

The Upper Jurassic Hexanchoid Elasmobranch *Notidanoides* n. g.

By

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With 9 figures in the text

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Abstract: An Upper Jurassic hexanchoid elasmobranch from Solnhofen is redescribed with particular reference to the anatomy of its neurocranium and jaws. Comparison with Recent sharks suggests that the fossil represents the extinct sister group of Recent hexanchoids. The Jurassic species is placed in a new genus, *Notidanoides*. It differs from living hexanchoids in lacking a basal angle and in having a broad braincase floor anterior to the orbital articulation of the palatoquadrate. In these respects *Notidanoides* closely resembles *Chlamydoselachus*.

Key words: Elasmobranchii (Hexanchoidei), Jurassic, anatomy, fossil, new taxon; Germany (Solnhofen), Bavaria.

Zusammenfassung: Anhand der Neubearbeitung eines hexanchoiden Elasmobranchiers aus dem Malm von Solnhofen wird die neue Gattung *Notidanoides* aufgestellt. Sie differiert von rezenten Hexanchoiden u.a. durch einen breiten Boden der Hirnkapsel vor der orbitalen Gelenkung des Palatoquadratus, so daß Ähnlichkeiten mit *Chlamydoselachus* bestehen.

Introduction

The Upper Jurassic elasmobranch fauna of the Solnhofen Limestone of Germany (and its lateral equivalent in France) is remarkably modern in appearance. Schweizer (1964) described a fairly complete specimen of the hexanchoid "*Notidanus*" *muensteri*, but concentrated mainly on the dentition. The present work will describe the endoskeletal anatomy of this form, particularly that of the head region. This description is almost entirely based on a single specimen, Pi 1210/3 in the Institut und Museum für Geologie und Paläontologie, Universität Tübingen (Fig. 1).

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Abbreviations in figures

add. f.: adductor fossa,	or: orbit,
bh.: basihyal,	or. art.: orbital articulation,
ch: ceratohyal,	or. pr.: orbital process,
ect. ch.: ectethmoid chamber,	pnw: postnasal wall,
ect. pr.: ectethmoid process,	po. art.: postorbital articulation,
fica: foramen for internal carotid artery,	po. pr.: postorbital process,
hym: hyomandibula,	post. cbr.: posterior ceratobranchial plate,
lot. pr.: lateral otic process,	pq: palatoquadrate,
Mc: Meckel's cartilage,	rb: rostral bar,
met: metapterygium,	r. fen.: rostral fenestra,
n. ioc.: notch for infraorbital sensory canal,	sc: scapulocoracoid,
oc. con.: occipital condyle,	v. pr.: vestibular process,
oc. dem.: occipital demi-centrum,	V, VII: facial-trigeminal foramen,
olf. cap.: olfactory capsule,	X: vagus foramen.

Living Hexanchoid Sharks

Among living elasmobranch fishes, the hexanchoids (six- and seven-gill sharks; cow sharks) are of considerable interest because of their supposedly primitive level of organization. They have long been considered a relict group, descended from distant hybodont or cladodont ancestors in the Paleozoic or early Mesozoic (e. g., WOODWARD, 1886 a, 1886 b; ROMER, 1966; SCHAEFFER, 1967). This premise is largely based on their amphistylic jaw suspension, with an orbital and postorbital articulation; the elongate basibranchial skeleton; long, slender cerato- and epibranchial elements; unfused scapulocoracoids; and a number of lesser characters, some of which are discussed below.

Three extant genera are recognized. Two of these are monotypic (*Notorynchus*, *Heptranchias*), while the remaining genus (*Hexanchus*) comprises two distinct species. Within this assemblage there is little anatomical variation. *Hexanchus* and *Notorynchus* are remarkably similar, differing mainly in the number of branchial arches (six in *Hexanchus*, seven in *Notorynchus*); and the number of cusps (serrations) on the lower lateral teeth (eight to ten in *Hexanchus*; four or five in *Notorynchus*). *Heptranchias* differs from *Hexanchus* and *Notorynchus* in its cranial morphology. The otico-occipital region is much shorter than the orbitotemporal-ethmoid region in *Heptranchias*, whereas these regions are of almost equal length in *Hexanchus* and *Notorynchus*. The postorbital process is much smaller in *Heptranchias*,

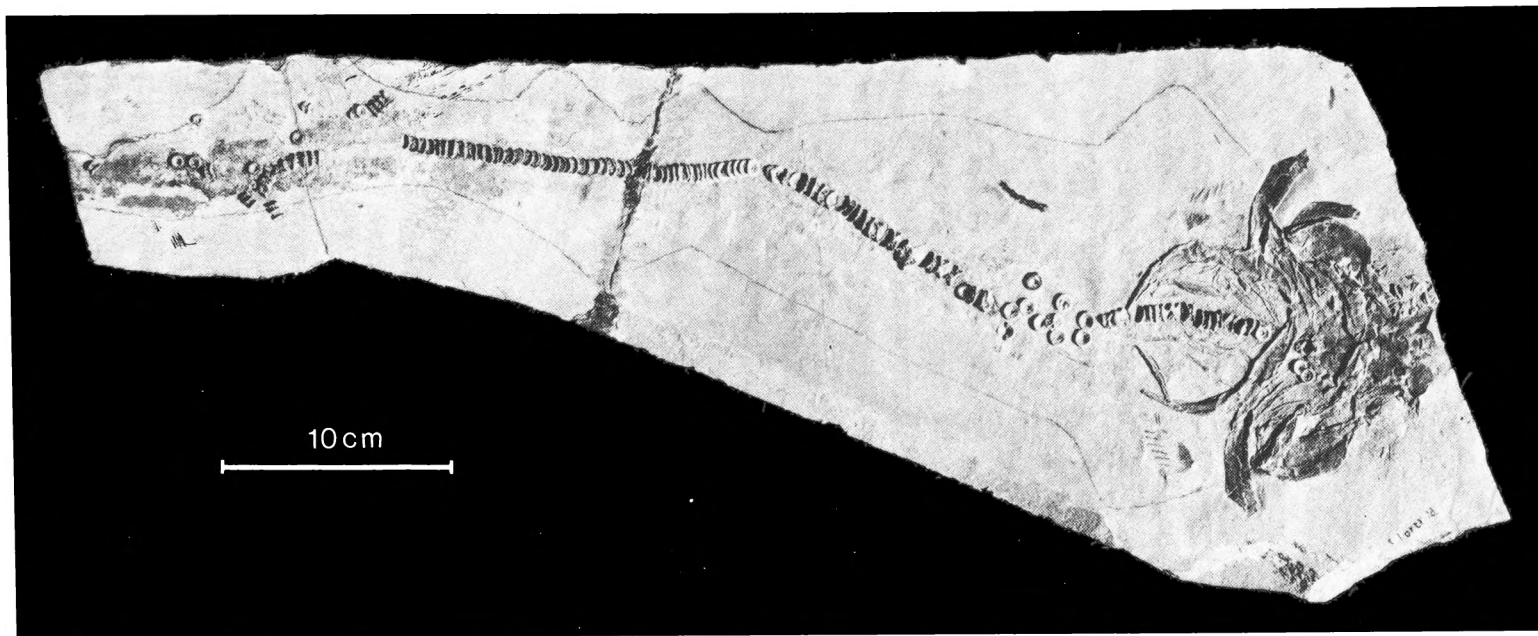


Fig. 1. Pi 1210/3, Universität Tübingen. Entire specimen, Nusplingen.

and the occiput does not project behind the otic capsules as in *Hexanchus* and *Notorynchus*. The postorbital articulation is much better developed in *Heptranchias* than in other hexanchoids (GEGENBAUR, 1872; HOLMGREN, 1941). The hyomandibular articulation with the cranium is much weaker in *Heptranchias* than in *Hexanchus* or *Notorynchus*, and the hyomandibula is a slender rod which plays only a minor role in mandibular support. The hyomandibula is slender in *Hexanchus vitulus*, but is broad and stout in *H. griseus* and *Notorynchus*; in these forms the hyomandibula provides much greater support for the jaws than in *Heptranchias* (GEGENBAUR, 1872). In *Heptranchias* the palatoquadrate adductor muscle has anterior and posterior divisions; in *Hexanchus* and *Notorynchus* this muscle is undivided.

The Frilled Shark (*Chlamydoselachus*) closely resembles hexanchoids, and has been united with them in some recent systematic treatments (e. g., COMPAGNO, 1973, 1977). Some fairly obvious differences have been noted, for example their dentition patterns and dental morphology, their scale morphology, and the absence of a postorbital palatoquadrate articulation (SMITH, 1937). Nevertheless *Chlamydoselachus* and hexanchoids are anatomically similar to each other in the number and structure of the visceral arches, paired fin morphology, and overall configuration (elongate body with a single dorsal fin located far posteriorly). Apart from a pristiophoroid (*Pliotrema*) and a trygonid stingray (*Hexatrygon*), hexanchoids and *Chlamydoselachus* are the only living elasmobranchs with more than five branchial arches and corresponding number of gill openings. Furthermore *Chlamydoselachus* resembles *Hexanchus* and *Notorynchus* in the proportions of its neurocranium, size of its postorbital process, the size and suspensory capability of its hyomandibula, and in its undivided adductor mandibulae muscle; i. e., *Chlamydoselachus*, *Hexanchus* and *Notorynchus* collectively differ from *Heptranchias* in all these respects.

Systematics

Order Hexanchiformes

Suborder Hexanchoidei COMPAGNO 1973

Notidanoides, new genus

Diagnosis: Hexanchoids with elongated trunk region; the gap between pectoral and pelvic fins is approximately three times the distance between pelvic and anal fins; dorsal fin inserted over the mid-region of the anal fin; teeth with maximum of three or four posterior serrations and lacking anterior serrations (anterior cutting edge smooth and well developed); strongly inclined median cusp in lower symphyseal tooth; seven or eight rows of lower lateral teeth; tooth replacement unsynchronized; vertebral column strongly calcified, with well developed tectospondylous centra and constricted notochord.

Derivation of name: Greek, *Notidanos*, triangular dorsal fin, plus - *oides*, resembling or similar to; i. e. "like *Notidanus*".

Discussion: The old generic name *Notidanus* has been applied both to fossil and living hexanchoids (e.g., CUVIER, 1817; GÜNTHER, 1870; WOODWARD, 1866 b, 1889; ARAMBOURG, 1952), but it is technically a junior synonym of *Hexanchus* and *Heptranchias*. These genera were distinguished by RAFINESQUE (1810) but were lumped together as *Notidanus* by CUVIER (1817). The name has continued to be used for fossil species, particularly those founded on isolated teeth, largely on the grounds that the number of branchial arches has not been determined in the fossils. Paradoxically, it has long been known that there are marked differences in the teeth of living hexanchoid taxa (e.g., WOODWARD, 1866 b), and attempts have been made to assign fossil hexanchoids to Recent genera using dental criteria (e.g., JORDAN, 1907; FOWLER, 1911; APPLIGATE & UYENO, 1968; WALDMAN, 1971; CAPPETTA, 1975; WARD, 1979; CASE, 1980; MAISEY & WOLFRAM, 1984). The teeth of *Notidanoides* share many "notidanid" features with those of *Hexanchus*, *Heptranchias* and *Notorynchus*, but are sufficiently different as to merit distinction as another tooth pattern (SCHWEIZER, 1964; MAISEY & WOLFRAM, 1984). This distinctiveness, coupled with what is known of the gross morphology of "*Notidanus*" *muensteri*, suggests that this species should not be referred to any of the three extant genera, nor to the invalid synonym *Notidanus*. The generic name *Notidanoides* is therefore proposed for this fossil species.

In a recent publication, PFEIL (1983, p. 23) erected another fossil hexanchoid genus, *Eonotidanus*, making the type species *Notidanus contrarius* MÜNSTER (1843). The species (and thus the genus) is founded upon a few isolated teeth from the Dogger (Middle Jurassic) of Rabenstein, Bavaria (see DE BEAUMONT, 1960, p. 35 and pl. 2, Figs. 41-43). PFEIL (1983) referred several other fossil species to *Eonotidanus*, including *Notidanus muensteri*. It is likely that this tooth pattern is primitive for hexanchoids, however (see SCHWEIZER, 1964; MAISEY & WOLFRAM, 1984), and species having this pattern are not necessarily congeneric. To avoid confusion and facilitate comparison in any future studies, I propose placing the relatively better known *Notidanus muensteri* in a new genus rather than assuming (as in PFEIL, 1983) it is congeneric with the poorly-founded genus *Eonotidanus*.

Notidanoides differs from Recent hexanchoids in several respects. In the latter, the trunk region between the pectoral and pelvic fins is shorter (no more than twice the distance between pelvic and anal fins). The dorsal fin is located just behind the pelvics in living hexanchoids (BASS et al., 1975), whereas it extends farther forward in *Notidanoides*. Tooth morphology differs between Recent hexanchoid species, but there is a consistently higher number of serrations than in *Notidanoides* (four or five in *Notorynchus*, eight or more in *Hexanchus* and *Heptranchias*), and in all living species the lateral teeth are serrated anteriorly. The crown and basal plate of the lower teeth are strongly flattened labio-lingually in Recent hexanchoids, instead of meeting at an angle as in *Notidanoides*. Recent hexanchoids have fewer rows of lower

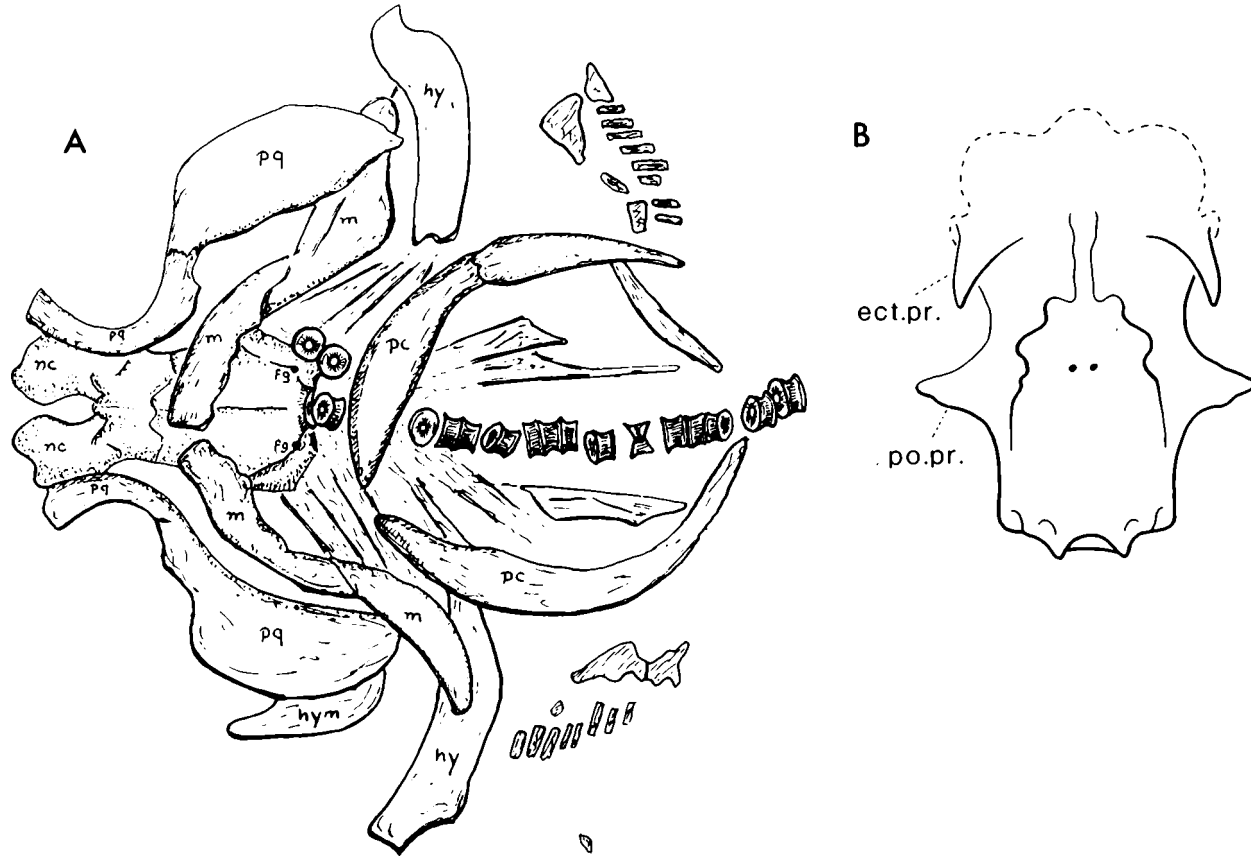


Fig. 2. (A) Anterior part of Pi 1210/3, from SCHWEIZER (1964, Fig. 7). Abbreviations differ from those in present description as follows; fg, glosso-pharyngeal foramen; hy, ceratohyal; m, Meckel's cartilage; nc, nasal capsule; pc, scapulocoracoid. (B) Restored outline of braincase according to MAISEY & WOLFRAM (1984).

lateral teeth than *Notidanoides* (five in *Heptranchias perlo* and *Hexanchus vitulus*, six in *Hexanchus griseus* and *Notorynchus cepedianus*), and their replacement is synchronized to form a nearly continuous cutting edge along the lower jaw. The vertebral column is poorly calcified in living hexanchoids, and only simple perichordal rings may form precaudally. Nevertheless the notochord is septate and constricted precaudally, and vertebral centra are sometimes present caudally (RIDEWOOD, 1921; COMPAGNO, 1977).

Type species: *Notidanus muensteri* L. AGASSIZ, Rech. sur les Poissons fossiles, 3, p. 222, pl. 27, Figs. 2, 3.

Referred species: *Notidanus arzöensis* G. DE BEAUMONT, 1960, Mém. Suisses de Paléont., 77, p. 38, figs. 23, 24, pl. 1, Figs. 39–41.

Notidanoides muensteri (AGASSIZ)

- 1833–1843 *Notidanus muensteri*. – L. AGASSIZ, Rech. sur les Poissons fossiles, 3, p. 222, pl. 27, Figs. 2, 3.
Notidanus wagneri. – L. AGASSIZ, *ibid.*, p. 377.
- 1849 *Notidanus muensteri*. – BEYRICH & FRISCHMANN, Zeitschr. Deutsch. Geol. Gesell., I: 423–447.
- 1852 *Notidanus muensteri*. – F. A. QUENSTEDT, Hdbk Petref.-K., p. 167, pl. 13, Fig. 4.
- 1858 *Notidanus muensteri*. – F. A. QUENSTEDT, Der Jura, p. 783, pl. 96, Figs. 33, 34.
- 1861 *Notidanus eximius*. – A. WAGNER, Abh. K. bay. Akad. Wiss., 9, p. 292, pl. 4, fig. 2.
- 1889 *Notidanus muensteri*. – A. S. WOODWARD, Cat. Foss. Fishes, 1, p. 158.
- 1937 *Notidanus muensteri*. – K. A. v. ZITTEL, Textbook of Palaeontology, 2, p. 72.
- 1964 *Notidanus muensteri*. – R. SCHWEIZER, Palaeontogr., 123 (A), p. 78, fig. 7, plate 11, fig. 4.
- 1983 *Eonotidanus muensteri*. – F. H. PFEIL, Palaeoichthyologica, p. 25.
- 1984 “*Notidanus muensteri*”. – J. G. MAISEY & K. WOLFRAM, Living Fossils, p. 170, fig. 2.

Previous study

Until the publication of SCHWEIZER's (1964) work, previous descriptions of the Solnhofen hexanchoids were superficial and dealt only with aspects of gross morphology and dentition (e.g., FRAAS, 1855; QUENSTEDT, 1858). SCHWEIZER (1964) figured and briefly mentioned parts of the cranial endoskeleton of Pi 1210/3, although he too concentrated upon the dental characteristics.

The neurocranium and jaws are known best from specimen no. Pi 1210/3, from Nusplingen, belonging to the Institut und Museum für Geologie und Paläontologie, Tübingen (SCHWEIZER, 1964, Fig. 7, pl. 11, Fig. 4; MAISEY & WOLFRAM, 1984, Fig. 2). As drawn by SCHWEIZER (1964, Fig. 7), the braincase of *N. muensteri* is elongate and fairly narrow, without a broad supraorbital

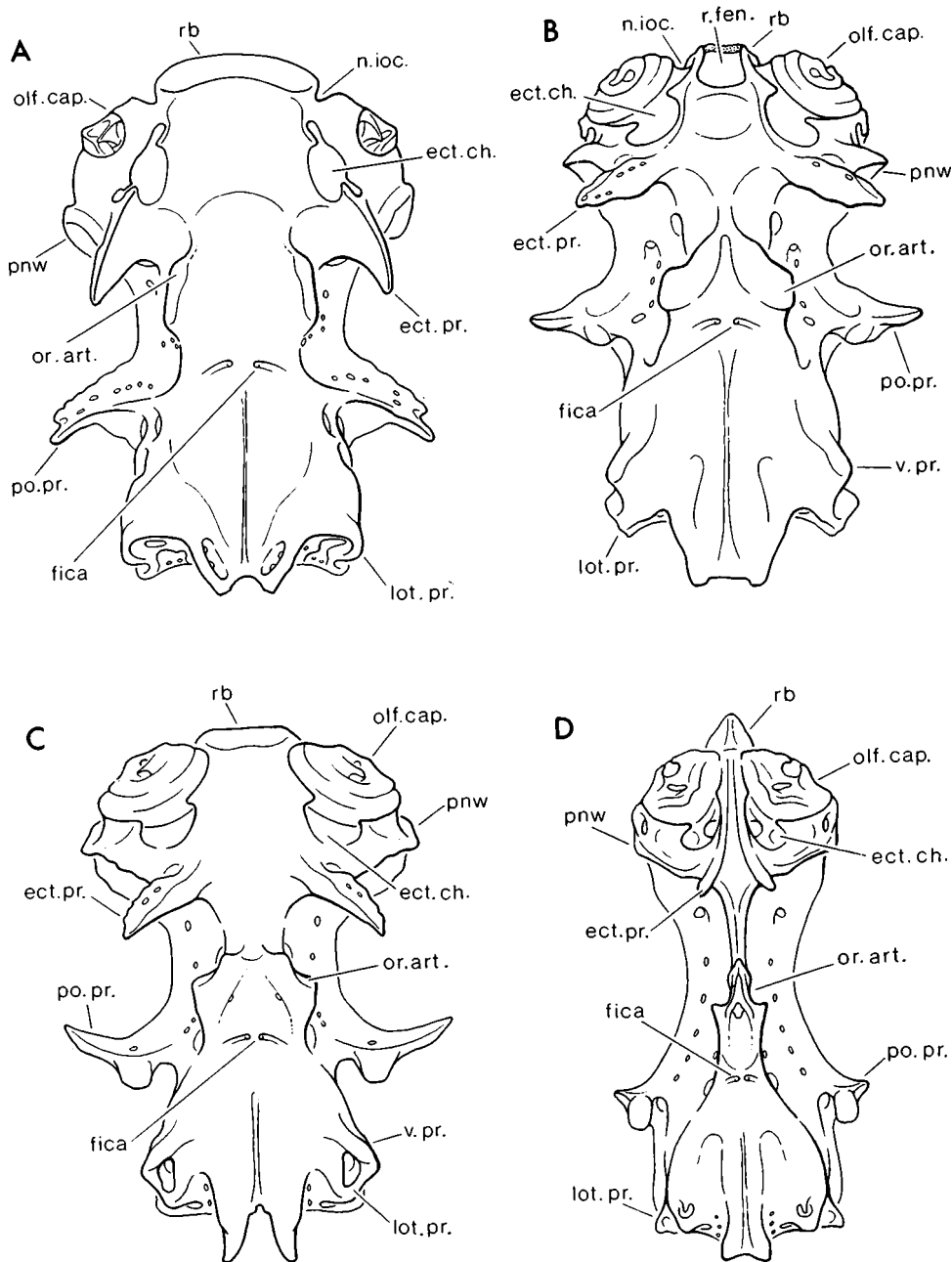


Fig. 3. The neurocranium of some Recent elasmobranchs in ventral view; (A) *Chlamydoselachus anguineus*, based on ALLIS and AMNH Vertebrate Paleontology Teaching Collection no. K 3-9; (B) *Notorynchus cepedianus*, from AMNH 49563; (C) *Hexanchus vitulus*, from AMNH 33475; (D) *Hepttranchias perlo*, from AMNH VP Teaching Collection no. AA 4-7.

roof to the orbit, and without a postorbital process (Fig. 2 A). Olfactory capsules were shown close together, separated by a gap which superficially resembles the precerebral fontanelle. The interorbital septum was shown as being broad, with transverse ridges both anteriorly and posteriorly (either of which might correspond to the basal angle of a modern hexanchoid braincase). Posteriorly the floor of the otico-occipital region was shown slightly broader than the interorbital septum. Paired foramina (supposedly for the glossopharyngeal nerves) and an occipital half-centrum were identified. As drawn by SCHWEIZER, the occiput does not project posteriorly beyond the otic capsules.

Comparison of SCHWEIZER's drawing with Recent hexanchoids would perhaps lead to the conclusion that the braincase of *N. muensteri* is most like that of *Heptranchias* (Fig. 3 D). In this form the neurocranium is narrow, with a narrow supraorbital roof and short postorbital process. The olfactory capsules lie close to the midline and the internasal septum and precerebral fontanelle are correspondingly narrow. The otico-occipital region is only slightly wider than the orbitotemporal region, and the occiput does not project behind the otic capsules.

Despite these apparent similarities, there are some striking disparities left unexplained by SCHWEIZER (1964). Firstly, the interorbital septum of *Heptranchias* is extremely narrow, with a prominent basal angle which allows the orbital articular surface for the palatoquadrate to jut abruptly downward in the posterior part of the orbit. There is no indication of such narrowing or projection of the interorbital septum in *Notidanoides*, according to SCHWEIZER. Secondly, the palatoquadrate of *Heptranchias* is somewhat triangular in outline, with an abbreviated palatine moiety that traverses beneath the braincase to meet its antimere symphyseally behind the olfactory capsules (Fig. 4). A curiously sigmoidal palatoquadrate is suggested by SCHWEIZER, which if accurately depicted would be radically different from that of any living hexanchoid, and would have a long and slender palatine part curving beneath the eye and extending anteriorly as far as the front of the olfactory capsule (i. e. about as far anteriorly as in *Chlamydoselachus*). The palatoquadrate ramus would thus have been approximately one-third longer than the mandibular ramus of Meckel's cartilage. No orbital process is shown on the palatoquadrate, and it is difficult to imagine how the braincase and jaws would have articulated given their disproportionate shapes and sizes.

An alternative interpretation of the braincase and jaws of Pi 1210/3 was given by MAISEY & WOLFRAM (1984), based on examination of casts and photographs (Fig. 2 B). The most noteworthy departure from SCHWEIZER's (1964, Fig. 7) version is reinterpretation of the curved anterior part of the palatoquadrates as supraorbital cartilages and (in part) the orbitonasal lamina. In that interpretation, the neurocranium appears much broader, and has a fundamentally different morphology from that suggested by

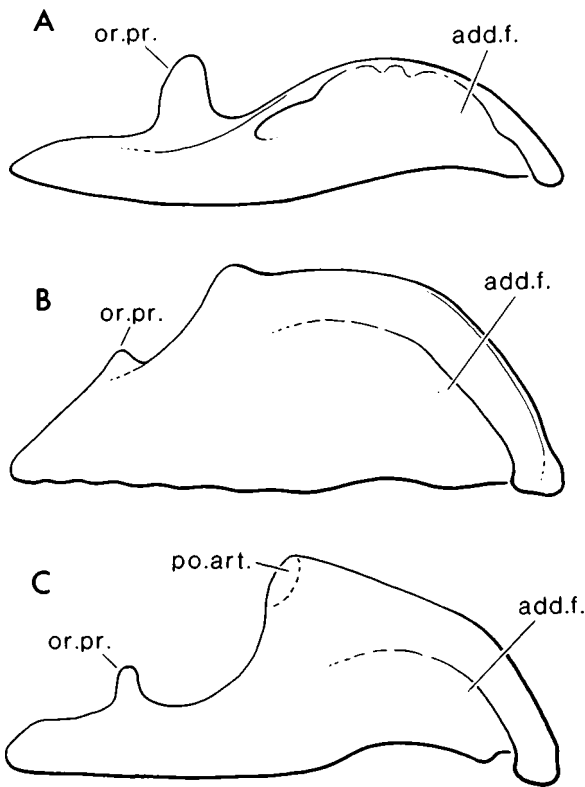


Fig. 4. Palatoquadrate of some Recent elasmobranchs in lateral view; (A) *Chlamydoselachus anguineus*, (AMNH VP Teaching Coll. no. K 3-9); (B) *Notorynchus cepedianus* (AMNH 49563); (C) *Heptranchias perlo* (AMNH VP Teaching Coll. no. AA 4-7).

SCHWEIZER. The palatoquadrate would be relatively short, although their precise extent and the suspensorial arrangement were not discussed.

Anatomy of the braincase

The ventral surface of the braincase is exposed in Pi 1210/3 (Figs. 5, 6). It is fairly complete, but parts of the otico-occipital region are overlain by the mandibles. Some other parts of the braincase have been damaged by earlier preparation, particularly where the cranial cartilage originally lay over the teeth. The most damaged areas are in the ethmoid region, the right orbital margin, and in the vicinity of the internal carotid foramen.

The ethmoid region is broad, with a short rounded rostral bar anteriorly (r. b., Fig. 6). There is an uncalcified fenestration of the rostral bar anteriorly similar to that in *Notorynchus* (r. f., Figs. 3, 6). The nasal capsules are spaced widely apart; the "Nasenkapsel" of SCHWEIZER (1964) are reinterpreted as parts of the internasal septum forming the lateral walls of the precerebral fontanelle. SCHWEIZER (1964, Fig. 7) showed a pair of supposed projections directed posteriorly and medially from the "Nasenkapsel" (Fig. 2 A). Although these "projections" resemble ectethmoid processes, they are simply folds in the floor of the orbitonasal lamina. These raised areas are not

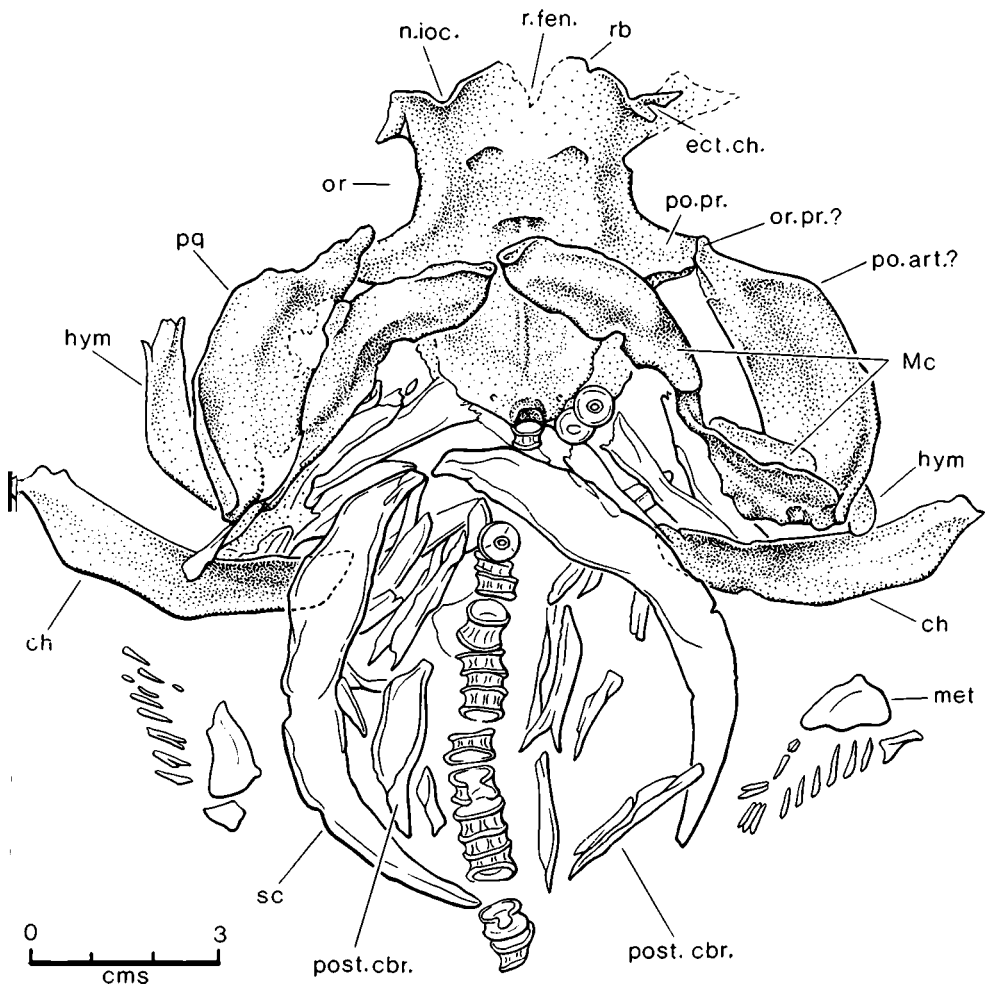


Fig. 5. New interpretation of Pi 1210/3, identifying the main endoskeletal components of the head region.

therefore the ectethmoid processes, but may reflect the internal position of olfactory canals leading to the nasal capsules.

The anterior margin of the rostral bar is indented on each side by a shallow notch (n. ioc., Fig. 6). A corresponding notch is present in *Chlamydoselachus*, where it is occupied by the posteriorly-reflected terminal branch of the infraorbital latero-sensory canal (JARVIK, 1942, Figs. 2, 4). The profundus and superficial ophthalmic nerves terminate near this groove in *Chlamydoselachus*, but do not occupy it. In *Hexanchus* and *Notorynchus* the rostral bar is broad and short, as in *Chlamydoselachus* and *Notidanoides*, but is not indented and the infraorbital latero-sensory canal is not reflected posteriorly as in *Chlamydoselachus* (e. g., *Notorynchus*; DANIEL, 1934, Figs. 45, 227, 228). The ethmoid region of *Hepttranchias* differs from all the above in being much narrower, with nasal capsules separated only by a narrow internasal septum

(Fig. 3). As in *Hexanchus* and *Notorynchus* the rostral bar (which is rudimentary) is not notched laterally for the infraorbital canal. Some short-snouted squaloids (e. g., *Aculeola*) also have a broad internasal septum and rostral bar, in which there may be shallow lateral indentations. In *Aculeola* the infraorbital canal lies in this emargination as in *Chlamydoselachus*, although the canal is not looped back on itself.

Immediately behind each marginal indentation in the rostral bar of Pi 1210/3 there is a pronounced groove bordered laterally by a raised ridge. In *Hexanchus*, *Notorynchus* and *Chlamydoselachus* this part of the internasal septum forms the mesial edge of the nasal fontanelle or ectethmoid chamber (GEGENBAUR, 1872; ALLIS, 1923; DANIEL, 1934; HOLMGREN, 1941).

This is also the case in *Hepttranchias*, but here the internasal septum is narrowly sandwiched by the olfactory capsules, and the ectethmoid chamber is correspondingly less commodious. *Notidanoides* is interpreted as having a large ectethmoid chamber as in *Chlamydoselachus*, *Notorynchus* and *Hexanchus*, of which only the inner margin is known in Pi 1210/3 (ect. ch. Fig. 6). In *Chlamydoselachus*, where the palatoquadrate extends beneath the internasal septum mesial to the olfactory capsules, the ectethmoid chamber is covered by a tough membrane (ALLIS, 1923), but in living hexanchoids (where the palatoquadrate symphysis lies behind the internasal lamina) such as membrane is absent. *Notidanoides* palatoquadrates similarly lay behind the internasal septum, and it may be that the ectethmoid chamber lacked a tough membranous covering. Despite this, as interpreted here, the olfactory region in *Notidanoides* is remarkably like that of *Chlamydoselachus* (see ALLIS, 1923, pl. ix; JARVIK, 1942, Fig. 4).

The postnasal wall is too badly damaged in Pi 1210/3 to determine whether an ectethmoid process was present (cf. MAISEY & WOLFRAM, 1984, Fig. 2). It is well developed in *Chlamydoselachus* and living hexanchoids, however, and one was probably also present in *Notidanoides* (ect. pr., Fig. 6).

The interorbital septum is broad and fairly flat in Pi 1210/3, with a gently arched transverse section. Only the floor of the interorbital region is seen, the orbital walls being crushed. The supraorbital cartilage projects laterally from each side of the interorbital septum. The overall impression gained from Pi 1210/3 is of a boxlike braincase between the orbits, lacking any suborbital shelf and covered by a broad orbital tectum.

The orbital region of *Notidanoides* thus resembles that of *Chlamydoselachus* in overall morphology. In living hexanchoids, by contrast, the interorbital septum has two distinctly different regions (Fig. 3). The anterior part is narrow and transversely rounded, extending from the postnasal wall posteriorly as far as the articular surface for the palatoquadrate orbital process (orb. art.). Just behind this articulation the braincase floor broadens at the "basal angle", although it narrows again level with the internal carotid foramina (fica, Fig. 3). This posterior region is much deeper dorsiventrally; the anterior part correspondingly slopes downward to meet it, at the "basal

angle". The lateral profile of this region is similar in all living hexanchoids, the main difference being that *Hepttranchias* has a much narrower interorbital septum than other hexanchoids.

In *Chlamydoselachus* two corresponding regions may be recognized, although the anterior part is much shorter than in Recent hexanchoids and the orbital articulation is located anteriorly in the orbit (ALLIS, 1923, pls. viii, ix). The basal angle is absent (ALLIS, 1923; HOLMGREN, 1941), although anterior to the orbital articulation the trabecular region curves dorsally. In embryo *Chlamydoselachus*, however, the basicranium is said to be flatter than in the adult (HOLMGREN, 1941, p. 9). Thus the weak adult basicranial flexure

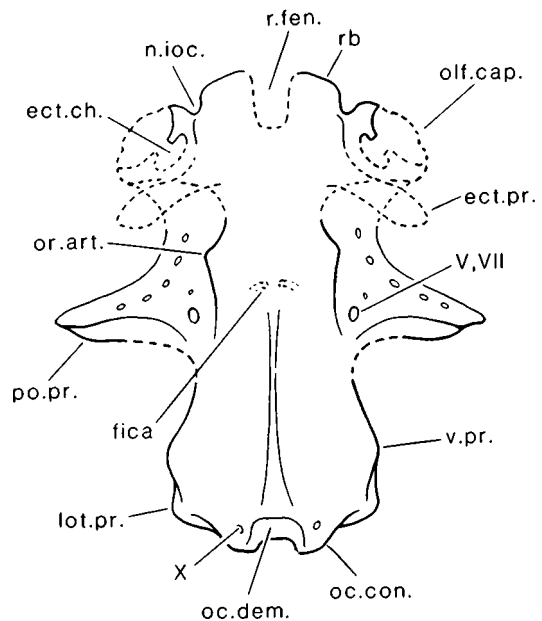


Fig. 6. Restored outline of *Notidanoides muensteri* braincase in ventral view, based on Pi 1210/3.

of *Chlamydoselachus* seems to be a derived condition ontogenetically, just like the basal angle (e. g., in *Squalus* and *Etmopterus*; SEWERTZOFF, 1899; DE BEER, 1937; HOLMGREN, 1940; JOLLIE, 1971). The relatively flat and unspecialized basicranium of *Notidanoides* suggests that a "basal angle" is primitively weak or absent in hexanchoids. Thus both ontogenetic and fossil evidence suggest that the pronounced "basal angle" of Recent hexanchoids is apomorphic. This raises some interesting questions concerning the relationships of hexanchoids to other elasmobranchs in which a "basal angle" is well developed (e. g., squaloids), especially in view of other similarities in their cranial anatomy (particularly among "short-snouted" forms such as *Aculeola*, *Oxynotus* and *Scymnorhinus*).

The positions of the internal carotid arteries are marked by shallow transverse grooves in Pi 1210/3. Their basicranial foramina have unfortunately

been obliterated, so it is unknown whether the vessels had separate openings or shared a common entrance. In *Chlamydoselachus* and Recent hexanchoids there are two foramina, located close to the ventral midline (GEGENBAUR, 1872; ALLIS, 1923; HOLMGREN, 1941). In living hexanchoids (but not *Chlamydoselachus*) these foramina lie a short distance behind the "basal angle" and the articular surface for the palatoquadrate orbital process. Although a basal angle seems to be lacking in *Notidanoides*, the position of the orbital articulation is suggested by a broadening of the basicranium just anterior to the carotids, followed posteriorly by a slight constriction level with the carotid impressions (orb. art., Fig. 6). Comparison with living hexanchoids and *Chlamydoselachus* leads me to believe that the orbital articulation lay towards the center of the orbit in *Notidanoides*, immediately anterior to the broadened part just mentioned (Fig. 7). In life, the orbital articulation may very well have sloped dorsally over this broader area, as in living hexanchoids.

The location of critical orbital foramina in *Notidanoides* cannot be made on the basis of available material. In living hexanchoids, as in other orbitostylic sharks, the orbital articulation lies between the optic nerve and efferent pseudobranchial artery (EDGEWORTH, 1935, MAISEY, 1980). While some orbital foramina are discernible in Pi 1210/3, none can be definitely identified as either the optic or efferent pseudobranchial foramen. The trigemino-facialis foramen is tentatively identified within the left orbit of Pi 1210/3, slightly behind the level of the orbital articulation (trf. f., Fig. 6). Other foramina in the orbital roof are probably for branches of the superficial ophthalmic nerve, supplying the supraorbital latero-sensory canal.

The supraorbital tectum expands posteriorly to meet the elongate postorbital process. The anterior (symphyseal) ends of the palatoquadrates lie directly over the tips of the postorbital processes in Pi 1210/3, from which they are separated by matrix. The left process is better exposed, and seems to lack a jugular canal and calcified lateral commissure. Aside from that, however, little can be discerned. Meckel's cartilages lie over this part of the braincase, so that only part of its posterior end is visible.

The otico-occipital region is relatively flat, but there is a median groove which reflects the position of the narrow notochordal canal is in many other Recent and fossil elasmobranchs. The occiput projects posteriorly behind the otic capsules as in *Chlamydoselachus*, *Notorynchus* and *Hexanchus*, and contains an occipital demi-centrum (oc. dem.) flanked by lateral condyles (co. con.). The ventral margin of the hyomandibular facet is marked by a low vestibular process (v. pr., Fig. 6; see GADOW, 1888), behind which lies the lateral otic process and glossopharyngeal canal. SCHWEIZER (1964, Fig. 7) identified a pair of glossopharyngeal foramina, on either side of the occiput, but comparison with Recent *Hexanchus* and *Notorynchus* suggests that these foramina are for the vagus nerve, since they are located much nearer to the posterior midline than the glossopharyngeal foramina (X, Fig. 6).

Jaws, visceral arches and shoulder girdle

Ventral reconstructions of the braincase and jaws in *Notidanoides* are shown in Figs. 7 and 8, along with comparable views of *Chlamydoselachus*, *Notorynchus*, and *Heptranchias*. In Fig. 7 the palatoquadrates and epihyals are shown in their proper articular relationship, and Fig. 8 shows the same with the addition of Meckel's cartilages, ceratohyals and basihyal. The palatoquadrates are indicated by a dashed line in Fig. 8, where obscured by other jaw elements. The modern examples are all taken from preserved dissections and show the jaws with the mouth closed; i. e., with no mandibular abduction or protrusion. In the reconstructions of *Notidanoides* an attempt has been made to locate the jaws in a similar "resting" configuration, although there is inevitably some artistic licence and author caprice. These views illustrate some of the differences in hexanchoid jaw suspension discussed in this section.

As mentioned earlier, the palatoquadrate of *Notidanoides* is much shorter than shown by SCHWEIZER (1964, Fig. 7). In Pi 1210/3 both palatoquadrates are exposed in lateral view, displaced outwards from their original position (Figs. 1, 5). The most evident feature is the expanded otic process and adductor fossa (add. f.), forming a broad insertion for adductor musculature. Its dorsal margin is gently rounded from the mandibular joint to the postorbital articulation. Anterior to this the dorsal margin swings steeply downward and the palatoquadrate tapers rapidly towards the symphysis. The postorbital articulation is vaguely defined and may not have been particularly strong. Nonetheless in Recent hexanchoids (even *Heptranchias*, which has a very strong postorbital articulation), the articular facet is located mesially (Fig. 7) and its extent is not readily apparent on the lateral surface of the palatoquadrate (Fig. 4 C; see GEGENBAUR, 1872; LUTHER, 1909; DANIEL, 1934). Furthermore the articular surfaces are generally uncalcified and are enclosed by a ligamentous bursa, which would be unlikely to fossilize. Even so, the tapered anterodorsal margin of each palatoquadrate in Pi 1210/3 bears an elongate groove or depression in its upper part (po. art.?, Fig. 5), which may reflect the original extent of the postorbital facet. This suggests that the articular surface was as extensive as in *Notorynchus* and *Hexanchus*; in *Heptranchias*, by contrast, this facet is much longer, extending more than two-thirds of the distance from the "top" of the otic process towards the orbital process (LUTHER, 1909, Fig. 6).

The palatine part of the palatoquadrate in *Notidanoides* resembles that of *Notorynchus* and *Hexanchus*. In *Heptranchias* the region between orbital and postorbital processes is deeply embayed into a strongly concave profile (GEGENBAUR, 1872; LUTHER, 1909). It may be that this feature caused SCHWEIZER (1964) to misidentify the curved orbital roof as part of the palatoquadrate in Pi 1210/3. In *Notidanoides*, *Hexanchus* and *Notorynchus* this region is more triangular, with a much less embayed dorsal margin (Fig. 4).

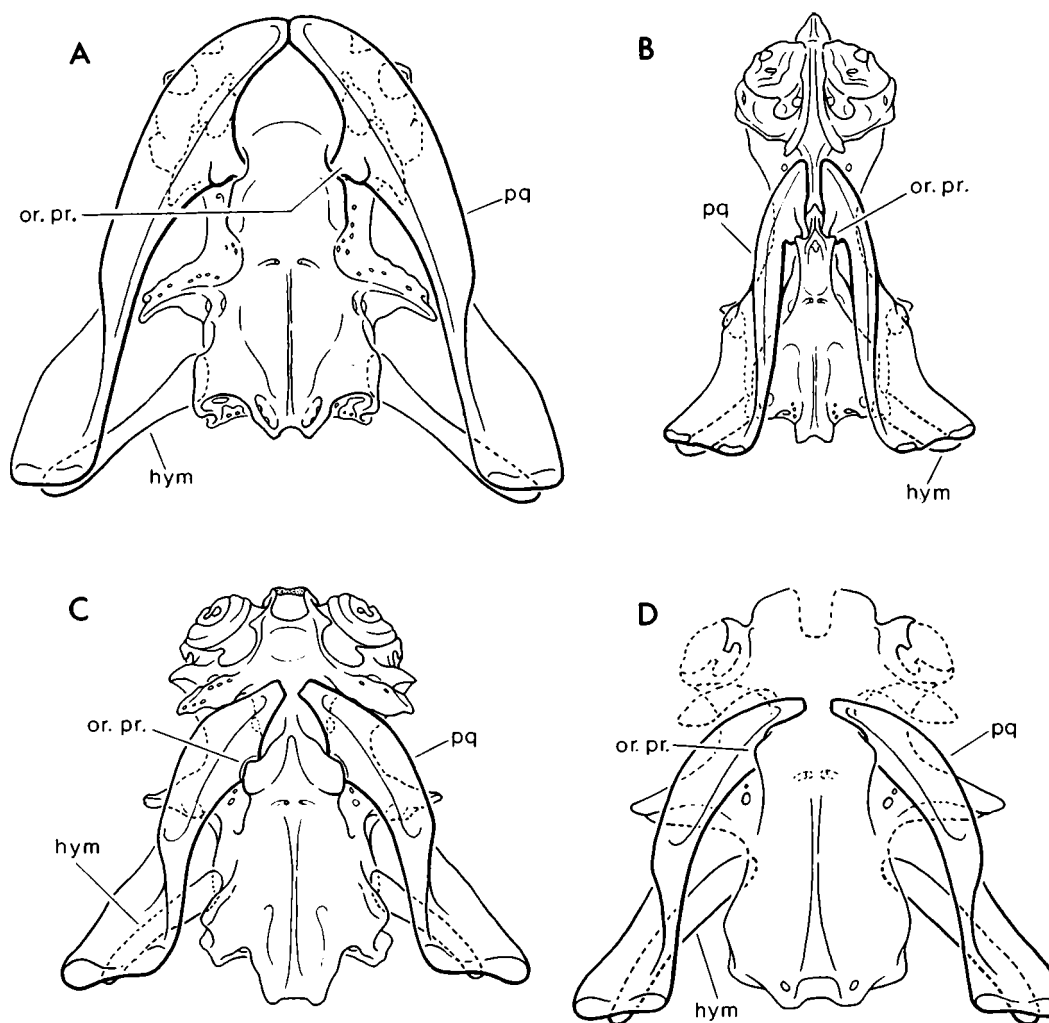


Fig. 7. Ventral views of neurocranium with palatoquadrate and hyomandibula in position (A) *Chlamydoselachus anguineus* (AMNH VP Teaching Coll. no. K 3-9); (B) *Heptatrachias perlo* (AMNH VP Teaching Coll. no. AA 4-7); (C) *Notorynchus cepedianus* (AMNH 49563); (D) *Notidanoides muensteri* (restored from Pi 1210/3).

The orbital process is poorly preserved, although its position is suggested by a bump behind the symphysis (or. pr.?, Fig. 5). In most orbitostylic elasmobranchs the orbital process is soft and uncalcified; consequently it may not have been completely preserved in Pi 1210/3. The orbital process probably articulated with the braincase in a mid-orbital position (Fig. 7). The palatine region would have been oriented obliquely below the braincase, with its symphysis level with the postnasal wall or even slightly posterior to it.

The quadrate part is about twice the length of the palatine moiety in *Notidanoides*. These proportions compare more favorably with those of

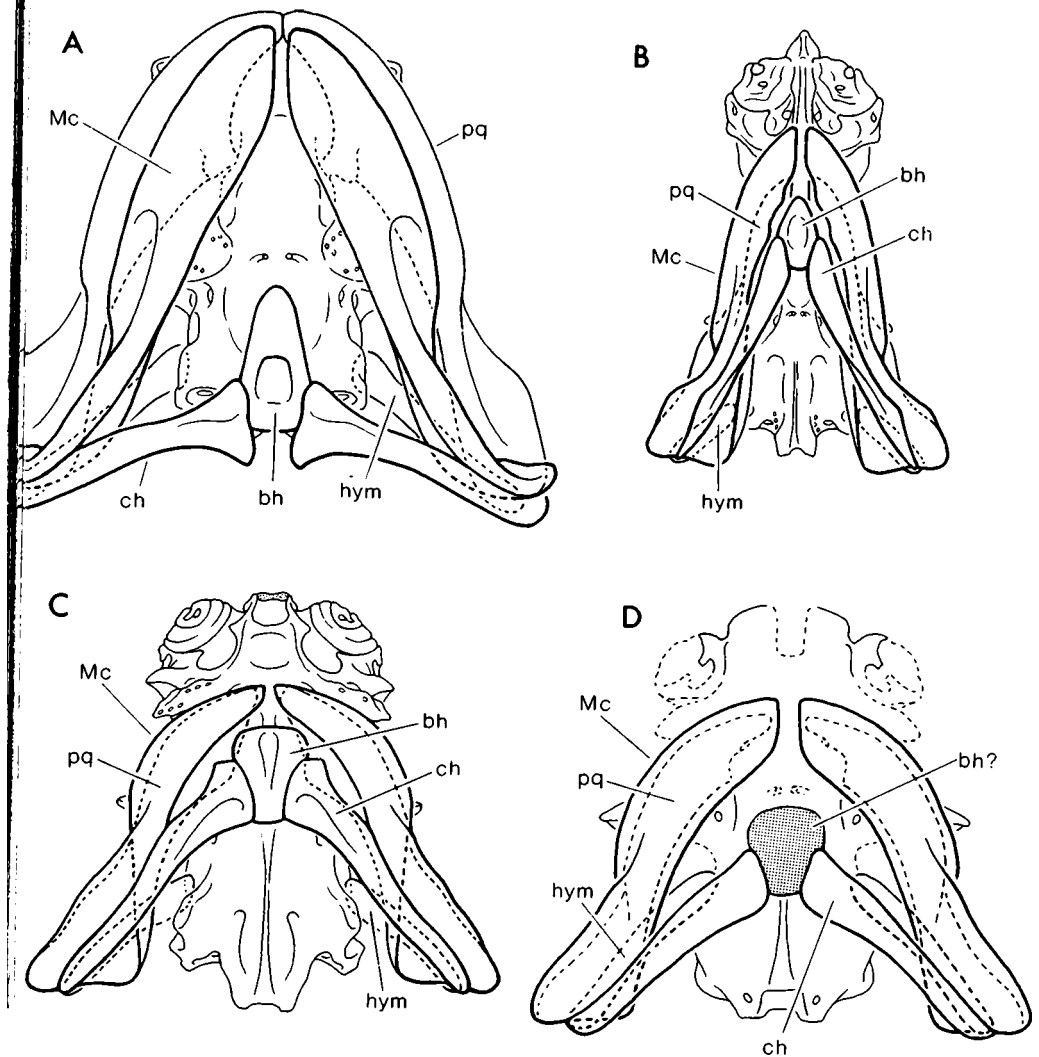


Fig. 8. Ventral views as in Fig. 7 but with Meckel's cartilage, ceratohyal and basihyal added; palatoquadrates shown by dashed line; basihyal of *Notidanoides* stippled.

Hexanchus and *Notorynchus* than with those of *Heptanchias*, but in *Notidanoides* the "quadrate" is relatively longer than in any Recent hexanchoid.

In *Chlamydoselachus* the palatoquadrate is much more elongate and slender than in any hexanchoid (Fig. 4 A), and there is an extremely long palatine bar extending beneath the ethmoid region (ALLIS, 1923). Although the palatoquadrate may make contact with the postorbital process during some phases of jaw movement (COMPAGNO, 1977), a postorbital articulation with a bursa and associated ligaments is absent (LUTHER, 1909). Thus the jaws of *Chlamydoselachus* and hexanchoids differ significantly in several respects. *Notidanoides* nevertheless resembles *Chlamydoselachus* in the elongate shape

of the otic process. In *Chlamydoselachus* this process is more than three times as long as deep. In *Notidanoides* it is almost 2 1/2 times as long. It is shorter in living hexanchoids (approximately 1 1/2 times the depth in *Hexanchus* and *Notorynchus*; almost equal length and depth in *Heptatranchias*).

Meckel's cartilage of *Notidanoides* are long and slender, but their exact shape is uncertain because of crushing in Pi 1210/3. Their length along the mandibular ramus is useful in determining the anterior extent of the jaws, however. Living hexanchoids have a pronounced underbite, in which the mandibular symphysis extends farther anteriorly than the palatoquadrate (Fig. 8). If we allow that the same was true in *Notidanoides*, measurements of upper and lower jaws of Pi 1210/3 confirm that very little of the palatine ramus was uncalcified and that the palatoquadrates did not extend below the ethmoid region as in *Chlamydoselachus*.

The hyoid and branchial arches are disarranged in Pi 1210/3, and not all elements have been reliably identified. I concur with SCHWEIZER's (1964, Fig. 7) identification of the ceratohyals ("Hyoidbogen") and one (probably the right) hyomandibular element (c. f. Figs. 2 A, 5). The left hyomandibula seems to be in place against the braincase, behind Meckel's cartilage. The ceratohyals have been displaced outwards, with their hyomandibular articulations at their outer extremities. Some features of the articular ends of these elements are preserved and compare closely with the articular surfaces in Recent hexanchoids. The visceral arches are too badly disturbed to determine their number and configuration, other than that the hypobranchials and ceratobranchials resemble those of *Chlamydoselachus* and hexanchoids in being elongate and slender. This may simply represent a primitive condition, however, since it occurs in *Synechodus* and *Sphenodus*, which may be allied to galeomorphs and *Heterodontus* (MAISEY, in press). Between the scapulocoracoids and vertebral column are two prominent elements, interpreted as the posteriormost pair of ceratobranchials (post. cbr., Fig. 5). In outline they resemble those of *Chlamydoselachus* very closely (GOODEY, 1910; ALLIS, 1923).

Comparison between *Notidanoides*, *Chlamydoselachus* and modern hexanchoids (Figs. 7, 8) suggests that jaw suspension in *Notidanoides* most closely resembled that of *Hexanchus* and *Notorynchus*. In all three taxa the gape is much wider than the maximum braincase width (at the postorbital process) and the jaws extend anteriorly only as far as the postnasal wall. *Chlamydoselachus* differs in lacking a postorbital articulation and in the anterior extent of its jaws beneath the ethmoid region, almost to the rostral bar. In Fig. 8, the transverse orientation of the ceratohyals in *Chlamydoselachus* is in contrast with the usually figured arrangement (e. g., GARMAN, 1885; ALLIS, 1923; SMITH, 1937), with the ceratohyals and Meckel's cartilages arranged in a chevron pattern. In specimens, there is considerable antero-posterior mobility of the basihyal-basibranchial skeleton. Discussion of this interesting phenomenon, and of its development during ontogeny, would be inappro-

appropriate in the present work, but it is anticipated that a note will be published on this elsewhere. The arrangement shown in Fig. 8 illustrates the extent to which the gape can be widened in *Chlamydoselachus*. Only when the ventral constrictors are strongly contracted is the basihyal brought much closer to the mandibular symphysis.

The scapulocoracoids in Pi 1210/3 are shaped like those of Recent hexanchoids, *Chlamydoselachus*, and the fossil taxa *Synechodus*, *Sphenodus* and *Palaeospinax* (GARMAN, 1885; DEAN, 1909; MAISEY, 1985, + in preparation). This may again represent a primitive pattern among living sharks. Traces of the pectoral fin skeleton are preserved, but nothing of significance can be determined.

Discussion

In this work, the sister group to Recent hexanchoids is thought to be *Chlamydoselachus*. These taxa share:

1. Overall body configuration (posterior position of single dorsal, the pelvics and anal fins; dorsal between pelvics and anal; elongate trunk between pelvics and pectorals).

2. More than five branchial clefts (known otherwise only in a sawshark, *Pliotrema*, and a trygonid, *Hexatrygon*).

Notidanoides and Recent hexanchoids differ from *Chlamydoselachus* in the following respects:

3. Upper and lower teeth distinctly different, with pointed multicuspid uppers and elongate, serrated lowers.

4. Lateral teeth bladelike, with several cusps along the cutting edge.

5. Posteriormost teeth small and buttonlike, unserrated.

Recent hexanchoids (*Hexanchus*, *Heptranchias*, *Notorynchus*) are united by the following features:

6. Precaudal vertebral centra weakly calcified (*Heptranchias*) or uncalcified (*Hexanchus*, *Notorynchus*).

7. Labio-lingually flattened teeth, with the root and crown lying in the same plane and the basal surface enlarged to form the "lingual" side of the root.

8. Basal angle well developed.

9. Braincase floor becomes narrow anterior to the orbital process.

These characters are not altogether satisfactory as synapomorphies. The notochord of *Chlamydoselachus* is partly constricted but is not septate precaudally (RIDEWOOD, 1921); in the present hypothesis this must be regarded as an independent reduction and loss in *Chlamydoselachus* and hexanchoids. Nevertheless there is some evidence of independent vertebral reduction among living hexanchoid taxa (MAISEY & WOLFRAM, 1984). The dental characters noted here are also found in some squaloids (e. g.,

Somniosus, *Oxynotus*) but are absent in apparently more primitive squaloids such as *Aculeola*. A basal angle is also well developed in most squaloids, although it is again less prominent in supposedly generalized taxa. The basicranium anterior to the basal angle is narrowed in *Scymnorhinus* and *Oxynotus*; but is fairly broad in *Squalus*. *Notidanoides* differs from living hexanchoids in all four characters. Instead, it resembles *Chlamydoselachus* (perhaps primitively) in having the tooth crown resting squarely on its root (SCHWEIZER, 1964), the basal angle weak or absent, and a broad basicranium anterior to the orbital articulation.

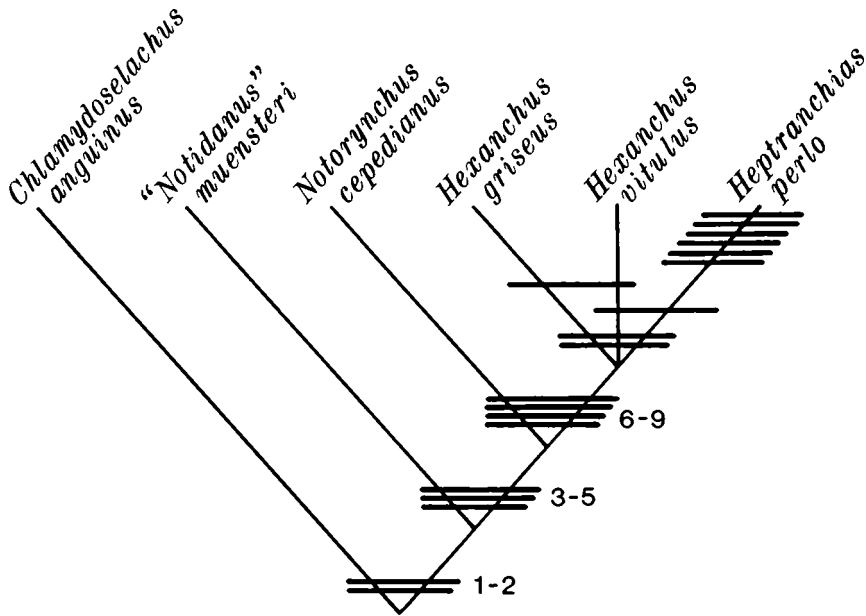


Fig. 9. Cladogram of relationships discussed in the text.

While there is no doubt that *Notidanoides* is closely related to Recent hexanchoids, it clearly differs from them (and resembles *Chlamydoselachus*) in some important respects. *Chlamydoselachus* differs from *Notidanoides* and living hexanchoids in the frontal position of its orbital articulation, the absence of a postorbital articulation, the extent of the palatoquadrate beneath the snout, and the peculiar morphology of its teeth. *Chlamydoselachus* differs from living hexanchoids (but not *Notidanoides*) in the absence of a basal angle. Its hyomandibular articulation also differs (HOLMGREN, 1941, p. 14), and its first gill-cleft is continuous across the throat, but neither character is known in *Notidanoides*. *Chlamydoselachus* resembles *Notidanoides* and living hexanchoids in gross morphology (single dorsal fin, which along with the anal and pelvics is located posteriorly, the dorsal lying between the pelvics and anal; elongated trunk region between pectorals and pelvics) and in having more than five branchial arches and gill openings.

Many of these differences in *Chlamydoselachus* can be considered autapomorphies which do not help in resolving its systematic position. The remaining differences are open to alternative explanations. *Chlamydoselachus* is regarded here as the sister group to all hexanchoids including *Notidanoides* (MAISEY & WOLFRAM, 1984). In this case, the absence of a postorbital articulation may also be derived for *Chlamydoselachus* (although the possibility still remains that the hexanchoid postorbital joint is secondary). The long palatine ramus of the palatoquadrate and absence of a basal angle would be primitive (a view supported by other fossils such as *Hybodus*, *Synechodus*, *Palaeospinax* and many Paleozoic selachians).

Alternatively, *Notidanoides* could be the sister taxon to *Chlamydoselachus* and living hexanchoids, but this hypothesis is less parsimonious than the first since it requires suppression of hexanchoid characters in *Chlamydoselachus*. If the postorbital articulation of hexanchoids and the elongate palatine ramus of *Chlamydoselachus* are both primitive characters (probably the simplest supposition), we may predict that both should be present in the most primitive members of each lineage and in their hypothetical extinct sister group.

Notidanoides muensteri resembles Recent hexanchoids in many details of its cranial anatomy. As we have seen, however, it shares some other features with the frilled shark, *Chlamydoselachus* (e. g. the lack of pronounced basal angle, and the arrangement of the snout). This raises some interesting questions concerning the interrelationships of living hexanchoids, *Notidanoides* and *Chlamydoselachus*. The most plausible hypothesis is that *Notidanoides* is the extinct plesiomorphic sister taxon to Recent hexanchoids (as suggested by MAISEY & WOLFRAM, 1984).

Conclusions

The common ancestor of *Chlamydoselachus* and hexanchoids probably had postorbital and orbital articulations for the palatoquadrate, no basal angle in the basicranium, an elongate palatine region, more than five branchial arches, an elongate, slender scapulocoracoid, a single dorsal fin and an elongated trunk with the dorsal, anal and pelvic fins located towards the tail.

Although *Chlamydoselachus* and hexanchoids possess a number of apparently primitive traits, these elasmobranchs share a suite of characters with other Recent sharks that are absent in the better known fossil elasmobranch taxa (MAISEY, 1984). The view that *Chlamydoselachus* and hexanchoids are distantly related (e. g., HOLMGREN, 1941) is no longer tenable, and in more recent surveys *Chlamydoselachus* is grouped with hexanchoids (e. g., COMPAGNO, 1973, 1977).

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