly the ventral surface is continuous with the occipital arch, as in other modern elasmobranchs.

VAGAL AND GLOSSOPHARYNGEAL CANALS: The topographic relationship of the glossopharyngeal and vagal openings differ in *Notorynchus* and *Chlamydoselachus*. According to Allis (1923), in *Chlamydoselachus* there is a large glossopharyngeal-vagal fossa, with the vagal foramen in its medial part and the glossopharyngeal foramen in its ventrolateral corner. By contrast, in *Notorynchus* the vagal foramen lies within the base of the notch formed by the posterior capsular wall and the occipital region, separate from the glossopharyngeal canal (as in *Hexanchus*; Shirai, 1992: pl. 21A). However, Allis (1923: fig. 10) illustrated two different arrangements in his specimen of *Chlamydoselachus*, with the right glossopharyngeal opening separated from the remainder of the fossa by a bridge of cartilage. If the posterior wall of the glossopharyngeal canal failed to develop completely in *Notorynchus* or *Hexanchus*, it would result in a deep fossa containing both the vagal and glossopharyngeal openings, much as in *Chlamydoselachus*. Variation in the extent of the posterior wall of the glossopharyngeal canal may therefore be decisive as to whether its exit also includes the vagal foramen in elasmobranchs. In *Heterodontus* and many other modern elasmobranchs the vagal and glossopharyngeal openings are separate (Daniel, 1915), but in extinct hybodont sharks there may be a deep glossopharyngeal-vagal fossa containing both nerves (Maisey, 1983). In addition, the posterior lateral line nerve (classically identified as the lateral line ramus of the vagal nerve) should also exit through this opening.

OCCIPITAL REGION

GENERAL: Anteriorly, the occipital block in *Notorynchus* is wedged firmly between the

otic capsules as in other modern elasmobranchs, with the vagal foramen positioned lateral to the foramen magnum. There are no ''condylar ridges'' for vertebral branches of the dorsal aorta like those described on either side of the occiput in *Chlamydoselachus* (Allis, 1923). Shirai (1992: pl. 2) illustrated large paired arches defining openings in the posterolateral margin of the basicranium in *Hexanchus*, but he did not identify them. They are positioned farther laterally than the condylar ridges in *Chlamydoselachus*, and it is uncertain whether they housed aortic vessels.

OCCIPITAL COTYLUS: In *Notorynchus*, a strong connection with the vertebral column is provided by a deep occipital cotylus (figs. 4, 6B). A similar cotylus is present in hybodonts and many Paleozoic sharks; Maisey, 1983). In most modern sharks (but not batoids), an occipital half-centrum is incorporated into the braincase, occupying the cotylus (= basioccipital fovea; Shirai, 1992). There are traces of an occipital half-centrum in *Notorynchus*, although it is poorly calcified and does not fill the entire cotylus. The lateral margins of the cotylus extend posteriorly to flank the hemicentrum and at least the first neural arch of the vertebral column. In *Chlamydoselachus*, there is also a well developed occipital connection (''condyle'' of Allis, 1923), bounded ventrally by condylar ridges which have a slightly convex posterior surface forming an articulation with a corresponding concavity of the first vertebra. Daniel (1934: fig. 47) depicted the lateral margin of the cotylus as contacting the first free basiventral in *Notorynchus*. Gegenbaur (1872) identified a condylar ridge in *Hexanchus* and *Notorynchus*, but did not find any real articulation.

According to Shute (1972), in *Squalus* the cranio-vertebral articulation includes paired occipital condyles, supposedly formed by a basidorsal which has fused to the posterior end of the parachordal. Each condyle articulates with the first free interdorsal, which is pierced by a dorsal nerve root as in more caudal elements, and its corresponding ventral root passes behind (not through) the condyle to supply the first metotic myotome. However the ''condyles'' to which Shute (1972) referred apparently do not correspond with the paired articular condyles on either side of the occipital region recognized by most other workers. These are situated in a ventrolateral position and have no connection with the dorsal arcualia, meeting instead with paired basiventrals (Compagno, 1988). The condyles are formed within cartilage of parachordal derivation, within the posteromedial part of the basicranium lying medial to the vagal canal. Thus, in modern sharks the principal cranio-vertebral articulation is provided by the occipital cotylus, usually incorporating an occipital half-centrum (one is absent in *Pristiophorus*; Shirai, 1992), and often buttressed by paired occipital condyles of parachordal origin, articulating with the anteriormost free basiventral. In addition, the hypotic lamina may extend posteriorly as supravagal and subvagal plates above and below the vagal canal (Compagno, 1988), which meet or fuse with basiventrals of the first one or two vertebral centra (e.g., *Carcharhinus*).

INTERNAL MORPHOLOGY

GENERAL: Digital imaging permits the endocranial and labyrinth cavities of *Notorynchus* to be rendered as negative morphospace, generating a virtual endocast that reveals many morphological features which can be compared with data obtained from conventional endocasts (figs. 7, 8).

ETHMOID AND FOREBRAIN REGIONS: In figure 7, the precerebral fontanelle is rendered arbitrarily as a solid area, because it has no physical boundary either with the endocranial cavity or the medial ends of the olfactory canals. The depicted upper limit of the fontanelle is also arbitrary. The transversely ridged surface appearance of the olfactory canals is merely an artifact of digital imaging from the CT scans. The internal shape of the fontanelle region is not rendered but can be seen in the horizontal, sagittal, and transverse slices depicted elsewhere in this work.

Anteriorly, each olfactory canal arises anterolaterally from the front (telencephalic) part of the prosencephalic chamber and extends outward toward the olfactory capsules (fig. 7A, D). The capsules themselves are missing from the scanned specimen, but the large space they formerly occupied is clearly

discernible although it is confluent with that of the ectethmoid chamber. The olfactory canals are more evident in dorsal than in ventral view, since they merge with the internasal plate ventrally. By contrast, in the *Squalus* endocast illustrated by Schaeffer (1981: fig.15; see fig. 8 here) the olfactory canals are well defined both dorsally and ventrally, because the lateral walls of the precerebral fontanelle intrude farther posteriorly between the olfactory capsules than in *Notorynchus*. In dorsal view, however, the olfactory canals in *Squalus* appear to diverge from the telencephalon behind the precerebral fontanelle, whereas in *Notorynchus* they arise from its lateral margins.

The precerebral fontanelle extends farther posteriorly between the olfactory canals in *Notorynchus* than in *Squalus*, and farther anteriorly in *Squalus* than in *Notorynchus*. Thus, it would be misleading simply to characterize the rostrum of *Squalus* as ''long'' and that of *Notorynchus* as ''short'', because the relative position of the precerebral fontanelle and olfactory canals accounts for some of the topological difference in the snout of these taxa. Nevertheless, the precerebral fontanelle of *Squalus* is more than double the length of its olfactory capsules, whereas in *Notorynchus* these structures are of approximately equal length, so the differing proportions of the ethmoid region in these taxa are both dimensional as well as topological. These differences can be summarized as follows: in *Squalus*, the precerebral fontanelle is elongated anteroposteriorly but does not intrude between the olfactory canals, although the rostral plate separates the canals from the fontanelle ventrally; in *Notorynchus* (and *Chlamydoselachus*; Allis, 1923), the fontanelle is not elongated anteroposteriorly, but intrudes between the olfactory canals dorsally, and the rostral plate does not separate the canals from the fontanelle floor.

The orbitonasal canal of *Notorynchus* opens anteriorly within the ectethmoid chamber (the usual neoselachian arrangement; Holmgren, 1941), but then passes posterolaterally through the postnasal wall, with its posterior end lying farther laterally, and the orbitonasal canals are therefore slightly convergent anteriorly (fig. 7A). Unlike in *Notorynchus*, the orbitonasal canals in *Squalus* pass posteromedially through the postnasal wall and are therefore strongly divergent anteriorly (fig. 8). Variation in the orientation of this canal cannot be accounted for simply by differences in the relative spacing of the olfactory capsules, but may be related to the angle at which the olfactory canals diverge, which in turn is related to the topological arrangement of the olfactory capsule with respect to the orbit. Thus, in *Notorynchus* the capsule lies entirely anterior to the orbit, and the orbitonasal canal simply passes anteriorly toward the ectethmoid chamber (fig. 7A, B). In *Squalus*, however, the anterior part of the orbit is expanded anteriorly to overlap part of the olfactory capsule, and the ectethmoid chamber is situated somewhat lateral to the front of the orbit (fig. 8B).

In *Notorynchus*, the floor of the telencephalic chamber rises anteriorly (fig. 7C), imparting a strong taper to this region, unlike the corresponding region in *Squalus* where the telencephalic chamber remains fairly deep for much of its length and is actually slightly deeper anterior to the optic foramen than farther posteriorly. In *Chlamydoselachus*, the telencephalic chamber is also tapered anteriorly, and its floor rises even farther dorsally than in *Notorynchus*. The floor of the precerebral fontanelle between the olfactory capsules is at almost the same level as the roof of the neurocranium behind the fontanelle in *Chlamydoselachus*, which is extremely shallow (Allis, 1923).

In modern elasmobranchs, the epiphysis arises from the membranous roof of the diencephalon between the optic lobes, but only reaches the cranial vault above the telencephalon and its opening therefore appears to be within the telencephalic chamber. From the CT scan there is no evidence of an epiphyseal canal in the roof of the cranium in *Notorynchus*. Schaeffer (1981) showed an epiphyseal canal in his *Squalus* endocast, and there is an epiphyseal foramen in the cranial roof of many squaloids, *Heptranchias*, and *Hexanchus*. A foramen is typically absent in *Chlamydoselachus*, *Squatina*, *Pristiophorus*, batoids, and many galeomorphs, but the epiphysis may form a notch in the posterior margin of the precerebral fontanelle (e.g., *Mustelus*, *Hemigaleus*), and there is a fora-

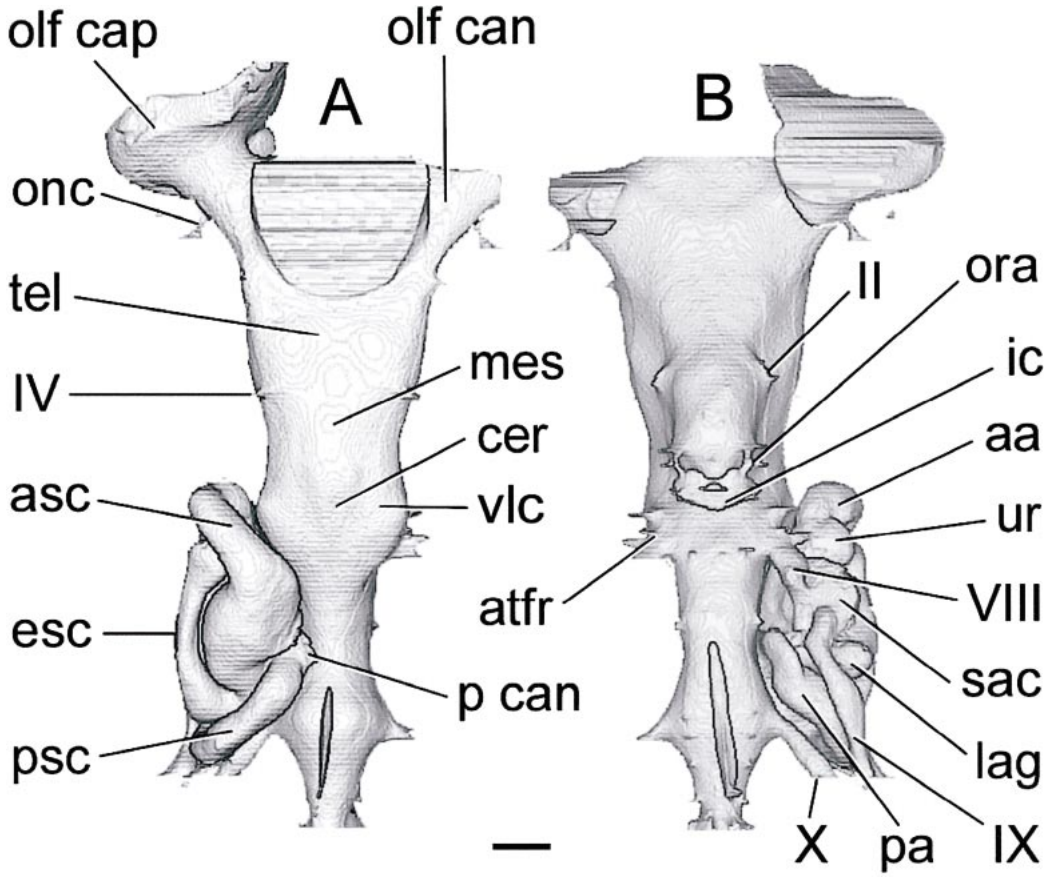
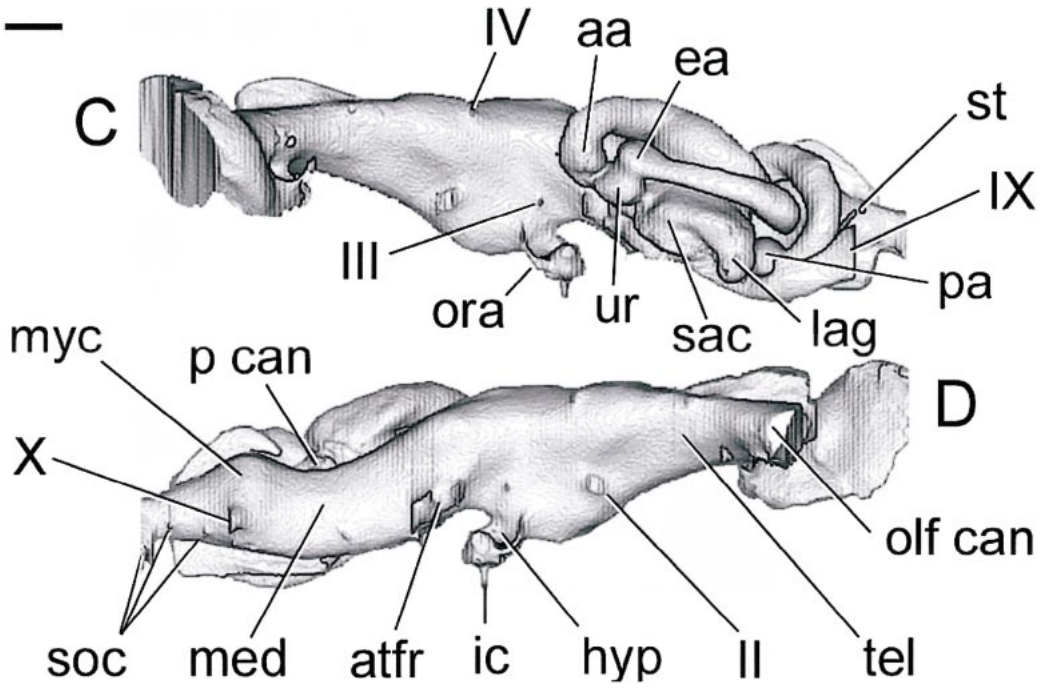


Fig. 7. Virtual endocast of *Notorynchus cepedianus* braincase rendered as negative morphospace from CT scans. Dorsal view (**A**); ventral view (**B**); lateral view, left side, with skeletal labyrinth in place (**C**); lateral view, right side, with skeletal labyrinth removed (**D**). Scale bar = 10 mm.

men in some galeomorphs (e.g., *Galeorhinus*). Whether an epiphyseal opening is present seems to depend on the anteroposterior extent of the cartilage forming the cranial vault, as the epiphysis may extend anteriorly to this and appear to lie within the precerebral fontanelle (in such cases the fontanelle cannot be considered entirely precranial; e.g., the *Orectolobus* braincase illustrated by Holmgren, 1941: fig. 42). It is uncertain whether the distribution of the epiphyseal foramen is of phylogenetic significance, and it can be ambiguous at species level because of intraspecific variation (e.g., in some squaloids; Shirai, 1992).

MESENCEPHALIC REGION: In *Notorynchus*, there is almost no discernible separation between the prosencephalic and mesencephalic chambers (fig. 7C, D), as in *Heterodontus*, *Squatina*, *Hexanchus*, *Notorynchus* and batoids. In *Squalus*, by contrast, these two regions are separated by a slight constriction, dorsal to the exit of the optic nerve (fig. 8C). The position of the optic lobes is indicated by the trochlear foramen, but in *Notorynchus* the lobes themselves are indistinct (they are better defined in *Squalus*). Thus, very few features of the brain are represented by morphological features in this part of the endocranial cavity dorsally or laterally. By contrast, the floor of the mesencephalic chamber contains a well-defined hypophyseal cavity, which in life housed the hypophysis, pituitary vein, median cephalic sinus of the internal carotids, and the efferent pseudobranchials (fig. 7B–D). A hypophyseal cavity is pre-



sent in most sharks, but this chamber is only weakly developed in *Pristiophorus* and is absent in batoids. As in *Chlamydoselachus*, the pituitary vein of *Notorynchus* leaves the cranial cavity via a foramen in the lateral wall of the hypophyseal chamber, emerging externally within the deep trigemino-pituitary fossa.

In some modern elasmobranchs the anterior part of the trabecular region forming the basis cranii is inflated internally to form a transverse presphenoid ledge (praesphenoïdvorsprung; Gegenbaur, 1872), often reaching the inner surface of the interorbital wall. However, such a ledge is not evident in *Notorynchus* (discussed further below).

LABYRINTH REGION: Parts of the labyrinth region (especially its medial wall) are not visible in the complete endocast of *Notorynchus*, and the structure has therefore been illustrated separately (fig. 9). As in *Squalus* (fig. 8), the vestibular chamber does not conform closely to the architecture of the membranous labyrinth it encloses, and it is not clearly differentiated into utricular or saccular regions (although the lagenar area is represented by a small bulge in the floor of the vestibular chamber).

The labyrinth chambers in modern elasmobranchs display many specializations toward low-frequency phonoreception, including isolation of the posterior semicircular canal, ascending preampullary canal, large perilymphatic fenestrae, a posterior canal duct, separation of the posterior utriculus containing the macula neglecta, and development of a medial capsular wall separating the skeletal labyrinth and main endocranial cavity (Maisey, 2001a). In *Notorynchus*, the ampullae of the anterior and external semicircular canals meet the utricular recess separately (fig. 9A, D). The floor of the saccular region lies in approximately the same plane as the cranial cavity, not below it as in osteichthyans and some extinct elasmobranchs. A short perilymphatic canal merges with the upper part of the posterior semicircular canal. In life, the membranous posterior utriculus is completely separated from the utricular recess and opens into the posterior semicircular canal via the posterior utriculo-saccular opening containing the macula neglecta (the

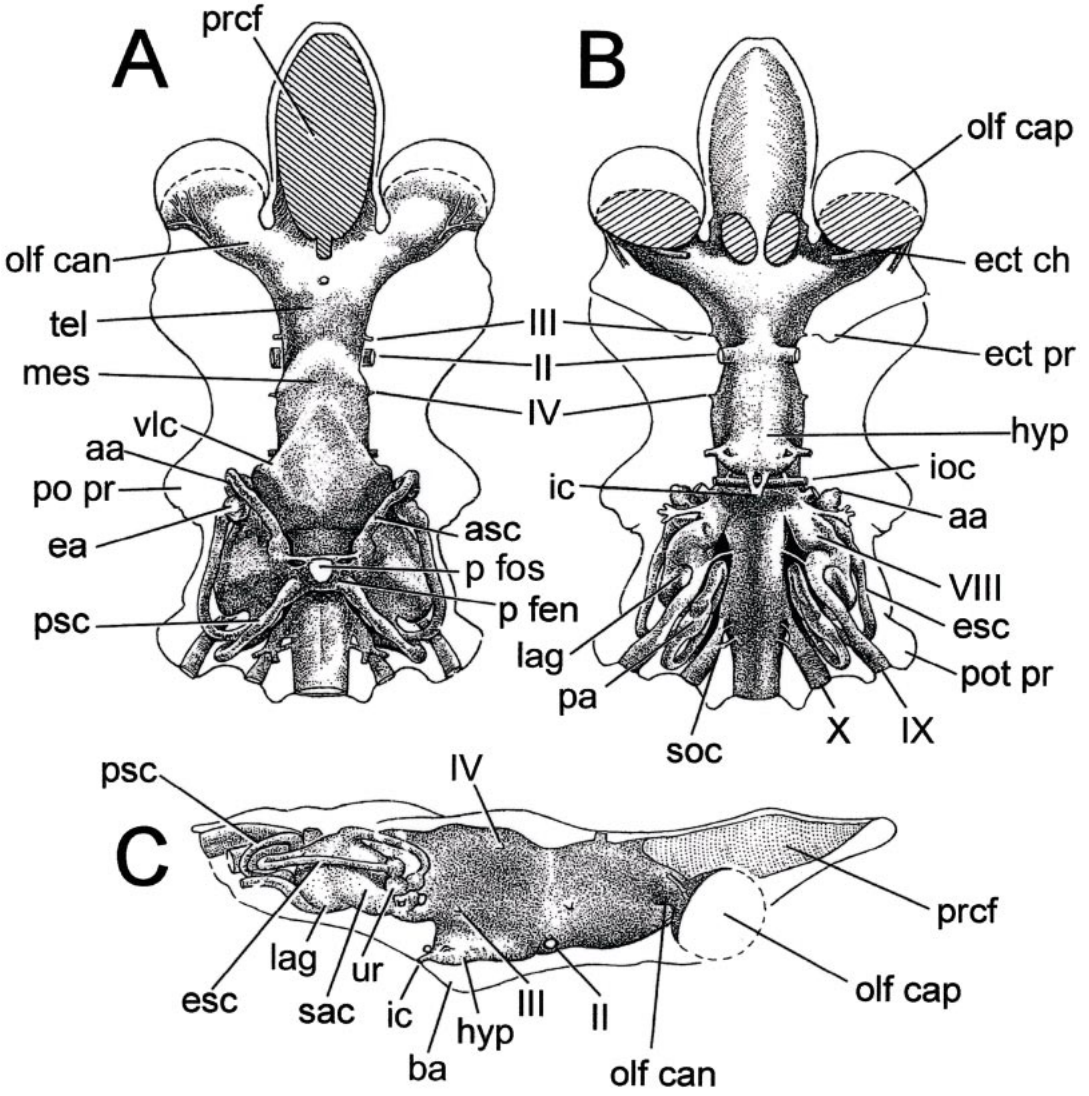


Fig. 8. Principal endocranial features in *Squalus acanthias* superimposed on outlines of the braincase. Dorsal view (**A**); ventral view (**B**); right lateral view (**C**). After Schaeffer (1981). No scale.

main phonoreceptor organ in elasmobranchs). By contrast, in osteichthyans and holocephalans both the utriculo-saccular opening and macula neglecta lie within the utriculus.

GLOSSOPHARYNGEAL AND VAGAL CANALS: The courses of the vagal and glossopharyngeal nerves can be partially traced through the virtual endocast of *Notorynchus*, except where their passages merge with the floor of the vestibular chamber (figs. 7B, C, 8A, C). The posterior semicircular canal provides a useful landmark, since it is located lateral to the vagal canal and medial to the glossopharyngeal canal. The latter arises at about the same level as the perilymphatic fenestrae farther dorsally, and is small as it exits the endocranial cavity. The canal then expands before passing in front of the ascending (preampullary) part of the posterior semicircular canal, where it gives off a dorsal branch that passes into the saccular region (probably representing the middle lateral line nerve). The glossopharyngeal canal then becomes

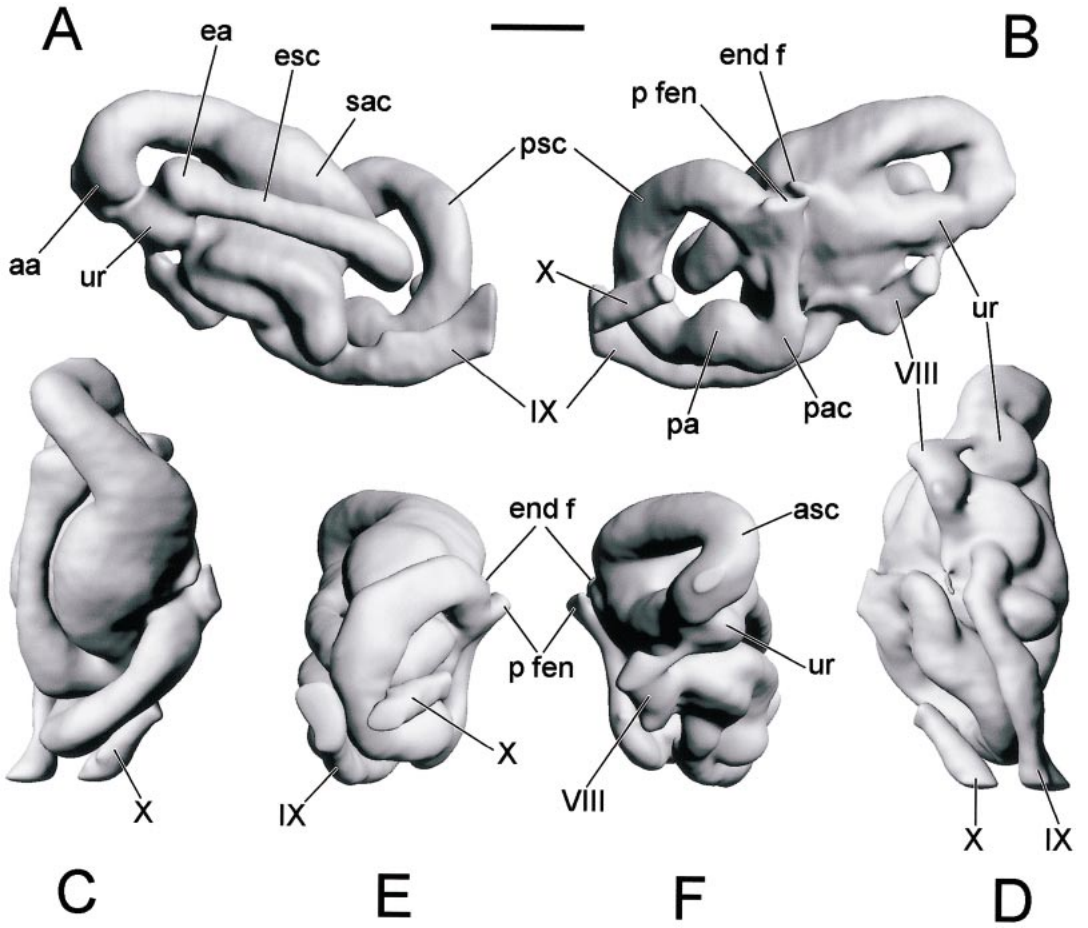


Fig. 9. Virtual endocast of the left labyrinth region in *Notorynchus*. (**A**) lateral view; (**B**) medial view; (**C**) dorsal view; (**D**) ventral view; (**E**) posterior view; (**F**) anterior view. Imaris/Surpass surface rendering.

indistinct as it enters a pocket housing the lagena. The canal separates from the pocket posteriorly (presumably within the passage formed by fusion of the hypotic lamina to the floor of the otic capsule, as discussed by Schaeffer, 1981) and then passes between the posterior semicircular canal (medially) and vestibular process (laterally) before turning dorsally to open on the posterolateral surface of the otic region.

The vagal canal is fairly uniform in diameter, and its path is considerably simpler than that of the glossopharyngeal canal. It first appears in transverse sections just behind the level of the horizontal semicircular canal, then extends posterolaterally between the medullary chamber and posterior semicircular canal. A small canal branches from it dorsally and then turns anteromedially, but this disappears before reaching the endocranial cavity. The identity of the small branch is uncertain, but it may correspond to the canal described in *Chlamydoselachus* by Allis (1923), in which there is a small vein coming from a plexus on the dorsal surface of the brain, considered by Gegenbaur (1872) to represent a primitive internal jugular vein. Slightly farther posteriorly, just behind the posterior semicircular canal, the vagal canal gives rise to a small dorsal passage (probably for the supratemporal lateral line nerve; figs. 3, 6B) which reaches the dorsal surface of

the braincase behind the glossopharyngeal canal.

CEREBELLAR AND MEDULLARY REGIONS: The cerebellar chamber encloses the dorsal part of the hindbrain and includes a large acustico-trigemino-facialis recess (figs. 10K, 11J, 12H). As in *Chlamydoselachus* (Allis, 1914), this recess is located in the lateral wall of the cerebellar chamber, adjacent to the dorsum sellae and just behind the level of the trigemino-pituitary fossa occupying the posteroventral part of the orbital wall externally (figs. 10I, 11A, 12G, H). The cerebellar chamber corresponds both topographically and morphologically to the large ''bay'' described by Allis (1923: 162) in the cranial cavity of *Chlamydoselachus*. This chamber is situated dorsal to the acustico-trigemino-facialis recess and immediately internal to the postorbital process. In *Chlamydoselachus*, the cerebellar chamber is evident in sagittal and horizontal slices through the cranial cavity published by Allis (1923: figs. 12, 58).

The cerebellar chamber in *Notorynchus* gradually widens dorsally into paired vestibulolateral (auricular) chambers housing the paired auricles of the cerebellum (fig. 7A). Vestibulolateral chambers are also well developed in *Squalus* (fig. 8A). In both *Notorynchus* and *Squalus*, the vestibulolateral chambers are prominent in dorsal view, but the ceiling of the cerebellar chamber in front of the parietal fossa decreases in height more gradually in these taxa than in *Chlamydoselachus*, making them less distinct in sagittal view (figs. 7D, 8C).

In *Notorynchus*, the medullary chamber becomes increasingly constricted as it passes beneath the parietal fossa farther posteriorly, and reaches its minimum height directly beneath the perilymphatic fenestrae (fig. 7D). As in other modern elasmobranchs, the medullary chamber is separated from the paired labyrinth chambers farther laterally by the chondrified medial wall of the otic capsule, and the two are connected only by passages for the octaval and glossopharyngeal nerves. For this reason, the entire labyrinth cavity appears as an almost separate object in the endocasts of both *Notorynchus* and *Squalus* (figs. 7, 8).

Just behind the otic capsules (and above the origin of the vagal nerve) in *Notorynchus* is the myelencephalic (medullary) chamber, marking the transition to the spino-occipital part of the brain stem (fig. 7D). A distinct medullary chamber is also present in other hexanchiforms, *Squatina* and many squaloids, but it is poorly developed in *Chlamydoselachus*, *Heterodontus*, galeomorphs, and batoids. Allis (1923: 163) remarked that in *Chlamydoselachus* the cranial cavity in this region ''is slightly enlarged, and the large vagal foramen lies in the middle of the lateral wall of this part of the cavity.''

MORPHOLOGY OF THE CRANIAL WALL

GENERAL: Originally, the neurocranium was scanned in the transverse plane, which clearly limits the extent of observations regarding variation within the cranial walls. Digital manipulation of the original transverse sections allows the virtual braincase to be resliced in any direction (figs. 10–12). In the following description, the braincase is examined by means of slices in the transverse, sagittal, and horizontal planes. In each case, the first image in each series of slices depicts the external form of the braincase and corresponds to one of the earlier views of the. Since only a small sample of representative slices can be published, some minor structures discussed in the following sections may not be evident in these views. Throughout this part of the description, references to the appropriate illustrations are simply indicated by key letters (A, B, etc.).

TRANSVERSE SECTIONS: All key letters in this part of the text refer to a series of transverse slices (fig. 10), in which the sequence passes anteroposteriorly (fig. 10A corresponds to fig. 6A). These slices reveal changes in the cross-sectional shape of the endocranial cavity, as well as variation in the thickness of its walls and the topographic relationship of certain landmark features inside and outside the braincase.

The main endocranial cavity (beginning immediately behind the precerebral fontanelle) is low and wide at the level of the olfactory canals (D), but is appreciably narrower farther posteriorly. The telencephalic chamber is roughly triangular in section and widest dorsolaterally (F), but farther poste-

riorly the mesencephalic region of the endocranial cavity deepens ventrally, until it becomes abruptly shallower again at the dorsum sellae (H). Behind the dorsum sellae the cerebellar chamber has a squarish cross section, although this shape is modified where passages for the octaval and glossopharyngeal nerves extend laterally. The cross-sectional shape gradually becomes more rounded farther posteriorly, and the medullary chamber has an oval cross section for much of its length between the main vestibular chambers, becoming almost circular as it passes through the occipital region, where it rapidly narrows to match the diameter of the dorsal nerve cord.

Slices through the rostral region reveal the depth of the precerebral fontanelle, as well as its flat floor (B). The lateral walls of the fontanelle extend dorsally and laterally around the ectethmoid chamber and olfactory capsule, and they also extend ventrally for a short distance to separate a concave area from the olfactory capsules ventrally (also seen in slice C). The floor of the fontanelle consists of the rostral and internasal plate (both probably representing anterior extensions of the trabeculae) and gradually thickens posteriorly. Although the dorsal and ventral surfaces of the fontanelle floor are both relatively flat, there is little correspondence between their features. The ethmoid region lacks a ventral keel in the floor of the internasal region. The ventral extensions of the internasal plate in *Notorynchus* become lower and wider posteriorly and eventually merge with the ventral margin of the ectethmoid process extending from the postnasal wall (C, D). Cartilage overlying the olfactory capsule becomes thicker posteriorly, and the ectethmoid chamber, olfactory canal, and orbitonasal canal are mostly developed within the thickness of the postnasal wall. The ectethmoid process extends ventrolaterally from the posterolateral margin of the postnasal wall and contains a large canal (discussed earlier) for the lateral ramule of the buccal + maxillary ramus (E).

In the anterior part of the orbit, the braincase wall is roughly triangular in transverse section, with a thick but narrow basicranium below the endocranial cavity (F). The interobital wall widens dorsally and expands laterally, forming a broad supraorbital shelf. There is a distinct lateral thickening of the interorbital wall just below the optic foramen, termed here the subocular ridge. This ridge becomes indistinct anteriorly and merges with the base of the ectethmoid process (E). In *Chlamydoselachus*, a corresponding ridge extends anterolaterally from behind and below the optic foramen to meet the postnasal wall, where it merges with the posterior margin of the ectethmoid process, and part of the ridge defines the upper anterior margin of the orbital articulation behind the optic foramen. In *Notorynchus*, this articular surface lies farther posteriorly and is not associated with the subocular ridge. The optic pedicel is not associated with this ridge but is situated farther posteriorly, where it arises laterally in the same transverse plane as the dorsum sellae (G, H). According to Allis (1923: pls. VIII, IX), the optic pedicel in *Chlamydoselachus* arises in a slightly more anterior position relative to the dorsum sellae. Supraorbital shelves extend the entire length of the orbit and are pierced by canals for dorsal rami of the superficial ophthalmic nerve from the level of the precerebral fontanelle to the postorbital processes (E–G).

The orbital articulation forms a massive, laterally directed thickening at the basal angle in the basis cranii in the posterior half of the orbit, and the external form of the basicranium here does not correspond with the shape of the endocranial cavity. The floor of the cranium is thinner between the paired processes forming the basal angle, where the cartilage is almost three times thicker (G). The basicranial cartilage again thickens at the level of the dorsum sellae farther posteriorly, where it is penetrated by passages for the internal carotids and the interorbital canal, and also contains the hypophyseal cavity (H, I).

In *Notorynchus*, the anterior ampulla is the anteriormost part of the skeletal labyrinth and is the first part of the vestibular system to appear in this series of transverse sections (I). In *Squalus* the anterior ampullae are again located between the postorbital processes, not behind them (fig. 8). Wells (1917: figs. 11–22) illustrated a series of transverse sections through the otic capsule of an adult *Squalus* braincase, some of which correspond to slices shown here. For example, her

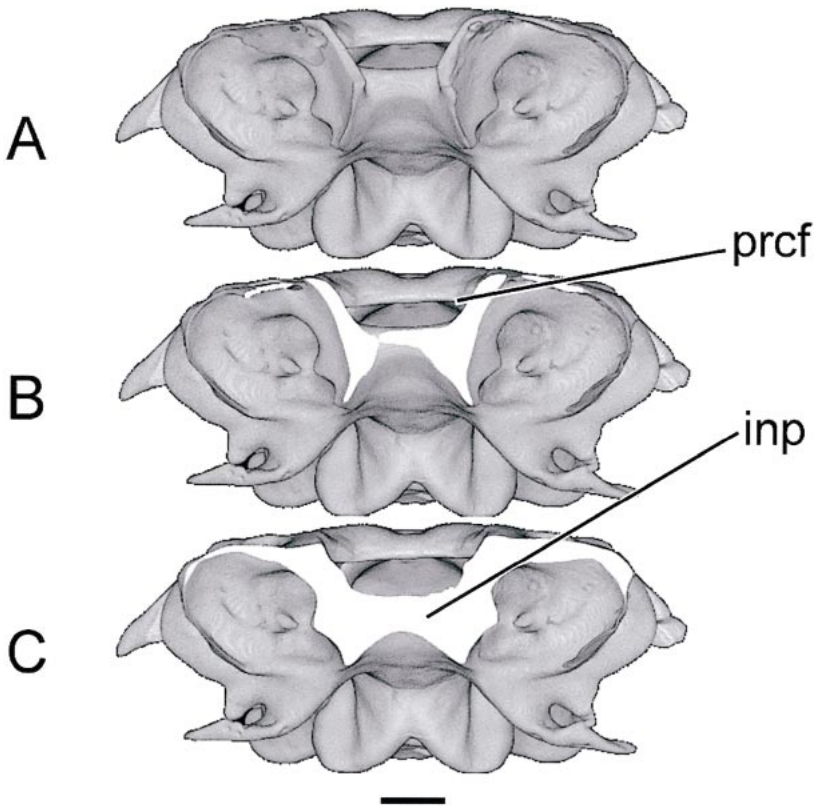


Fig. 10. *Notorynchus cepedianus* neurocranium digitally resliced in transverse plane (corresponding to x–y axes of original CT scans). Sequence (A–U) passes from front to back of braincase. View A corresponds to figure 4A. Scale bar = 10 mm.

anteriormost section (her fig. 11) shows the anterior ampulla connected to the ascending part of the anterior canal as in section I here.

In *Notorynchus* (as in modern elasmobranchs generally), the medial capsular wall is chondrified throughout the length of the medullary region, separating the labyrinth almost entirely from the endocranial cavity (fig. 9). According to Goodrich (1930) this wall develops mainly as an upgrowth from the parachordal. In *Notorynchus*, the utricular recess lies immediately behind the anterior ampulla, meeting it between the postorbital processes (J, K). A similar arrangement is found in *Squalus* (fig. 8) although it was not illustrated by Wells (1917). The octaval canal in *Notorynchus* branches away from the endocranial cavity ventrally, passing through the medial capsular wall (L; see also fig. 9A). Wells (1917: fig. 13) showed a similar arrangement in *Squalus*. However, her section also shows a passage for the hyomandibular ramus passing posteriorly through the basicranial cartilage below the capsule at this level, whereas in *Notorynchus* there is no corresponding passage. The glossopharyngeal canal seems to merge with the saccular chamber ventrally (M–O); in life, however, the glossopharyngeal nerve is separated from the vestibular apparatus by the membranous floor of the saccular chamber (Norris, 1929). Wells (1917: fig. 19) similarly identified the position of the glossopharyngeal canal within the floor of the chamber in *Squalus*.

In the midregion of the *Notorynchus* labyrinth, the medial capsular wall is penetrated by openings for the perilymphatic fenestrae dorsally (Q), much as Wells (1917: figs. 17, 18) showed in *Squalus*. In *Notorynchus*, the roof of the medullary chamber (formed by the taenia medialis) is considerably lower than the capsules on either side, giving rise

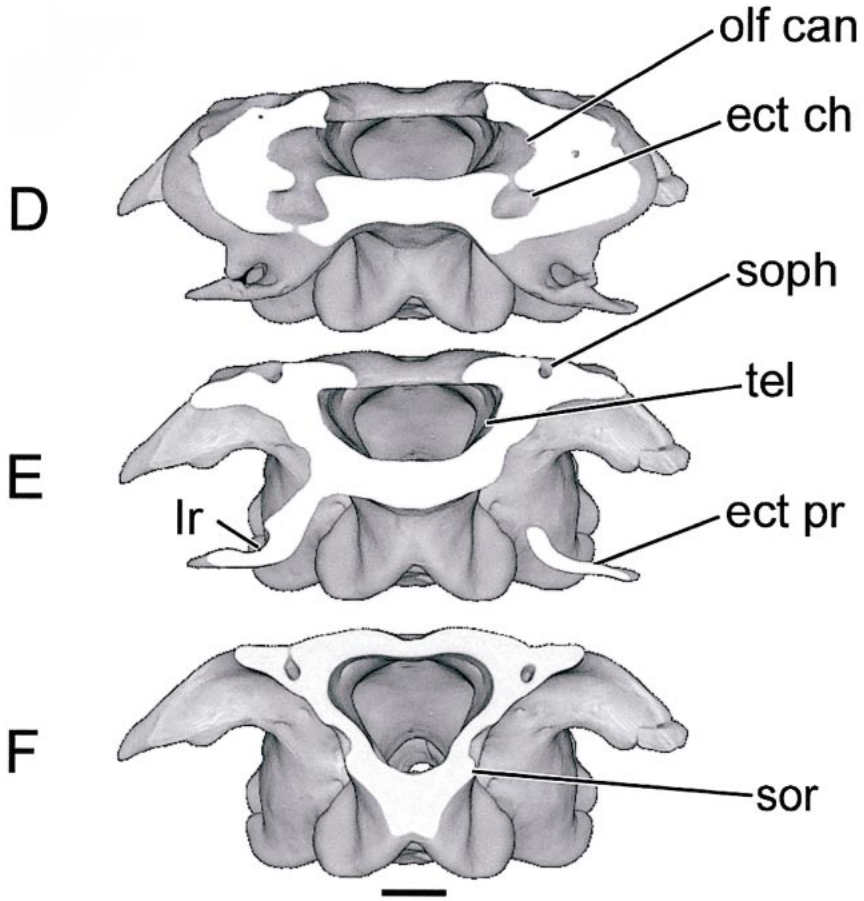


Fig. 10. Continued.

to the parietal fossa (L–S). By contrast in *Squalus* the parietal fossa is relatively shallow (Wells, 1917: figs. 15,16). The ascending (preampullary) part of the posterior semicircular canal is seen between the endocranial cavity and glossopharyngeal canal (which begins to reemerge ventrally from the saccular floor; Q). It is not easy to identify the preampullary part of this canal in the sections of *Squalus* shown by Wells (1917); comparison with slice Q suggests that the canal labelled ''VIII'' in her figure 18 is the ascending preampullary region of the posterior canal, since the octaval nerve should not extend so far posteriorly. The canal shown immediately lateral to this in her section is probably the glossopharyngeal canal passing lateral to the canal. In *Notorynchus*, the lagenar chamber forms a small recess in the floor of the saccular region just dorsolateral to the glossopharyngeal canal (Q). In *Squalus*, this seems to be represented by the lateralmost part of the vestibular chamber depicted by Wells (1917: fig. 18).

Transverse sections through the posterior part of the otic region in *Notorynchus* show the returning path of the external semicircular canal between the upper and lower parts of the posterior canal, and the glossopharyngeal canal is completely surrounded by cartilage (S). In corresponding slices through the capsule in *Squalus*, Wells (1917: figs. 21, 22) showed the posterior semicircular canal sandwiched between the glossopharyngeal and vagal canals, but in *Notorynchus* the vagal nerve leaves the cranial cavity slightly

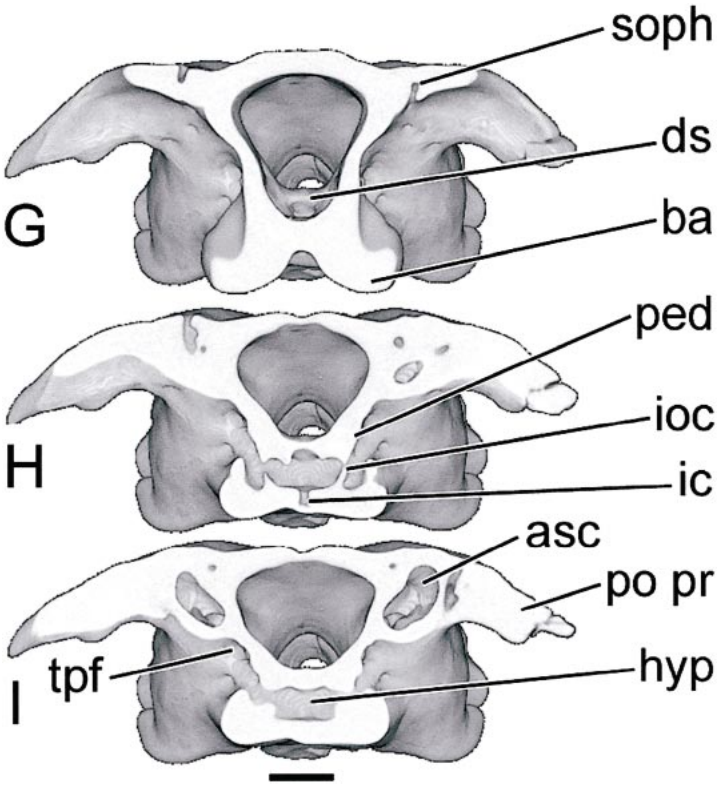


Fig. 10. Continued.

farther posteriorly, and its canal does not therefore appear in section S. For this reason, the posterior semicircular canal is located instead between the medullary chamber and glossopharyngeal canal. Unfortunately, the origin of the vagal canal cannot be seen in the sections shown here, but its subsequent passage and the canal for its small dorsal ramus are visible (T). Canals for some of the spino-occipital nerves can also be observed, passing posterolaterally from the endocranial cavity. The anteriormost spino-occipital nerves emerged into the glossopharyngeal canal and shared this common exit from the braincase (T), but those situated farther posteriorly lay behind the canal and their passages open directly onto the external surface of the braincase. Wells (1917) did not illustrate the equivalent region in *Squalus*.

SAGITTAL SECTIONS: All key letters in this part of the text refer to a series of slices in the sagittal plane (fig. 11). These slices are sequenced beginning on the left side of the braincase (A, corresponding to fig. 5B), passing progressively deeper to reach the midline (G), and then continuing partway into the right side. Slices B–H therefore reveal features at increasing depths within the braincase, while slices I and J are the approximate equivalents of G and F, respectively, the principal difference being that views G and F are directed medially, whereas I and J are directed laterally.

Slice B cuts the postnasal wall through the canal for the buccal branch of the anterodorsal lateral line nerve. The postnasal wall meets the cartilage forming the roof of the olfactory and orbital regions dorsally, completely separating the canals for the olfactory and optic nerves. The same slice also cuts through the supraorbital shelf above the orbit, as well as the tip of the postorbital process. In slices closer to the midline, the orbitonasal canal is seen passing through the

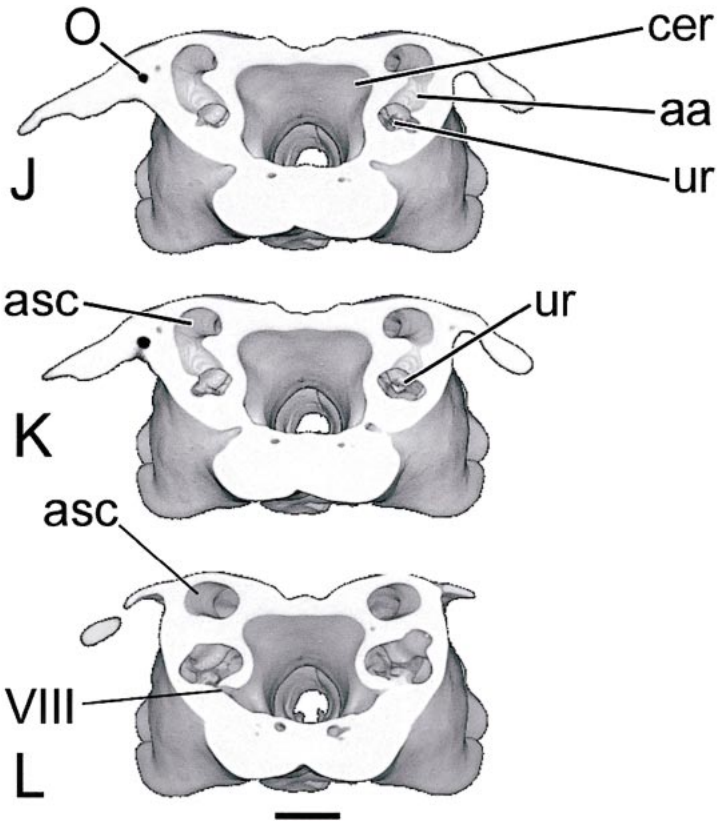


Fig. 10. Continued.

postnasal wall from the orbit into the ectethmoid chamber of the olfactory region (C). The main passage for the superficial ophthalmic ramus penetrates the supraorbital shelf anterodorsally, and canals for several ramules of this nerve also extend upward (D). The anterior opening for the olfactory canal is visible in several of these slices but is not actually cut until slice E, and in subsequent slices the canal of the opposite side can be seen lateral to the precerebral fontanelle.

In slice B, the otic capsule is cut superficially, revealing the outer part of the anteroposterior ramus of the external semicircular canal dorsally, and the lateral part of the saccular chamber farther ventrally. Behind this chamber, the glossopharyngeal canal is sectioned near to its exit on the posterolateral margin of the otic region. The vestibular process forms a distinct ventral projection between the exposed parts of the sacculus and glossopharyngeal canal. Slice C also reveals some features of the vestibular region, including sections through all three semicircular canals. The external semicircular canal (which is cut at two levels) is bracketed by the anterior and posterior canals and underlain by the saccular and lagenar chambers (the latter is seen better in slice D). The dorsal ramus of the vagal canal lies either immediately above the posterior semicircular canal (B) or just behind it (C, D), but the main vagal canal lies slightly more medially (its posterolateral wall is clipped in slices C and D and the entire canal is cut in E). Slice D exposes the external and anterior ampullae, as well as the utricular recess to which both ampullae are connected (in this section the external ampulla connects ventrally with the recess). The glossopharyngeal canal has

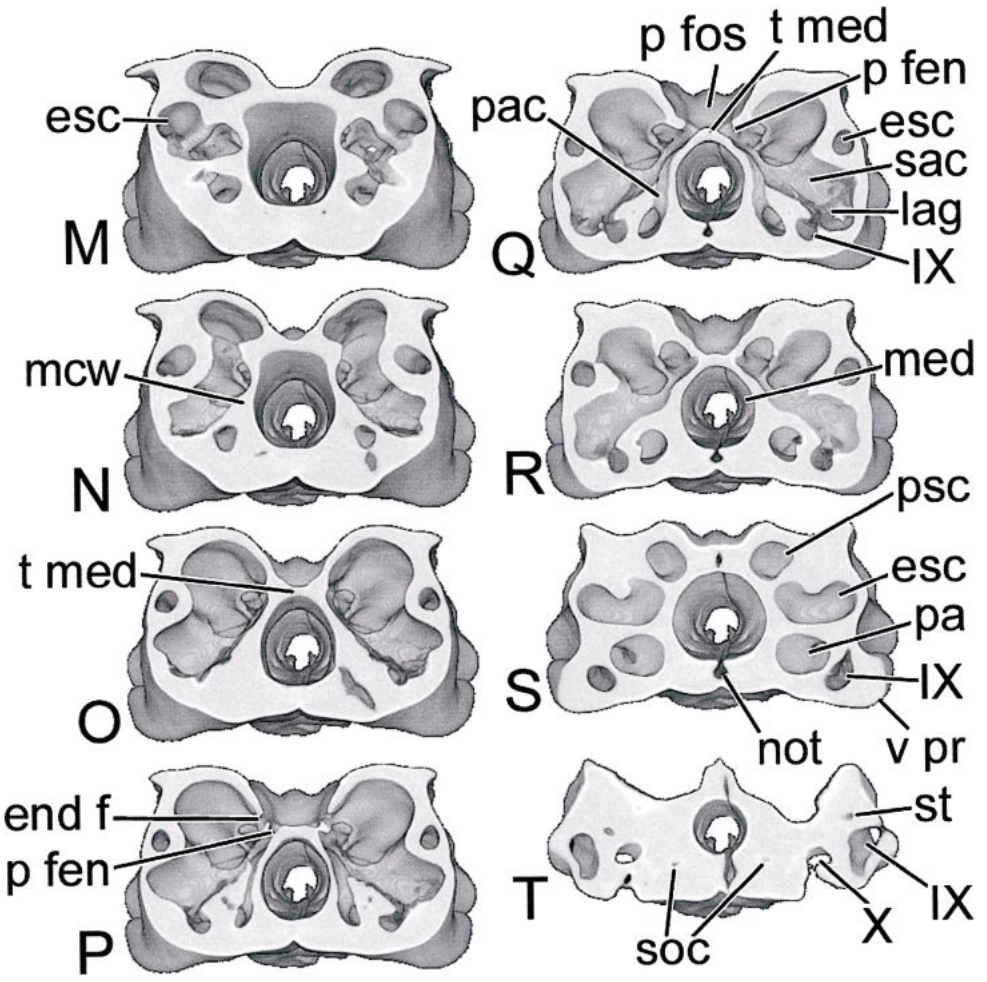


Fig. 10. Continued.

merged with the floor of the saccular chamber in slice D and is no longer distinct.

The posterior ampulla is the closest of the three to the midline and is not seen until slice E; it lies between the glossopharyngeal canal anteriorly and vagal canal posteriorly. The external semicircular canal merges with the vestibular chamber posteriorly, and its subsequent course through this region is indistinct (in life the membranous canal actually extends anteriorly within the vestibular chamber to meet the anterior semicircular canal, as in all modern elasmobranchs, but this cannot be seen in endocasts; Schaeffer, 1981; Maisey, 2001A). Farther medially, cartilage forming the inner wall of the utricular recess helps define the acustico-trigemino-facialis recess, which marks the point at which the octaval nerve enters the vestibular chamber (E). The glossopharyngeal canal is partly separated from the floor of the chamber and extends toward its medial wall. The ascending (preampullary) ramus of the posterior semicircular canal is positioned deep beneath the main vestibular chamber (F, J). The relationship of this canal to the perilymphatic fenestrae dorsally is not particularly evident in sagittal view, and it is seen better in transverse and horizontal sections.

The main endocranial cavity is seen only in deeper sagittal sections. The medial capsular wall bulges medially, obscuring the

medullary chamber from view (F). The basis cranii is extraordinarily thick in the vicinity of the basal angle, enclosing the oculomotor canal and hypophyseal cavity, and the passage for the optic nerve also passes through this cartilage just anterior to the basal angle. The hypophyseal pit is broad from side to side, but its anteroposterior extent is short (F–J). Its posterior limit is defined by the prominent dorsum sellae which overhangs the posterior part of the pit and the canals for the internal carotid arteries (G, I). Farther posteriorly, passages for several spino-occipital nerves pass through the basicranial cartilage (F, J), and in slices close to the midline the notochordal canal extends anteriorly from the occipital cotylus (H). The medullary chamber is expanded dorsally before reaching the cotylus, forming the prominent myencephalic chamber. This chamber contains the exit of the vagal nerve in the midlle part of its lateral wall and the internal openings of the spino-occipital nerve canals along the lateral margins of its floor.

A narrow canal extends from the endocranial cavity into the basicranial cartilage at the ventral midline, just anterior to the main part of the hypophyseal cavity and near the presumed anterior limit of the polar cartilages (H). The canal is tentatively identified as a vestigial hypophyseal duct, although it is separated by cartilage from the main hypophyseal cavity farther posteriorly. In modern adult elasmobranchs, the hypophyseal fenestra typically becomes obliterated during ontogeny (this area is among the last to chondrify; De Beer, 1931), although a fenestra is present in some adult *Etmopterus* (Holmgren, 1940). An open hypophyseal fenestra and duct is present in many fossil elasmobranchs (e.g., hybodonts, *Orthacanthus*; Schaeffer, 1981; Maisey, 1982, 1983), and closure of the duct in adults has been considered a neoselachian synapomorphy (Maisey, 1984). A similar canal has also been illustrated in sagittal views of the braincase in *Heptranchias* and *Hexanchus* (Gegenbaur, 1872) and *Echinorhinus* (Shirai, 1992). In modern elasmobranchs, therefore, persistence of the hypophyseal canal has a very restricted systematic distribution and has so far been found only in orbitostylic sharks with a prominent basal angle. In modern hexanchiforms, the hypophyseal fenestra is closed in the adult and the hypophyseal canal extends only partway into the basis cranii, but clearly in some squaloids the canal remains open. There is no evidence of a similar canal in the sagittal section of the adult braincase in *Chlamydoselachus* (Allis, 1923), although an open hypophyseal fenestra seems to be present in earlier stages of development (e.g., the 127-mm embryo figured by Holmgren, 1941: fig. 7).

Closure of the hypophyseal duct may be ontogenetically delayed in sharks with a strong basal angle, as the fenestra is still open in the latest embryonic stages of *Squalus* (59 mm) and *Etmopterus* (55 mm) investigated by Holmgren (1940). However, there seems to be no correlation between the timing of closure and the elimination of the embryonic angle between the trabeculae and parachordals in taxa where the basal angle is absent. For example, according to Holmgren (1940) in ''*Scyllium*'' (= *Scyliorhinus*) the fenestra is closed in the 40-mm stage, and in *Torpedo* it disappears in the 31-mm stage, although in both cases basicranial flexure between the trabeculae and parachordals is not eliminated until later stages. In *Raja*, however, closure of the fenestra is delayed until the 60-mm stage, after the basis cranii becomes straightened. From a phylogenetic perspective, persistence of the canal into the adult is undoubtedly a primitive state for elasmobranchs generally, and presence of the canal could be considered a plesiomorphic character of orbitostylic sharks that was retained by hexanchiforms and *Echinorhinus* and lost in various other lineages. Since the duct is only present in modern elasmobranchs with a basal angle (which is itself a unique character of hexanchiforms and squaloids), however, its persistence here may be secondarily related to retention of the angle into adulthood, and therefore could be regarded as an apomorphic (though homoplaseous) feature.

HORIZONTAL SECTIONS: All key letters in this part of the text refer to a series of slices in the horizontal plane (fig. 12). These are sequenced beginning dorsally (A, corresponding to fig. 3), and then pass progressively farther ventrally. These views provide a useful ''plan view'' of the braincase and

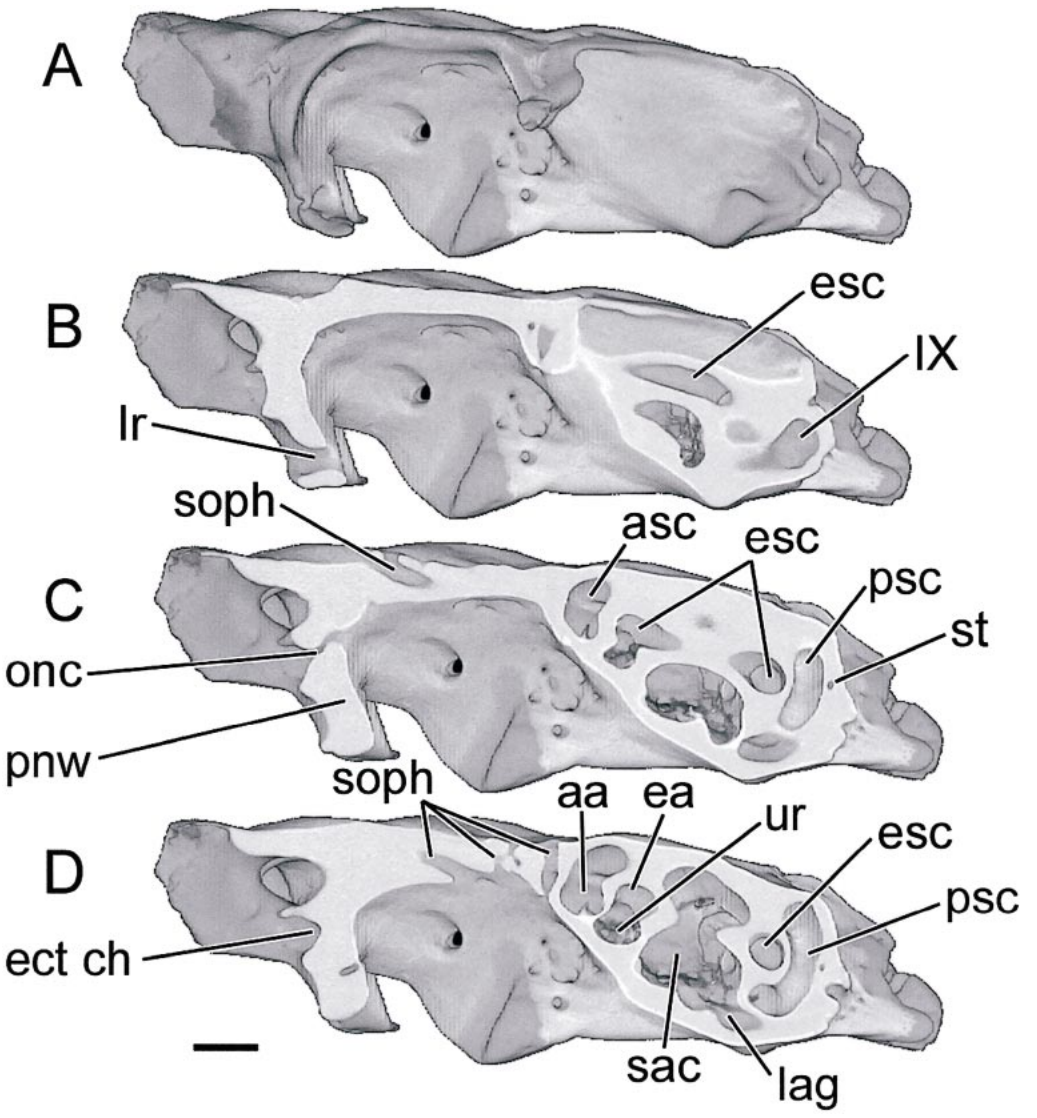


Fig. 11. *Notorynchus cepedianus* braincase, digitally resliced in sagittal plane (corresponding to x–z axes of original CT scans). Sequence (A–J) passes from left to right of braincase. View A corresponds to figure 3B. Scale bar = 10 mm.

are particularly informative about the anteroposterior topographic relationship of endocranial structures to external morphology. Only the left side of each slice is shown, although each view extends slightly beyond the midline to ensure that no structures were inadvertently cropped.

The most superficial horizontal slices pass through the thickness of the supraorbital shelf, cutting passages for several branches of the superficial ophthalmic ramus, as well as the olfactory canal and trochlear nerve (B). Canals for additional branches of the superficial ophthalmic ramus are also present in the postorbital process (C, D). Farther anteriorly, features revealed in horizontal sections include the orbitonasal canal within the postnasal wall (D, E), the optic and oculomotor canals, and the trigemino-pituitary fossa in the back of the orbit (G). Deeper

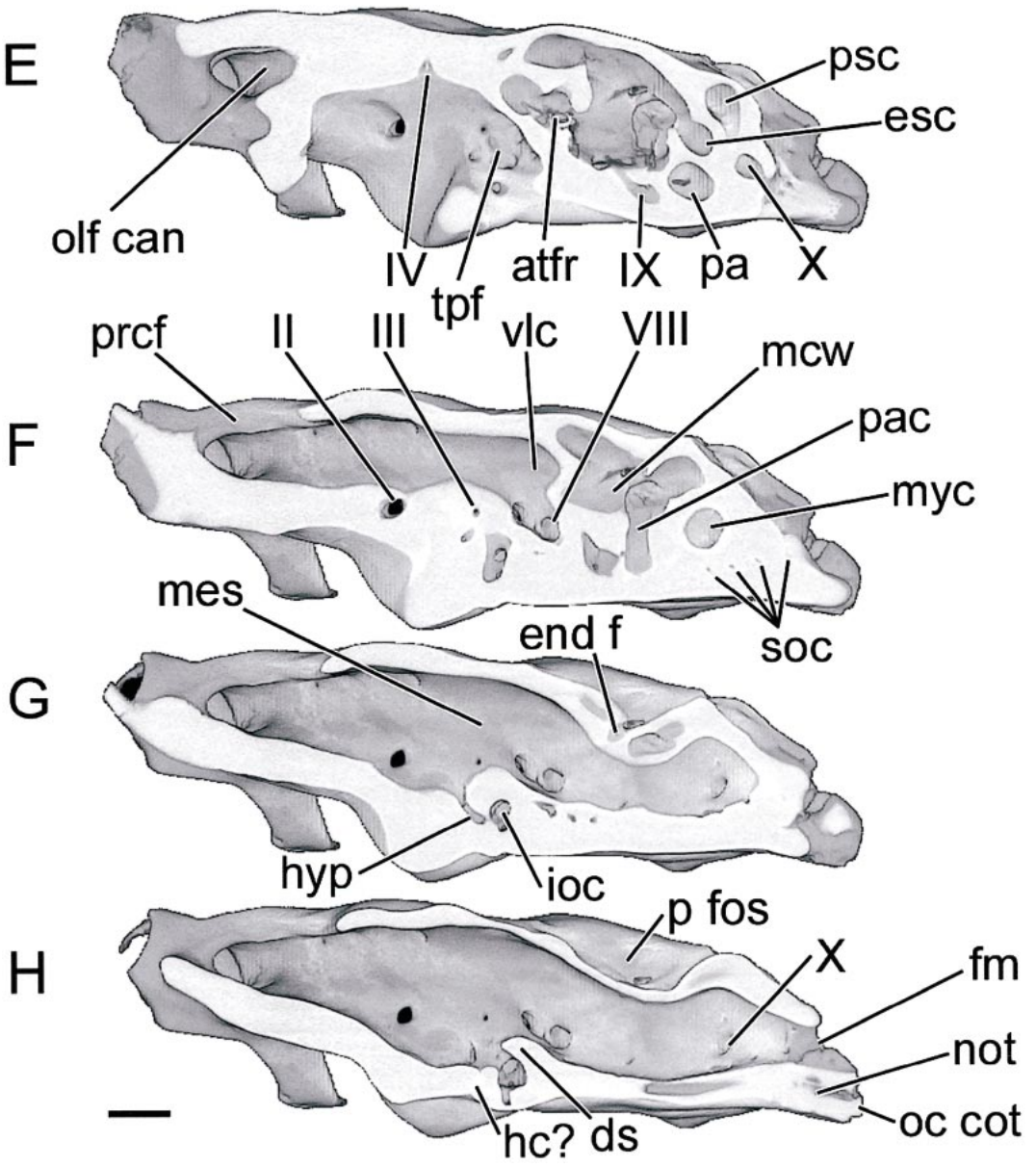


Fig. 11. Continued.

slices through the ethmoid region pass through the buccal canal for the anterodorsal lateral line nerve in the ectethmoid process (M).

In the otic region, the anterior semicircular canal is the first part of the labyrinth to be exposed in horizontal sections (B); by contrast, the posterior canal is seen only in deeper slices (D). At this level the anterior ampulla and utricular recess have already been cut anteriorly, showing that the entire labyrinth system is inclined anterodorsally relative to the long axis of the braincase. The anterior ampulla is located adjacent to the base of the postorbital process (C, D). The paired perilymphatic canal connects with its

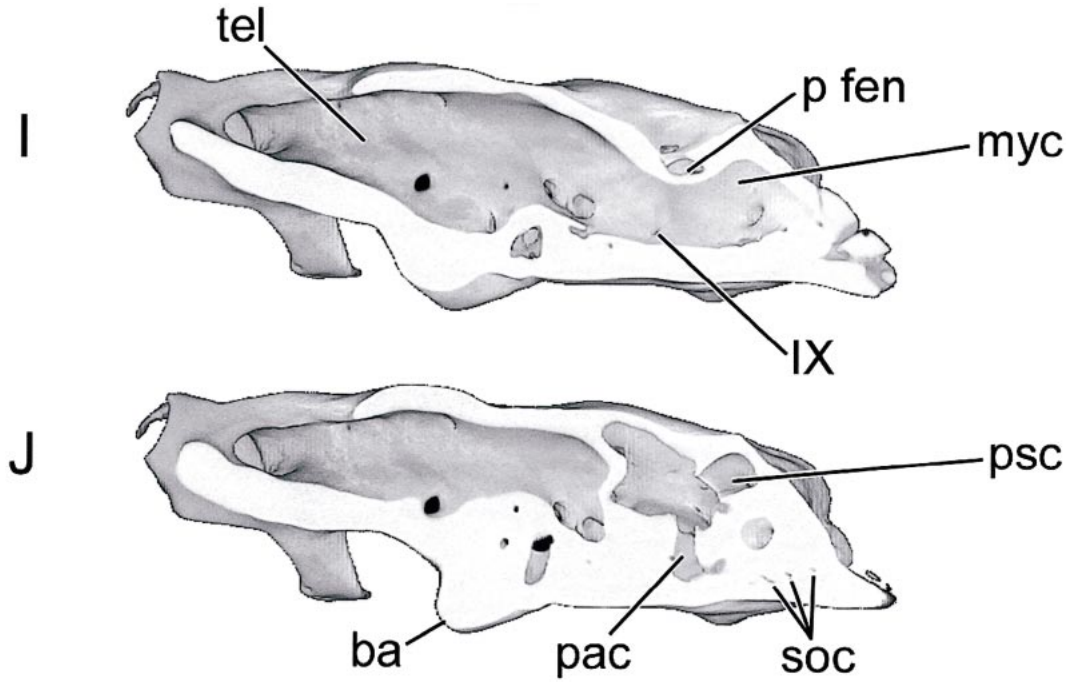


Fig. 11. Continued.

corresponding posterior semicircular canal medially, within the lateral walls of the parietal fossa (D, E). The ascending (preampullary) part of this canal lies immediately lateral to the perilymphatic fenestra. Thus, the posterior semicircular canal in *Notorynchus* describes a virtually complete circuit (Maisey, 2001a), and is completely separated from the anterior one as in *Squalus* (figs. 8, 9). The posterior semicircular canal extends into the cartilage forming the base of the postotic process, which also contains the glossopharyngeal canal (I, J). The external semicircular canal curves progressively deeper around the exterior of the saccular region (E–J) and eventually passes between the saccular space and posterior semicircular canal.

The floor of the vestibular chamber has a very complex morphology, incorporating the lagenar chamber and the passage for the octaval nerve, as well as parts of the glossopharyngeal canal (technically the latter lies below the capsule, but now appears confluent with the chamber because the membranous floor to the capsule is unchondrified). The octaval canal enters the vestibular chamber from the acustico-trigemino-facialis recess anteromedially, immediately behind the dorsum sellae (H–J). A similar arrangement has been described in *Chlamydoselachus* (Allis, 1914, 1923), except that its recess is located slightly farther anteriorly with respect to the dorsum sellae, which lies immediately below the anterior margin of the recess rather than in front of it as in *Notorynchus*. The octaval canal branches within the thickness of the cartilage in the scanned specimen, suggesting that the anterior (utricular) and posterior (vestibular) branches of the nerve divided within the capsular wall (Maisey, 2001a). The octaval canals in the *Squalus* endocasts prepared by Schaeffer (1981) do not branch, suggesting that either the nerve divided within the labyrinth, or the two branches shared a common canal.

In progressively deeper slices (J–M) the dorsum sellae separates the hypophyseal chamber from the posterior part of the endocranial cavity. The passage for the efferent pseudobranchial artery is situated in the lateral wall of the hypophyseal chamber (J). The canal enters the orbit immediately in

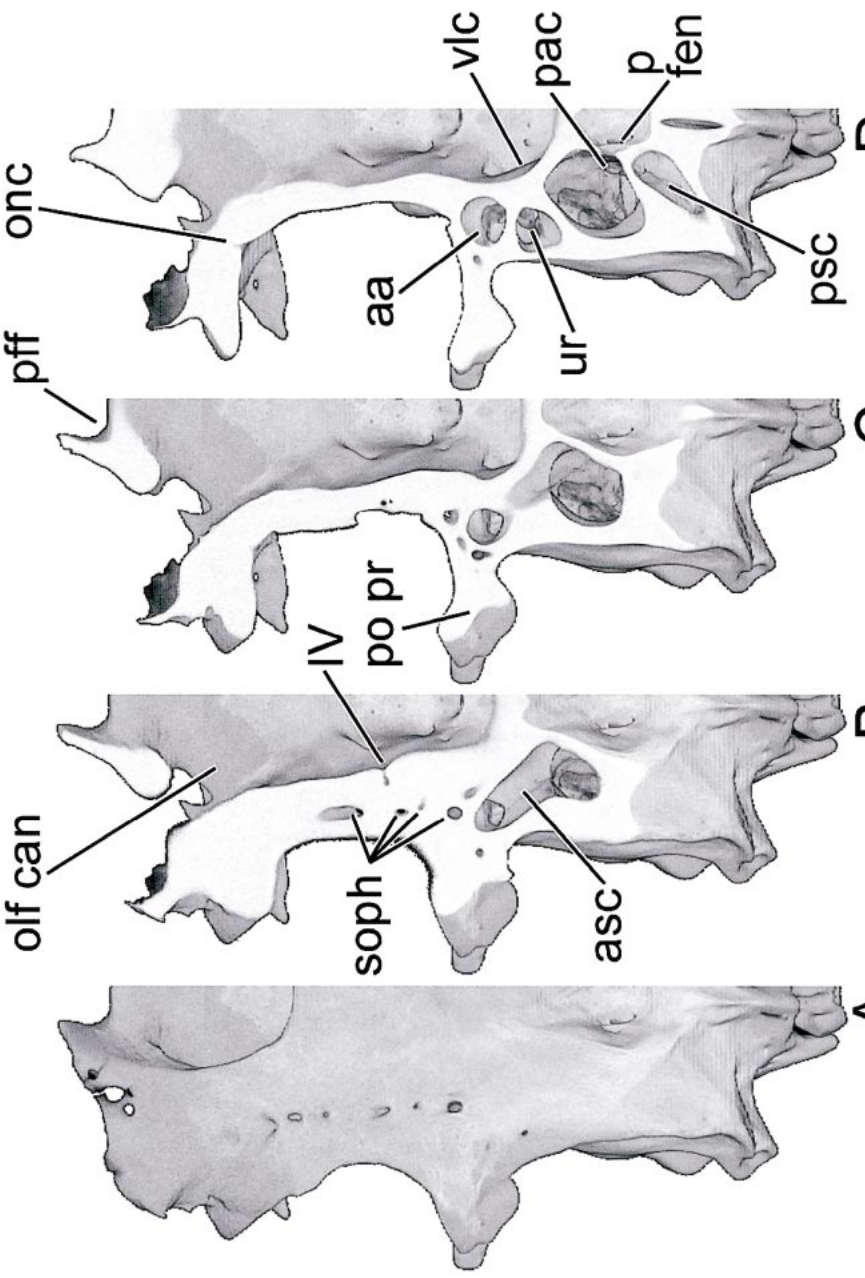


Fig. 12. *Notorynchus cepedianus* braincase digitally resliced in horizontal plane (corresponding to y–z axes of original CT scans). Sequence (A–P) passes from top to bottom of braincase. Left side only. View A corresponds to figure 1. Scale bar = 10 mm.

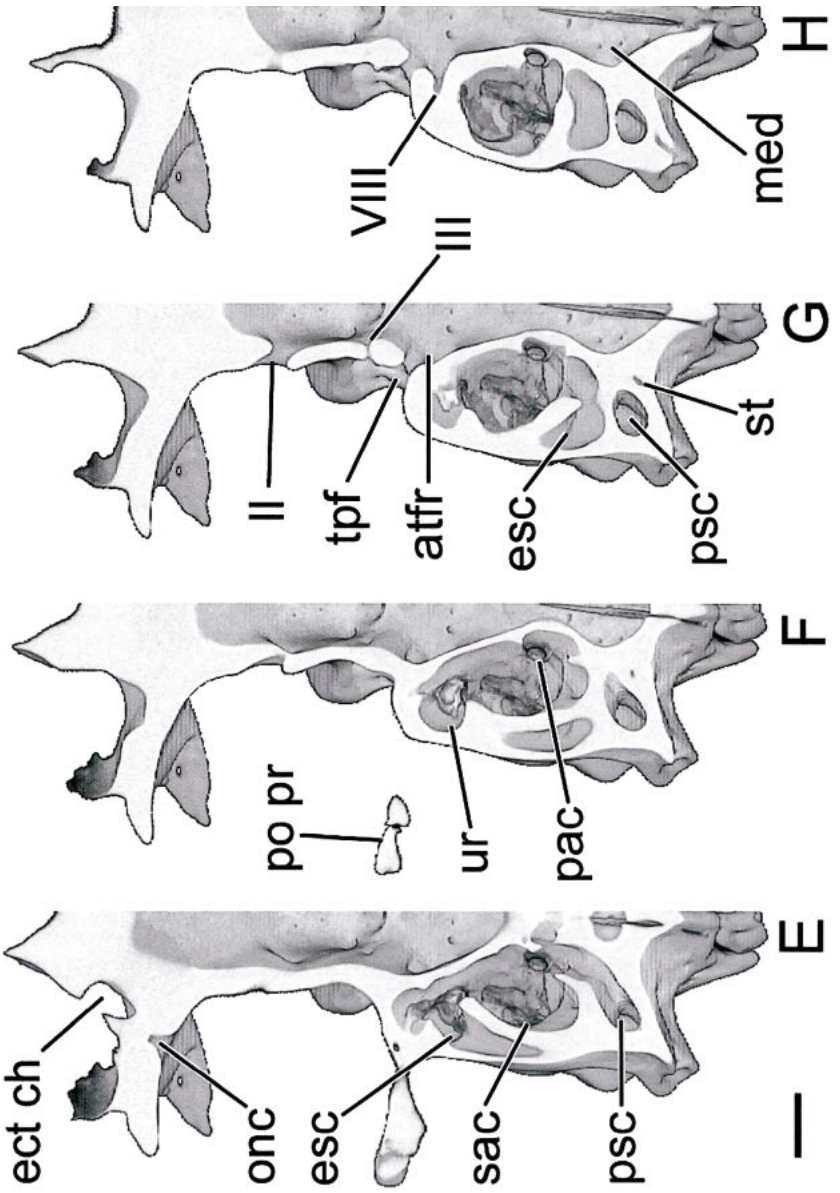
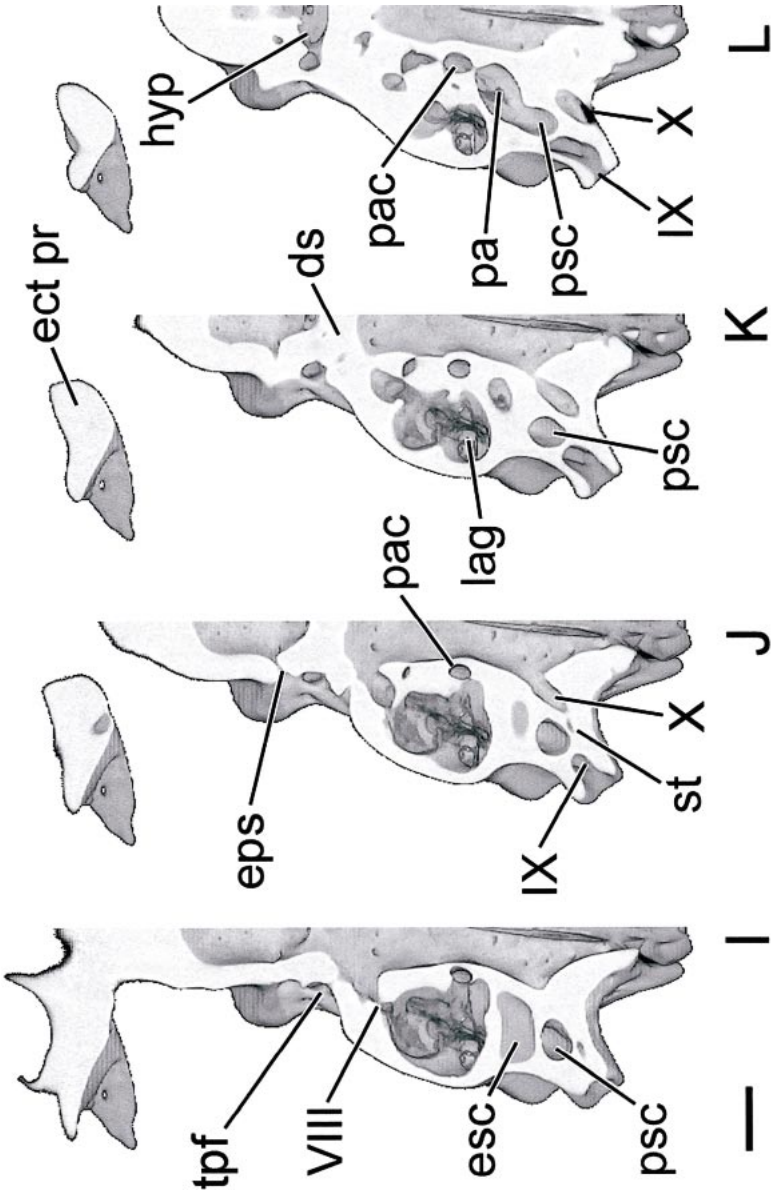


Fig. 12. Continued.



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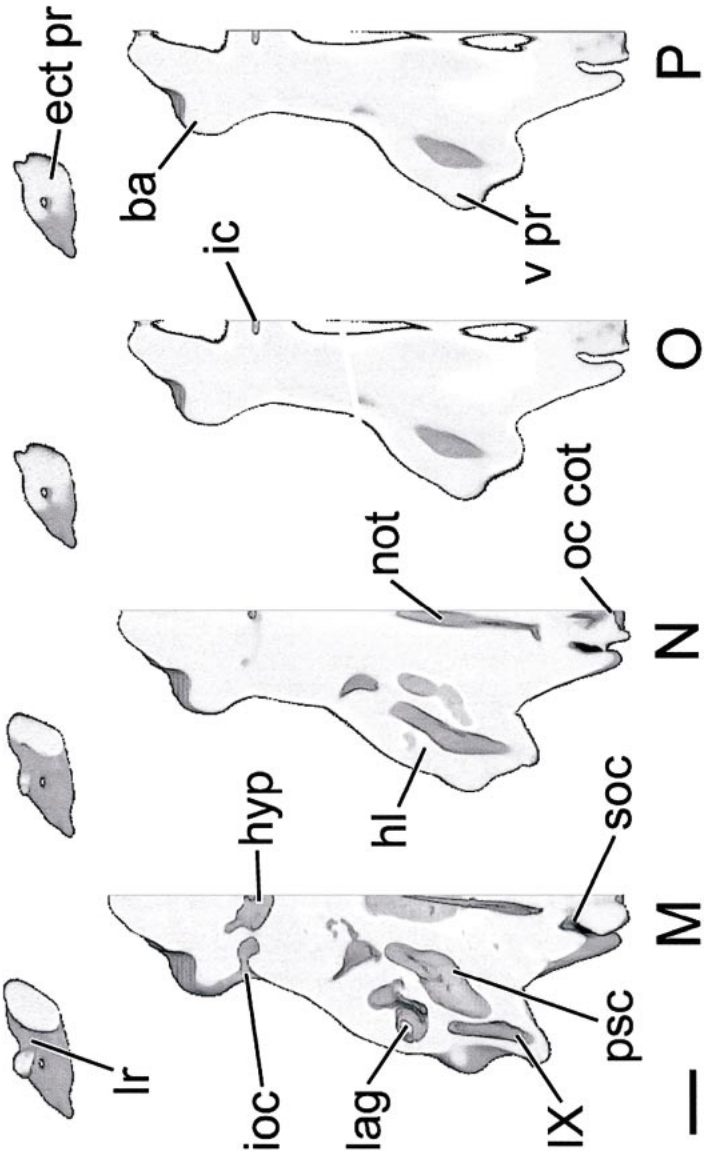

Fig. 12. Continued.

front of the trigemino-pituitary fossa and directly above the basal angle (see also fig. 5B). The horizontal slices clearly show that the floor of the vestibular chamber and medullary chamber lie in approximately the same plane (K, L). Slightly deeper within the hypophyseal chamber is the interorbital canal (M). Passages for the internal carotid arteries are located within the floor of the chamber (N, O). The vestigial hypophyseal canal discussed earlier is difficult to detect in horizontal sections.

The course of the vagal nerve and its dorsal ramus can be seen in slices F–L. The notochordal canal is exposed in deeper slices through the basis cranii (its slightly asymmetric appearance is probably caused by slight shrinkage and internal tearing of cartilage when the specimen was originally preserved). The glossopharyngeal canal passes deeper within the cartilage of the basicranium than any of the other cranial nerves, but it does not extend laterally into the vestibular process (M–P).

DISCUSSION

Interpretation of Endocranial Morphology from CT Scans

The present work demonstrates that cranial morphology in modern elasmobranchs can be studied successfully using digitally processed images obtained from CT scans, revealing otherwise inaccessible details. Images of the external cranial surface earlier in this work are certainly as informative as conventional photographs, and in some respects they are clearer (for example in emphasizing the positions of small foramina). Internal cranial features are also clearly revealed, and digitally processed images of the endocranium provide new morphological data that can contribute enormously to phylogenetic investigations. Clearly, CT scanning cannot be construed as a replacement or an alternative for traditional dissected or cleared-and-stained preparations. However, the ease with which scans can be obtained, coupled with advances in computerized imaging, makes CT scanning an increasingly valuable resource to comparative morphologists, especially when rare or irreplaceable type and/or voucher specimens are involved.

One of the great advantages virtual imaging from CT scans has over conventional serial sectioning or grinding techniques is the potential to investigate the three-dimensional relationships between internal and external morphospace, in addition to those aspects which are only evident in sections. For example, the cranial endocast of *Notorynchus* has been combined with external views of the braincase in figure 13 to create composite dorsal and ventral views. The topographic relationships of certain endocranial and external features are readily seen, including the alignment of the anterior ampulla with respect to the postorbital process and hypophyseal chamber, and the topographic relationship of external features in the otic region to the semicircular, vagal, and glossopharyngeal canals.

As might be expected, endocranial features of *Notorynchus* revealed by CT scanning agree closely with many of Schaeffer's (1981) observations of silicone endocasts prepared from *Squalus* braincases (fig. 8). However, some differences are also noted in the topographic arrangement of certain structures in the braincases of *Notorynchus* and *Squalus*. For example, in *Squalus* the hypophyseal chamber is positioned farther anteriorly relative to the postorbital process than in *Notorynchus*, although both taxa agree in the position of the process with respect to the anterior ampulla (cf. figs. 7, 8). The thickest part of the basicranium (forming the basal angle) is also positioned differently in these taxa; in *Squalus* it lies more or less directly below the hypophyseal chamber, a considerable distance behind the exit of the optic nerve, but in *Notorynchus* it is positioned farther anteriorly, below and just behind the optic nerve canal. The differing relative positions of these structures invites further developmental investigation and phylogenetic analysis. There may well be a developmental correlation between the size and extent of the basal angle and position of the hypophyseal chamber in orbitostylic sharks, and this may also have some bearing on the position and extent of the hypophyseal duct. Unfortunately, preparing silicone endocasts obliterates the braincase and destroys the original relationships between internal and external fea-

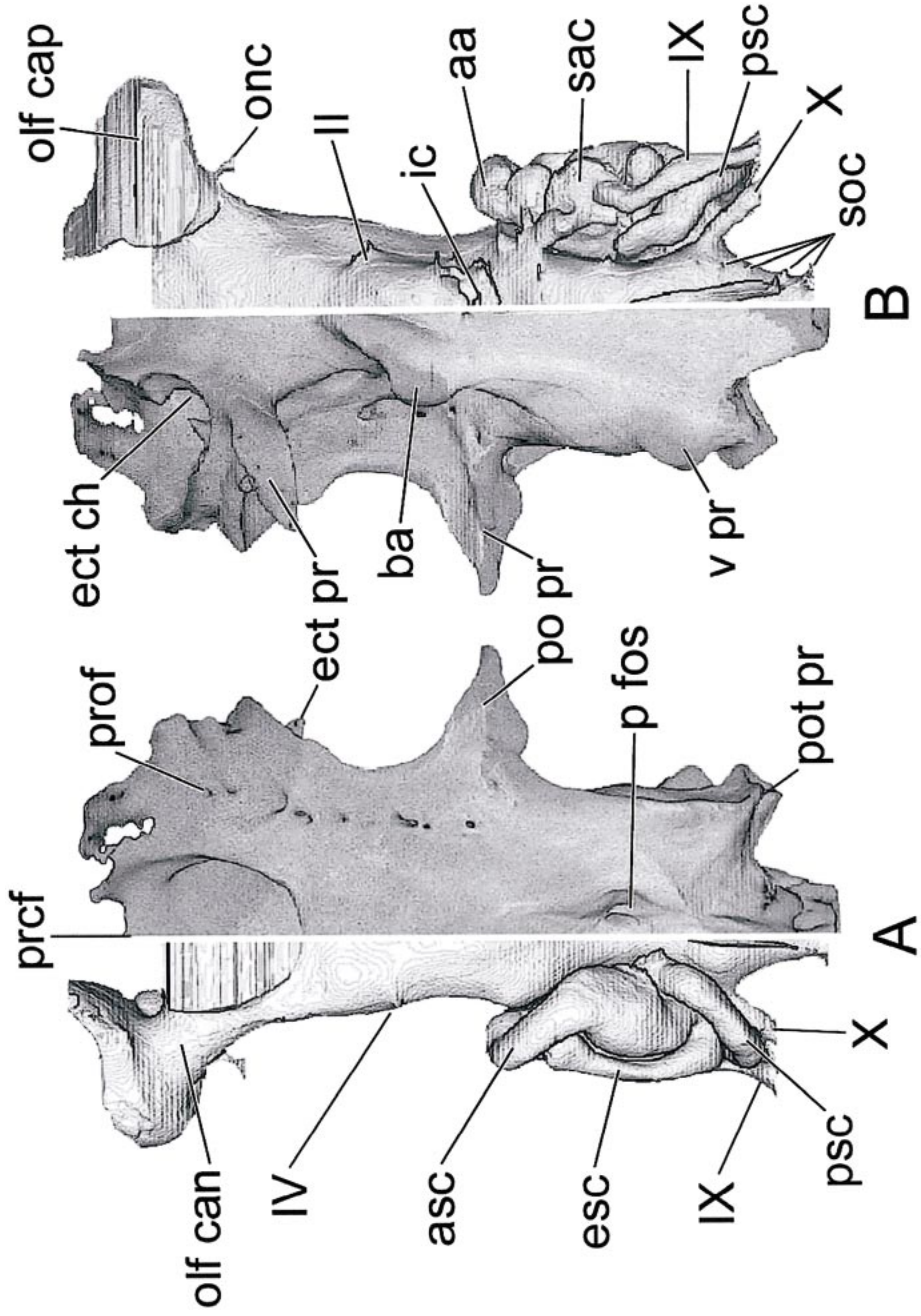

Fig. 13. Composite digital images of *Notorynchus cepedianus* braincase (external virtual image with left side removed) and virtual endocast in dorsal (**A**) and ventral (**B**) views. Anterior to top. Scale bar = 10 mm.

tures, whereas CT scanning and appropriate imaging protocols can easily document them.

The difficulties inherent in reconstructions of endocranial morphology in fossils have already been discussed at length elsewhere (Stensiö, 1963; Maisey, 2001a) and will not be repeated here. Historically, the comparative basis for interpreting endocranial features in extinct vertebrates has been extremely limited. For example, in many earlier studies of placoderm braincases a modern elasmobranch paradigm was followed, but ongoing investigations of the braincase in several extinct elasmobranchs (especially Paleozoic taxa) cast doubt on the validity of many morphological and phylogenetic statements in those earlier studies. Technological improvements over the past century (beginning with serial grinding, sectioning, and acid preparation, and now scanning and digital preparation) have gradually increased the availability of phylogenetically informative data about endocranial morphology in early craniates, and they hold great promise for improving our knowledge even further in the future.

Comparative Remarks

The following remarks are not intended to provide a detailed comparison or analysis of cranial morphology in elasmobranchs, or even in neoselachians; instead, they merely expand on some issues noted during the course of preparing this work. Since several of the features discussed here represent important landmarks developmentally, a discussion of their systematic distribution and morphological relationships to other structures may be useful.

Ventral Nasal/Ethmoid Keel: In *Notorynchus* there is no cartilaginous keel in the ventral midline of the nasal or ethmoid region (figs. 1B, 4, 6A). There is also no keel in the Upper Jurassic hexanchiform *Notidanoides* (Maisey, 1986), nor in the extinct neoselachian *Synechodus* (Maisey, 1985). By contrast, a well-developed median keel is present within the floor of the nasal septum in some extinct sharks (e.g., *Hybodus*, *Orthacanthus*: Schaeffer, 1981; Maisey, 1983), and is closely associated with the anterior (ethmopalatine) part of the palatoquadrates. Absence of such a keel has been considered a neoselachian synapomorphy (Maisey, 1984) but the situation is actually more complicated. In *Squalus* a narrow keel (rostral carina of Wells, 1917; ''carène sous-rostral'' of Devillers, 1958) extends along the ventral midline of the rostrum onto the nasal plate, and an extremely narrow keel-like nasal plate is present in some other squaloids (e.g., *Scymnorhinus*, *Etmopterus*, *Deania*; Holmgren, 1941). Holmgren (1940) described a median ''keel-process of the basis cranii'' in *Etmopterus* embryos, and he also identified a raised ''median area'' in the embryonic ethmoid region of many sharks and batoids (supposedly formed at the anterior contact between the paired trabecular plates). Additionally, Shirai (1992) noted the presence of a slender ''suborbital keel-process'' in adult *Centroscyllium*. Thus, a median ethmoidal keel is not absent in all modern elasmobranchs, although it may be absent in all galeomorphs.

Further complicating this issue, a median ethmoidal keel is apparently absent in some fossil non-neoselachian sharks (e.g., *Tristychius*, *Akmonistion*, *Tribodus*; Dick, 1978; Coates and Sequeira, 1998; Maisey and De Carvalho, 1997) and also in the primitive stem chondrichthyan *Pucapampella* (Maisey, 2001b; Maisey and Anderson, 2001). If a keel is primitively absent in chondrichthyans and early elasmobranchs, its presence may represent a synapomorphy of an extensive elasmobranch clade including (but not necessarily restricted to) xenacanths, hybodonts, and neoselachians, with the keel becoming independently reduced or lost in several neoselachian lineages. Reduction or absence of the ethmoid keel in neoselachians (and in hybodonts such as *Tribodus*) is often (though not invariably) associated with the presence of a highly kinetic (orbitostylic or fully hyostylic) mandibular apparatus (sensu Maisey, 1980). It is also possible that the keel became secondarily better developed in certain taxa (e.g., *Hybodus*, *Orthacanthus*).

Postnasal Wall: A postnasal (antorbital) wall is well developed in many modern elasmobranchs including *Notorynchus* (Fig. 5B), as well as in *Hybodus* and many Paleozoic sharks (Schaeffer, 1981; Maisey, 1983; Williams, 1998). In some Paleozoic sharks the

postnasal wall is not preserved although the olfactory canals are well developed immediately in front of the orbits and the wall may therefore have been weak or absent.

PRESPHENOID LEDGE: A presphenoid ledge is absent in *Notorynchus*, but one is present in *Squalus*, immediately below the optic nerve and the posterior part of the telencephalon (Marinelli and Strenger, 1959: fig. 162). Neither Goodey (1910) nor Allis (1923) identified a presphenoid ledge in *Chlamydoselachus*, although the basis cranii is distinctly thickened at its expected position. According to Gegenbaur (1872) a presphenoid ledge is absent in *Squatina*, batoids, *Heterodontus* and some galeomorphs (e.g., *Mitsukurina*) but is present in *Heptranchias*, *Squalus*, *Dalatias*, *Deania*, *Galeus*, and *Mustelus*. He did not identify the ledge in *Hexanchus*, although he showed a slight thickening of the basis cranii just anterior to the optic foramen, apparently corresponding to the ledge in *Heptranchias*. Shirai's (1992) sagittal sections suggest that a presphenoid ledge is present in *Centroscyllium* and *Squaliolus* but not in *Echinorhinus* or *Pristiophorus*. It is concluded that presence of a presphenoid ledge is highly variable in modern elasmobranchs and its distribution lacks a clear phylogenetic distribution, although it tends to be (1) present in most (but not all) orbitostylic sharks and (2) absent in batoids and most (but not all) galeomorphs.

POSITION OF OPTIC FORAMEN: The floor of the endocranial cavity in modern elasmobranchs sometimes includes a pocket between the presphenoid ledge and dorsum sellae (e.g., *Squalus*: Marinelli, and Strenger, 1959: fig. 162). Where such a pocket is developed it usually contains the endocranial opening of the optic foramen, low down on the interorbital wall (e.g., *Dalatias*, *Deania*, *Squaliolus*, *Galeus*). In *Heptranchias*, *Squalus*, *Centroscyllium* and *Mustelus* the optic foramen lies just at the anterolateral border of the pocket, and in *Chlamydoselachus* the foramen is positioned just above the presphenoid ledge, not within a pocket. The presphenoid ledge and a pocket are both absent in batoids and some other modern elasmobranchs (e.g., *Squatina*). In forms lacking a presphenoid ledge the pocket is poorly defined anteriorly and the optic foramen is more variable in position (e.g., in *Squatina* the optic foramen has an unusual position in the upper part of the interorbital cartilage, anterior to the trochlear foramen). As with the presphenoid ridge, no clear phylogenetic picture emerges from these observations, but there may be some correlation between the location of the optic foramen and the presence or absence both of the pocket and the presphenoid ledge.

The arrangement of the optic, trochlear, and efferent pseudobranchial foramina in *Chlamydoselachus* differs from that of other modern elasmobranchs. Its optic foramen is located anterior to the exit of the superficial ophthalmic ramus, instead of below it (as in *Notorynchus*) or behind it (as in *Heptranchias* and most other modern elasmobranchs). The optic nerve describes an unusually circuitous path in the orbit, curving anteriorly around the orbital process to reach the eyeball (as does the central retinal artery, which exits with the optic nerve; Allis, 1923: pls. 4, 19).

POSITION OF TROCHLEAR AND OCULOMOTOR FORAMINA: In modern elasmobranchs, the oculomotor foramen is invariably located near the margin of the dorsum sellae, often at its junction with the interorbital cartilage, and it therefore provides a relatively fixed developmental and morphological reference point. In many orbitostylic elasmobranchs the endocranial exits for the optic, trochlear, and oculomotor nerves are almost equidistant from each other, describing an equilateral triangle with the optic foramen anteriorly, the oculomotor foramen posteriorly, and the trochlear foramen at its apex (e.g., *Chlamydoselachus*, hexanchiforms, *Squalus*, *Squaliolus*, *Pristiophorus*). An imaginary line drawn between the optic and oculomotor foramina at the base of this triangle would pass through the foramen magnum in all these taxa. Different configurations of these openings occur in other taxa. For example, in *Squatina* the optic foramen is elevated to the same level as the trochlear foramen farther posteriorly, and in *Galeus* and *Mustelus* the optic foramen lies farther ventrally, below the level of the oculomotor foramen. In both cases, an imaginary line drawn between the optic and oculomotor foramina will pass obliquely and will miss the foramen magnum

(passing below it in *Squatina* and above it in *Galeus* and *Mustelus*).

There are important discrepancies between Goodey's (1910) and Allis' (1923) descriptions regarding the positions of the trochlear and oculomotor foramina in *Chlamydoselachus*, apparently because the earlier author failed to observe the trochlear foramen correctly. Thus, the trochlear foramen of Goodey (1910) is the oculomotor foramen of Allis (1923), and the oculomotor foramen in Goodey's (1910) account probably corresponds to the efferent pseudobranchial foramen of Allis (1923). The arrangement shown by Allis (1923) is certainly more in line with that of many other elasmobranchs and is confirmed by the embryonic *Chlamydoselachus* material illustrated by Holmgren (1941: fig. 8).

Basal Angle and Orbital Articulation: A basal angle (figs. 4, 5) is present in all extant hexanchiforms and squaloids, and its lateral surface characteristically articulates with the palatoquadrate orbital process in the posterior part of the orbit (fig. 2). The ontogenetic development of the basal angle is best known in *Squalus* (Holmgren, 1941; El-Toubi, 1949; Devillers, 1958, Jollie, 1971), where it supposedly results from retention of the original 45° orientation of the polar cartilages with respect to the parachordals after the trabeculae become reoriented approximately parallel with the parachordals, probably because the embryonic basicranial cartilages become fused before cephalic flexure is completely eliminated. The basal angle in hexanchiforms probably formed in similar fashion, since it is located at the presumed junction between the trabeculae, parachordals, and polar cartilages (if present), but this requires confirmation from ontogenetic investigations.

The orbital articulation is positioned between the optic foramen and efferent pseudobranchial foramina in all orbitostylic sharks, regardless of whether a basal angle is present (Maisey, 1980). Since the ophthalmic artery leaves the braincase via the optic foramen, the orbital process also effectively always separates this vessel from the efferent pseudobranchial and ophthalmic arteries. According to Allis (1923), in *Chlamydoselachus* the optic nerve is confined to a groove in the surface of the orbital articulation, into which it is pressed by the orbital process of the palatoquadrate. Conversely, *Heptranchias* differs from other hexanchiforms and *Chlamydoselachus* in having a much narrower interorbital septum.

The orbital articulation is restricted to the posterior region of the orbit (i.e., at the junction of the trabecular-polar cartilage and the parachordal) *only* in those orbitostylic elasmobranchs in which a basal angle is present (e.g., hexanchiforms, squaloids; fig. 2). Unfortunately, the development of the head in orbitostylic sharks has only been investigated in taxa possessing a basal angle. It has sometimes been suggested that the orbital articulation in these forms is homologous with the basitrabecular process in other gnathostomes (e.g., Gardiner, 1984). The transverse shelf-like process of the polar cartilage in *Squalus* and *Etmopterus* has been identified as a basitrabecular process (Holmgren, 1940), but it clearly lies some distance behind the palatoquadrate orbital process, which borders the trabeculae and does not extend posteriorly as far as the polar cartilage. In osteichthyans (including tetrapods), the basitrabecular process is positioned anterior to the palatine nerve (Goodrich, 1930: fig. 284). In *Squalus*, however, the orbital articulation is located much farther anteriorly relative to the palatine nerve, and in *Chlamydoselachus* and *Squatina* (both of which lack a basal angle) the articulation is even more remote from the palatine nerve. Furthermore, in *Chlamydoselachus* the anterior end of the orbital articulation overlaps the ectethmoid process, giving rise to a broad suborbital platform in the *anterior* part of the orbit (Maisey, 1980).

Although the orbital articulation in orbitostylic sharks resembles the palatobasal one in osteichthyans, topographically, confinement of the orbital articulation to the posterior part of the orbit in hexanchiforms and squaloids may represent a derived state, probably related to development of the basal angle, secondarily resembling the topography of the basitrabecular process of other gnathostomes. All modern sharks with a basal angle are orbitostylic, but not all orbitostylic sharks have a basal angle (e.g., *Chlamydoselachus*, *Squatina*, *Pristiophorus*). In the Upper Jurassic hexanchiform *Notidanoides*,

the basicranium is flat (even allowing for compression of the fossil during preservation), and there is no sign of a basal angle. However, *Notidanoides* probably had an orbital articulation, as the palatoquadrate has a strong orbital process; Maisey, 1986).

The consistent topographic relationship of the orbital articulation with respect to the optic foramen, efferent pseudobranchial foramen, optic pedicel, and rectus musculature (whether or not a basal angle is present) has been regarded as a unique feature of orbitostylic neoselachians (Maisey, 1980). The anterior palatoquadrate articulation of other neoselachians (e.g., galeomorphs, *Heterodontus*) certainly does not have the same configuration and lies far anterior to the efferent pseudobranchial foramen and polar cartilage. Conversely, modern orbitostylic sharks have (at best) only a ligamentous connection between the symphyseal region of the palatoquadrates and ethmoid region. However, the orbital articulation of *Notorynchus* and other orbitostylic sharks is widely regarded as homologous with the anterior (ethmopalatine) articulation of other elasmobranchs. For example, Holmgren (1941) repeatedly referred to a ''palatobasal process'' with an articular surface for the palatoquadrate not only in *Chlamydoselachus*, hexanchiforms, and squaloids, but also in *Heterodontus* and galeomorphs, and he clearly regarded the articulations as homologous in all these taxa. Wilga (2002) identified the articular surface for the palatoquadrate orbital process as an ''ethmopalatine groove'', even though in many orbitostylic sharks the articulation is far removed from the ethmoid region. Admittedly, the position of the orbital articulation in orbitostylic sharks is highly variable (Maisey, 1980); in *Notorynchus* it is located almost level with the postorbital processes, but in other modern hexanchiforms, *Notidanoides*, and *Chlamydoselachus*, it lies slightly farther anteriorly in the orbit. Thus, the orbital articulation is confined to the posterior part of the orbit only in sharks with a pronounced basal angle (hexanchiforms and squaloids). From an evolutionary viewpoint, therefore, it might be argued that this arrangement was primitively derived from a more anterior articulation and subsequently displaced toward the back of the orbit in those sharks which acquired a strong basal angle. Some morphological support for this is found in the position of the efferent pseudobranchial foramen, which is always close to the posterior margin of the orbital articulation in orbitostylic sharks and lies immediately behind the anterior articulation in extinct sharks such as *Cladodoides*, *Tamiobatis*, and *Orthacanthus* (Schaeffer, 1981; Maisey, 1983), even though the articulation occupies different positions in the orbit.

Several recently published phylogenies based on morphology have postulated a close phylogenetic relationship between orbitostylic sharks and batoids (which are completely hyostylic and have no palatoquadrate articulations with the braincase; Shirai, 1992, 1996; Carvalho, 1996; Carvalho and Maisey, 1996). According to those hypotheses, batoids are inferred to have lost the orbitostylic suspensorial arrangement. However, there is molecular evidence that batoids are not ''derived sharks'' (Douady et al., 2003), and there is strong molecular support for an alternative phylogenetic hypothesis in which batoids and modern sharks are sister groups (Maisey et al., in press). In that scheme, orbitostyly is a cladistically derived pattern that characterizes a monophyletic group of neoselachians (orbitostylic sharks; Maisey, 1980), which includes hexanchiforms, *Chlamydoselachus*, squaloids, squatinoids and pristiophoroids.

POSTORBITAL PROCESS, LATERAL COMMISSURE, AND PREFACIAL COMMISSURE: In actinopterygians, the lateral commissure surrounds the lateral head vein and orbital artery (De Beer, 1937). By contrast, In modern elasmobranchs the commissure encloses the lateral head vein but not the orbital artery (Holmgren, 1940, 1941). The extent of the lateral commissure, the degree to which it becomes chondrified, and its relationship to other structures (apart from the lateral head vein) all vary considerably in neoselachians. In *Squatina* and many squaloids (e.g., *Oxynotus*, *Scymnodon*, *Centrophorus*, *Somniosus*), the lateral commissure completely surrounds the lateral head vein, although the jugular canal may be quite small (most squaloids) or inflated (*Squatina*). However, in *Squalus* and *Centrophorus* the lateral head vein and hyomandibular ramus pass through

separate canals, and (according to De Beer, 1937) the medial wall of the jugular canal in *Squalus* is formed from the prefacial commissure (derived ontogenetically from the basal plate), while its outer wall is formed by the lateral commissure. The prefacial commissure in this form therefore separates the hyomandibular trunk from the jugular canal and the lateral commissure. Different conditions of the hyomandibular trunk, lateral head vein, the lateral and prefacial commissures in orbitostylic sharks include the following: (1) Prefacial commissure and hyomandibular foramen located medial and slightly anterior to a ''complete'' lateral commissure; the hyomandibular trunk accompanies the lateral head vein posteriorly through a jugular canal (e.g., *Squatina*). (2) Prefacial commissure and hyomandibular foramen lie ventral and medial to a ''complete'' lateral commissure; the hyomandibular trunk passes behind the lateral commissure and the palatine nerve exits below it (e.g., *Squalus*). (3) Prefacial commissure and hyomandibular foramen are both ventral and medial to primary postorbital process (lateral commissure absent); hyomandibular trunk and lateral head vein pass below the postorbital process (e.g., *Notorynchus*).

According to Schaeffer (1981) the hyomandibular trunk emerges from the braincase behind the postorbital process in *Cladodoides* and *Orthacanthus*. This may reflect a more posterior position of the prefacial commissure in those taxa (similar to the situation described above in *Squalus*, but with a completely chondrified lateral commissure; Maisey, 1983: 27).

Slightly different arrangements are found in other modern elasmobranchs, although in most forms the lateral commissure is unchondrified or absent and a jugular canal is not developed; for example, the prefacial commissure is absent in galeomorphs and the hyomandibular trunk may lack a discrete foramen altogether (Holmgren, 1941). A ''complete'' postorbital process (with a large jugular canal) occurs in many extinct elasmobranchs (Schaeffer, 1981) and may represent a primitive elasmobranch condition. Holmgren's (1941) argument that the lateral head vein did not pass through the canal in early sharks does not withstand critical examination (see also Maisey, 1983: 27).

POSTORBITAL PROCESS AND OTIC CAPSULE: In *Notorynchus* the anterior ampulla of the vestibular region is located in the same transverse plane as the postorbital process (fig. 10 H, I). During the development of *Squalus*, *Heterodontus*, and *Torpedo*, the anteriormost part of the otic capsule extends forward as far as the lateral commissure (Holmgren, 1940: figs. 67, 119, 140), and in *Etmopterus*, *Scyliorhinus*, and *Raja* it can extend slightly farther anteriorly (Holmgren, 1940: figs. 86, 103, 109, 114, 128). In modern carcharhiniform sharks, however, the postorbital process is usually positioned on the lateral wall of the capsule, well behind the level of the anterior ampulla (Compagno, 1988: fig. 6.12). In hybodonts the postorbital process is also located on the lateral wall of the otic capsule, although its anteroposterior extent is variable (e.g., *Hybodus*, *Tribodus*; Maisey, 1983; Maisey and Carvalho, 1997).

Orthacanthus and *Tamiobatis* both have a comparatively long otic region, and their anterior ampulla is located some distance behind the postorbital process (Schaeffer, 1981). The anterior ampulla is also located well behind the postorbital process in the Devonian stem chondrichthyan *Pucapampella* (Maisey, 2001b; Maisey and Anderson, 2001) and also in primitive actinopterygians (e.g., *Kansasiella*; Poplin, 1974: figs. 12, 22, 30), where the otic region is clearly not elongated. When compared with *Notorynchus*, the postorbital process in *Orthacanthus* is located anteriorly not only with respect to the otic capsule, but also to the passages for the facial, trigeminal and anterior lateral line nerves within the cranial wall. The mesencephalic chamber is proportionately longer in *Orthacanthus* and *Tamiobatis* than in *Notorynchus* and *Squalus*, but endocranial structures of the orbital region also seem to be positioned farther posteriorly in these fossils, so these differences evidently involve more than just the proportions of the otic region. For example, in both *Squalus* and *Notorynchus* the optic lobe of the mesencephalic chamber has a midorbital position, whereas in *Orthacanthus* it lies farther posteriorly, in line with the postorbital process, suggesting

a somewhat different position for the embryonic lateral commissure.

To summarize, although the developmental relationships of the lateral commissure, the prefacial commissure, and the otic capsule are highly conserved in gnathostomes, there is clearly some localized variation in their arrangement which may have phylogenetic significance. Primitively, the otic capsule was probably located entirely behind the postorbital process in gnathostomes, but in neoselachians and some extinct sharks the lateral commissure is plastered onto the lateral or anterolateral wall of the capsule.

OTIC CAPSULE MORPHOLOGY: The anterior part of the medial capsular wall in *Notorynchus* contributes to the acustico-trigemino-facialis recess (sensu Allis, 1914, 1923) within the endocranial cavity. According to Schaeffer (1981: fig. 14), *Orthacanthus* lacks an acustico-trigemino-facialis recess. Such absence could be explained by the incomplete chondrification of the medial capsular wall in *Orthacanthus*, as this cartilage helps define the wall of the recess in modern elasmobranchs. In *Cladodoides*, however, CT scanning suggests that the prefacial commisure was chondrified and formed a wall behind the main exits of the facial and trigeminal nerves in the expected position of an acustico-trigemino-facialis recess. It is therefore entirely possible that in *Orthacanthus* an acustico-trigemino-facialis recess was present although its walls may not have chondrified. The medial capsular wall is chondrified in hybodonts (e.g., *Hybodus*; Maisey, 1983: 32), and CT scanning suggests that an acustico-trigemino-facialis recess was also well developed.

Several specializations for low-frequency semidirectional phonoreception have been identified in modern elasmobranchs, many of which are reflected by the architecture of the skeletal labyrinth cavity. Features include separation of the posterior semicircular canal, which describes an almost complete circle and is connected to the vestibular region by a single duct; separation of the utricular and saccular chambers; perilymphatic fenestrae; and a deep parietal fossa (Maisey, 2001a). In addition, the macula neglecta of modern elasmobranchs is greatly enlarged, and is confined to an area within or immediately adjacent to the duct connecting the posterior semicircular canal to the vestibular region, but this feature cannot be determined in CT scans of the braincase.

Orthacanthus and some other Paleozoic sharks lack most of these features, although a parietal fossa is usually present. The cartilaginous lateral walls of the parietal fossa in *Orthacanthus* extend deep inside the braincase, however, and probably no direct communication existed between the macula neglecta and the perilymphatic canals as in modern elasmobranchs. As restored by Schaeffer (1981), the floor of the saccular chamber in *Orthacanthus* seems to be level with that of the medullary region, rather than extending below it. This arrangement characterizes modern elasmobranchs and certain hybodonts (e.g., *Hybodus*, *Tribodus*). By contrast, in some Paleozoic sharks the saccular chambers seem to have extended much farther ventrally (as in osteichthyans), although in fossils where the floor of the sacculus was unchondrified the glossopharyngeal canal may sometimes appear confluent with the saccular space, creating the illusion of a deeper saccular chamber.

PARIETAL (ENDOLYMPHATIC) FOSSA AND POSTERIOR DORSAL FONTANELLE: There is some developmental and paleontological evidence (reviewed in Maisey and Anderson, 2001) that the parietal fossa is homologous with the posterior dorsal fontanelle of osteichthyans, and that both these openings represent parts of a primitive otico-occipital fissure. One plausible evolutionary scenario is that primitively the fontanelle was continuous with the otico-occipital fissure (as a posterior dorsal fontanelle; e.g., *Pucapampella*; Maisey, 2001b), and that more advanced elasmobranchs acquired a posterior tectum which isolated the parietal fossa from the otico-occipital fissure (which is primitively retained in a number of Paleozoic sharks). According to this scenario, the parietal fossa of modern elasmobranchs can be regarded as a posterior dorsal fontanelle that is separated from the primitive cranial fissure by a posterior tectum.

BASICRANIAL CIRCLE: In gnathostomes, the dorsal aorta generally divides on either side of the notochord, and the paired vessels (lateral aortae, internal carotids) anterior to the

notochord subsequently converge and form a cephalic circle (Bertin, 1958), which is almost entirely confined to the posterior (parachordal) region of the basicranium. Differences in the basicranial circle mostly involve the shape of the cephalic ''circle'', and the extent to which the arteries lie beneath or within the parachordal cartilage (in fact, considerably greater variation of both these variables has been noted than is at present documented in the literature). In *Notorynchus*, most of the vessels forming the circle are situated below (i.e., external to) the basicranium, and the internal carotids trace a bell-shaped path. A similar arrangement is also found in other modern elasmobranchs, and this was considered a derived condition by Schaeffer (1981). In some extinct elasmobranchs, the lateral aortae are essentially straight or divergent anteriorly, but do not adopt an outward curve (e.g., *Hybodus*, *Cladoselache*, *Tamiobatis*, *Orthacanthus*). The cephalic circle was largely external to the braincase in hybodonts (Maisey, 1982, 1983), but in many Paleozoic sharks the lateral aortae and internal carotids are partly buried within the basicranial cartilage (Schaeffer, 1981; Williams, 1998). Thus, *Notorynchus* shares two important derived features of its cephalic circle with other neoselachians; the outward swing of its lateral aortae, and the extensive exposure of the lateral aortae and internal carotids.

Holmgren (1942) noted that in modern elasmobranchs the internal carotid foramina may lie a considerable distance behind the hypophyseal foramen (from which they are separated by the precarotid commissure; De Beer, 1931). According to Gross (1937), in ''*Cladodus*'' *wildungensis* the internal carotids entered the braincase via the hypophyseal foramen, and CT scanning suggests that the precarotid commissure was absent (in preparation). The commissure may also be absent in the stethacanthid *Akmonistion* (Coates and Sequeira, 1998) and possibly in *Tamiobatis vetustus*, but in other Paleozoic sharks there is an extensive commissure separating the internal carotid foramina and hypophyseal fenestra (e.g., *Orthacanthus*, ''*Tamiobatis* sp.'', *Cladoselache*, *Hybodus*: Schaeffer, 1981; Maisey, 1983; Williams, 1998). The area around the hypophysis is among the last to chondrify in the braincase of modern elasmobranchs (De Beer, 1931), and the presence or absence of the precarotid commissure in extinct sharks may reflect variation in the timing of chondrification as well as actual differences in the basicranial aortic circle.

OCCIPITAL ARCH: Schaeffer (1981) presented a convincing argument that having the occipital arch wedged to a greater or lesser degree between the otic capsules is a derived condition in elasmobranchs, not seen in other gnathostomes apart from a few teleosts (e.g., *Clupea*, mormyroids and some pholidophorids). In his phylogenetic discussion, he recognized two states: (1) occipital arch projecting behind capsules, with separate foramina for spino-occipital nerves, and (2) arch not projecting behind capsules, with most spino-occipital nerves leaving braincase through the vagal canal. The first of these states was said to characterize all chondrichthyans; the second supposedly represented a synapomorphy of *Hybodus* and neoselachians. However, in chimaeroids there is no evidence that the occipital block extends anteriorly between the otic capsules to any appreciable extent, a condition which is clearly different from that found in some early sharks such as *Orthacanthus*, *Tamiobatis*, *Akmonistion*, and *Cladodoides*, where the occipital arch does extend at least some distance between the capsules (Schaeffer, 1981; Coates and Sequeira, 1998; Maisey, 2001C). Furthermore, the occiput projects appreciably behind the posterior wall of the otic capsule in some modern elasmobranchs (e.g., *Notorynchus*, *Hexanchus*). Schaeffer's (1981: 59) proposal that ''the relatively forward position of the occipital arch in neoselachians accounts for the fact that the occipitospinal nerves leave the braincase through the vagal canal or behind the condyles . . . rather than separately along the sides of the occipital segment'' does not hold true for all neoselachians or hybodonts, because in *Notorynchus* and *Hybodus* the spino-occipital nerves are located on the lateral surface of the occipital block rather than entirely within the vagal canal. Collectively, these observations suggest that Schaeffer's (1981) proposals regarding occipital arch arrangement (especially that the ''short'' occipital block is a synapomorphy of neoselachians and hybodont

sharks) require some reappraisal and refinement. There is certainly a tendency toward shortening the occipital region in neoselachians and hybodonts, but no clear-cut phylogenetic pattern has yet emerged.

In gnathostomes generally, the parachordals project posteriorly and give rise to a variable number of neural arches (= occipital and preoccipital arches; Goodrich, 1930). In modern elasmobranchs (and most lower vertebrates) these become fused with the synotic tectum and posterior walls of the otic capsules. However this fusion evidently has a complex evolutionary history and seems to have occurred independently in osteichthyans and chondrichthyans (perhaps several times; Maisey, 2001b). In many Paleozoic sharks the occipital region is separated from the otic region dorsally by the persistent otico-occipital fissure, but in modern elasmobranchs and hybodonts this fissure is closed and the occipital arches are fused with the otic region.

Endocranial Features as Phylogenetic Characters

Only some of the morphological features noted in *Notorynchus* have been included in previous phylogenetic analyses of elasmobranchs. The following list combines features which have previously been considered phylogenetically informative (i.e., they have appeared at one time or another in previously published phylogenetic analyses), as well as many other whose phylogenetic potential is largely untested. Characters listed in parentheses may not occur primitively within the group or within all extant representatives. An asterisk denotes an internal cranial feature.

A. Craniate Characters
- chondral neurocranium surrounding the brain
- chambered, platybasic endocranial cavity with hypophyseal opening*
- trabecular and parachordal cartilages forming basis cranii*
- otic capsule with ampullae, maculae, and semicircular canals*
- olfactory capsules

B. Gnathostome Characters
- trabeculae with a rostral extension dorsum sellae and deep hypophyseal chamber*
- articulations for palatoquadrate and epihyal
- optic pedicel
- separate superficial ophthalmic division of trigemino-facialis complex
- lateral commissure
- endolymphatic ducts
- external semicircular canal*
- macula neglecta*
- (utricular recess)*
- orbitonasal canal
- ectethmoid chamber?

C. Chondrichthyan Characters
- prismatically calcified cartilage, no chondral centers of ossification
- (single-unit braincase; not in certain stem chondrichthyans)

D. Elasmobranch Characters
- precerebral fontanelle
- parietal fossa
- posterior position of hyomandibular articulation
- (specializations in otic region for low-frequency phonoreception; see Maisey, 2001a)*
- (Floor of saccular chamber level with medullary region)*
- (perilymphatic canals)*
- (ectethmoid process)
- (otic capsule protrudes between postorbital processes)*
- (otic capsule with chondrified medial wall)*
- (glossopharyngeal canal)*
- (dorsal otic ridge lacks horizontal crests; see Coates and Sequeira, 1998)
- (posterior tectum present)
- (vestibular process)
- (postotic process)
- (occipital region wedged between otic capsules posteriorly)

E. Neoselachian (= crown elasmobranch) Characters
- flat internasal plate
- (no ethmoidal keel)
- occipital hemicentrum
- (postorbital process ventrally unchondrified)
- (hypophyseal duct closed externally)

F. Orbitostylic Shark Characters
- orbital articulation extends into orbit

(basal angle)
(hypophyseal duct associated with basal angle)*

G. Hexanchiform Characters
postorbital articulation
braincase poorly calcified

This list is clearly dominated by external features except at very generalized levels (e.g., craniates, gnathostomes). The only significant exception to this is in the ear region, where 16 apomorphic features (7 of which are associated with low-frequency semidirectional phonoreception) have been identified in the elasmobranch labyrinth (Maisey, 2001a; not listed separately above). One additional character of the elasmobranch ear region is noted here (floor of saccular chamber level with that of the medullary region). This bias is undoubtedly artificial, since the ear region has been investigated in much more detail, and many features of the endocranial cavity will probably be discovered as investigations proceed. Historically, endocranial morphology has not been widely utilized in higher-level systematic studies of elasmobranchs (or other vertebrate groups), perhaps reflecting the difficulties in obtaining such data. Hopefully, the present study has demonstrated that endocranial morphology can be a rich source of phylogenetically informative characters at many levels. It certainly deserves greater attention by future investigators using modern noninvasive scanning and imaging technologies.

A detailed discussion of all the characters listed above is beyond the scope of this work. The most fundamental craniate and gnathostome characters undoubtedly reflect phylogenetically deep-rooted and relatively immutable patterns of gnathostome structure and development within major evolutionary clades. For example, there are fundamental differences in the skeletal labyrinth morphology of gnathostomes and agnathan craniates and between modern elasmobranchs and other gnathostomes (Maisey, 2001a). Similarly, in all gnathostomes the cranium supports or articulates with parts of the visceral skeleton (e.g., palatoquadrate, epihyal), and each type of articulation has a distinct and unique relationship with parts of the braincase that have their own distinct and unique ontogenetic origins. The hyomandibular articulation with the otic capsule is another conservative gnathostome feature, although its posterior position on the capsular wall is apparently a derived feature of elasmobranchs.

The differing relationships between endocranial features associated with the mid- and hindbrain in modern and extinct elasmobranchs probably involve many developmental factors that are as yet poorly understood. The observations discussed briefly in the previous section have broader implications for the role of fossils in future developmental studies, since they show that some patterns of structural and topographic relationship may not be revealed by modern ontogenetic studies and exist only in extinct taxa. This is not an entirely new revelation, but it certainly underscores the increasing relevance of paleontology to modern evolutionary-developmental investigations.

Unfortunately, many of the features identified in this work cannot be incorporated into phylogenetic analyses of craniates or gnathostomes until many more taxa are sampled. Such features therefore offer a potentially rich but still largely untapped source of characters at many phylogenetic levels, yet they show great promise in resolving problematic phylogenetic issues. A comprehensive program of scanning and imaging endocranial features in Recent and fossil elasmobranchs (indeed, in all vertebrate groups) should provide many more characters for inclusion in future phylogenetic analyses, and may perhaps improve our understanding of several crucial problems in lower vertebrate evolution.

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