BULLETIN DE L'INSTITUT ROYAL DES SCIENCES NATURELLES DE BELGIQUE, BIOLOGIE, 76: 147-189, 2006
BULLETIN VAN HET KONINKLIJK BELGISCH INSTITUUT VOOR NATUURWETENSCHAPPEN, BIOLOGIE, 76: 147-189, 2006

Otolith evidence concerning interrelationships of caproid, zeiform and tetraodontiform fishes

by Dirk NOLF & James C. TYLER

Abstract

Otolith features are used to test osteology-based hypotheses about interrelationships among caproid, zeiform and tetraodontiform fishes and intrarelationships of the taxa within each concerned group. Otolith morphology suggests that caproids are the plesiomorphic sister group of [zeiforms + tetraodontiforms]. In zeiforms, otolith data are in reasonable agreement with the homogeneity of the families defined upon osteology, but they are of little use in supporting interrelationships among these families. Problematic cases are the plesiomorphic otoliths of *Parazen* and *Zenion,* which would group these two taxa as a plesiomorphic sister group of all other zeiforms. The placement of *Parazen* as sister to [*Cyttopsis* + *Stethopristes*] in parazenids and *Zenion* as sister to [*Capromimus* + *Cytomimus*] in zeniontids, however, is logically consistent within both families. In tetraodontiforms, otoliths exhibit a broad range of very different morphologies, but there are no apparent contradictions with the osteology-based phylogenetic hypotheses. The main interest of otolith morphologies among tetraodontiforms is the evidence that strongly supports the recognition of three clades within balistids, and the confirmation of tetraodontids and diodontids as, respectively, plesiomorphic and apomorphic sister groups.

Key words: otoliths, Caproidei, Zeiformes, Tetraodontiformes, phylogeny.

Introduction

The order Zeiformes comprises mostly deep-bodied benthic fishes found in marine waters worldwide. Many species of the order are deep-sea fishes, found at depths that may exceed 1000 m. Some species, however, especially in the family Zeidae, live at depths of 100-300 m, and, in European waters, *Zeus faber* occurs usually between 50 and 150 m but is occasionally caught as shallow as 10 m (NELSON, 2006, QUERO *et al.*, 2003). There are six Recent families (some divided into subfamilies, see section on classification), with about 16 genera and 32 species. Fig. 1 provides a pictorial overview of a representative of each of the recognized Recent families and subfamilies.

There are approximately 350 species of extant Tetraodontiformes, grouped in ten families of great diversity in body form and osteological structure (Fig. 2). Most of these families are found in warm and temperate shallow marine waters worldwide, with a few families absent from the Atlantic and eastern Pacific Oceans. They include the primitive, deep-water, bottom-dwelling Triacanthodidae, but most families are more typical of shallow water and often are associated with coral reefs or surrounding sea grass beds and continental sand / mud flats: the Triacanthidae, Balistidae, Monacanthidae, Aracanidae, Ostraciidae, Tetraodontidae and Diodontidae. One family, the Triodontidae, has a single extant species found in deep Indo-western Pacific bottom waters, whereas the three species of Molidae are oceanic pelagic.

The phylogenetic relationships of the various clades of zeiform and tetraodontiform fishes and the affinities of both groups to other teleost taxa have been the subject of many studies during the last 25 years. An overview of the published work and a modern cladistic synthesis of the now available data is presented in two recently published papers: TYLER *et al.* (2003) and SANTINI & TYLER (2003), treating, respectively, the zeiforms and the tetraodontiforms. Except for some schematic drawings of extant triacanthodid otoliths in TYLER (1968) and a synoptic note by SCHWARZHANS (1996) in a paper on fossil otoliths, very little has been done on the systematic interpretation of the otoliths of these two orders of fishes.

WINTERBOTTOM (1974) suggested that at least some zeiforms might be related to tétraodontiforms. ROSEN (1984) provided argumentation for a group comprising caproids, tetraodontiforms and zeiforms, with the latter two being sister groups. TYLER *et al.* (2003) provided strong evidence for the monophyly of zeiforms and discussed a possible relationship of zeiforms with tetraodontiforms and caproids, but they concluded that such relationships were ambiguous. These putative relationships will be evaluated herein on the basis of otoliths.

We herein provide an overview of the previously published illustrations of zeiform and tetraodontiform otoliths and an extensive series of new figures, covering almost all existing Recent subfamilial and higher clades. After a brief iconographic and descriptive overview, otolith morphology is used to test the phylogenetic hypotheses based upon osteological features, and some new affinities are proposed on the basis of the otoliths. We believe that our coverage is very satisfactory in providing an overall survey of otolith mor-

phology in the various tetraodontiform clades, but the same cannot be said about our survey of the intraspecific variability of the otoliths of these fishes.
A significant problem is that tetraodontiform otoliths cannot be dissected from museum specimens without severe external damage to the fishes because the classical dissection method through the gill apertures cannot be applied. Moreover, many tetraodontiform otoliths show fine salient structures and crests that are readily attacked by the preliminary formalin fixation that had been applied to most preserved specimens. Also, only in a limited number of cases was it possible to give even a small overview of the intraspecific otolith variability. This is because, unfortunately, in many cases the otolith of only a single specimen was available. A single otolith provides some idea of the structure in that species and how that species may be related to other taxa, but it does not adequately define the otolith morphology of that species. The same is true for the illustration of ontogenetic changes. Therefore, the present study should be considered a preliminary overview that still requires much additional information in such a speciose and highly diversified group as tetraodontiforms.

Otolith terminology

All the materials studied herein are saccular otoliths. Except for some brief remarks on the lagaenar and utricular otoliths of *Balistes* and *Zeus* in two papers by ASSIS (2003 and 2005), these two types of otoliths, which are very small in the groups studied herein, have scarcely been used in systematic studies and almost no collections of them are available. Fig. 3 provides an overview of the terminology first proposed by CHAINE & DUVERGIER (1934) and now universally used for saccular otoliths; this generalized scheme is reproduced herein. Because many taxa of the groups studied herein have strongly modified otoliths, the figure of Chaine & Duvergier is followed by selected examples of some zeiform and tetraodontiform otoliths, where the homologies of their specialized structures are indicated with the standard terminology.
We also figure an otolith of a myctophid and of a gadid fish because these otoliths have a well-marked collicular crest, a structure that is also visible in the otoliths of several zeiforms and of some tetraodontiforms. Collicular crests are structures that occur in the otoliths of many deep-water fishes with large otoliths, e.g., myctophids, beryciforms and gadiforms. These ridges emerge near to and parallel to the crista inferior. In all groups (often unrelated), collicular crests are located near the caudal crista inferior. When they occur in gadiform otoliths, they always occupy a central position (this is at the transition of the ostial and caudal crista inferior), which feature constitutes a synapomorphy for gadiforms. Manifest collicular crests with an ostial position are unknown in all groups of fishes. Although the collicular crests of zeiforms often occupy a central position, they are manifestly caudal structures, which is evident when their otoliths are compared with those of *Antigonia* (Fig. 6). Collicular crests have often been called "pseudocolliculum" in various papers on otoliths, a term of useless and inappropriate jargon (the structure has nothing "pseudo" about it), whereas "collicular crest" is concise, standard language that says exactly what is intended.

Classification of zeiforms and tetraodontiforms; iconography and brief descriptions of their otoliths

Preliminary note concerning the iconography. - To make our figures as understandable and comparable as possible, we tried to represent all specimens by their left otoliths. Right otoliths were figured only if no left ones were available, or when the right otoliths provided some additional information. When a figure represents a right otolith, this is always mentioned directly on the plate, and when both left and right otoliths are figured, the left specimen is figured on the left side and the right specimen on the right side, according to the CHAINE & DUVERGIER (1934) principle of representing otoliths. Locality and collection data are provided in an addendum. All scale bars represent one millimeter. The annotations Fig. a,b and c are used to indicate, respectively, ventral, inner (= mesial) and posterior views. Figures without a letter annotation show inner views.

ZEIFORMES

Plesion:

[CRETAZEIDAE, extinct; Late Campanian/Early Maastrichtian; Nardò, Puglia, Italy; otoliths unknown]

CYTTOIDEI

CYTTIDAE

Available iconography:

Cyttus australis (RICHARDSON, 1843)
Pl. 1, Fig. 3

Cyttus novaezelandiae (ARTHUR, 1885)
Pl. 1, Figs. 4–6

Cyttus traversi HUTTON, 1872
Pl. 1, Figs. 1–2
SMALE *et al.*, 1995, pl. 45, fig. D1

Cyttid otoliths are characterized by a very strong constriction along the antero-posterior midline, and by the absence or only rudimentary development of collicula. In the rather small otoliths of *Cyttus australis* and *C. novaezelandiae* figured herein, collicula are completely lacking and the distal portions of the ostium and the cauda are hollowed out. In the two figured large otoliths of *C. traversi,* rudimentary collicula are formed. In all cyttids, neither the ostium nor the cauda shows a ventral expansion. This readily allows cyttid otoliths to be distinguished from those of oreosomatids, which otherwise have a very similar outline. In *Cyttus australis* and *C. traversi,* the swollen upper portion of the ventral area is small and elongate; in *C. novaezelandiae,* it is more extended ventrally. All examined otoliths have a well-formed collicular crest.

ZEOIDEI
OREOSOMATIDAE, Pseudocyttinae
Available iconography:

Pseudocyttus maculatus (GILCHRIST, 1906)
Pl. 1, Figs. 7–9
GON & HEEMSTRA, 1990, fig. 3, p. 227
SMALE *et al.*, 1995, pl. 46, figs. D1–2

For general features of oreosomatid otoliths, see Oreosomatidae, Oreosomatinae, herein. *Pseudocyttus* otoliths may be distinguished from those of the other oreosomatids by their somewhat stronger antero-posterior constriction and their rather wide dorsal area, but examination of a large series of all oreosomatid species would be necessary to confirm these differences.

OREOSOMATIDAE, Oreosomatinae
Available iconography:

Allocyttus folletti MYERS, 1960
Pl. 2, Fig. 3
NOLF, 1985, fig. 55E, p. 73

Allocyttus niger JAMES, INADA & NAKAMURA, 1988
Pl. 2, Figs. 1–2

Allocyttus verrucosus (GILCHRIST, 1906)
Pl. 2, Fig. 4
SMALE *et al.*, 1995, pl. 46, figs. A1–3

Neocyttus helgae (HOLT & BYRNE, 1908)
Pl. 2, Fig. 5, drawn by W. Schwarzhans

Neocyttus rhomboidalis GILCHRIST, 1906
Pl. 2, Fig. 6, redrawn after Smale *et al.*, 1995
Smale *et al.*, 1995, pl. 46, figs. B1–3

Oreosoma atlanticum CUVIER, 1829
Pl. 2, Fig. 7, redrawn after SMALE *et al.*, 1995
SMALE *et al.*, 1995, pl. 46, figs. C2–3

Oreosomatid otoliths are characterized by strong ventral expansions of the ostium and of the posterior end of the cauda. Both expansions are filled with well-developed collicular formations of swollen aspect. The available material does not permit pertinent comments about differences among the taxa constituting the family.

PARAZENIDAE, Parazeninae
Available iconography:

Parazen pacificus KAMOHARA, 1935
Pl. 3, Figs. 1–2
KOTLYAR, 2001, fig. 1d, p. 689
NOLF, 1985, fig. 55A, p. 73
OHE, 1985, fig. 112, p. 76
SCHWARZHANS, 1980, fig. 362, p. 110

Among parazenids, the monotypic subfamily Parazeninae displays the plesiomorphic otolith condition. The posterior constriction is almost nonexistant in the specimen figured herein, but Ohe (1985) figured a specimen with a more marked posterior constriction. The presence of a crista superior and a crista inferior that are clearly divided into ostial and caudal portions also is a plesiomorphic feature. For other features, see Cyttopsinae.

PARAZENIDAE, Cyttopsinae
Available iconography:

Cyttopsis cypho (FOWLER, 1934)
Pl. 3, Fig. 3
RIVATON & BOURRET, 1999, pl. 144, figs. 7–11

Cyttopsis roseus (LOWE, 1843)
Pl. 3, Fig. 4
ASSIS, 2004, fig. 56, p. 118
CAMPANA, 2004, p. 277 (sac., utr., lag.)
CHAINE, 1958, pl. p. 236
OHE, 1985, fig. 114, p. 76, as *Zen itea*

Stethopristes eos GILBERT, 1905
Pl. 3, Fig. 5
KOTLYAR & PARIN, 1990, fig. 5, p. 110
RIVATON & BOURRET, 1999, pl. 144, figs. 12–13

Otoliths of the Cyttopsinae are rather similar to those of oreosomatids in their outline, but they do not exhibit the ventral expansions of the ostium and of the posterior end of the cauda as in the latter family. Their collicula are marked, but they do not show as much hypertrophy as in oreosomatids. Swelling of the central upper part of the ventral area is visible but is not as strongly marked as in parazenin otoliths.

ZENIONTIDAE
Available iconography:

Capromimus abbreviatus (HECTOR, 1874)
Pl. 3, Fig. 6

Cyttomimus stelgis GILBERT, 1905
Pl. 3, Fig. 7
KOTLYAR & PARIN, 1990, fig. 5, p. 110
RIVATON & BOURRET, 1999, pl. 144, figs. 5–6

Zenion hololepis (GOODE & BEAN, 1896)
Pl. 4, Fig. 6
KOTLYAR & PARIN, 1990, fig. 5, p. 110
NOLF & CAPPETTA, 1989, pl. 14, fig. 12
SMALE *et al.*, 1995, pl. 45, fig. C2

Zenion japonicus KAMOHARA, 1934
Pl. 4, Fig. 1
NOLF, 1985, fig. 55B, p. 73
OHE, 1985, fig. 116, p. 76, as *Zenion pacificum*

Zenion longipinnis KOTTHAUS, 1970
Pl. 4, Figs. 7–8
RIVATON & BOURRET, 1999, pl. 144, figs. 1–2

Zenion sp.
RIVATON & BOURRET, 1999, pl. 144, figs. 3–4

Zenion sp.
SCHWARZHANS, 1980, fig. 361, p. 110

Zeniontids can easily be divided into two groups on the basis of their otolith morphology: *Zenion* and [*Capromimus* +

Cyttomimus]. The most plesiomorphic condition (very rudimentary antero-posterior constriction) is present in *Zenion*. Both groups have swollen collicula. In *Zenion* the collicula are centrally located, whereas in *Capromimus* and *Cyttomimus* the collicula are reduced to small swellings at the extreme anterior and posterior ends of the otoliths. In *Cyttomimus*, the swollen central upper part of the ventral area is more strongly developed and concentrated in the most central part of the otolith; the collicula protrude on the anterior and posterior sides of the otolith, and ventrally the beginning of the formation of an anterior and posterior lobe is visible.

GRAMMICOLEPIDIDAE, Macrurocyttinae
Contained genus: *Macrurocyttus*; otoliths unknown.

GRAMMICOLEPIDIDAE, Grammicolepidinae
Available iconography:

Grammicolepis brachiusculus POEY, 1873
Pl. 5, Figs. 1–2
CAMPANA, 2004, pl. on p. 276, as *Daramattus americanus*
OHE, 1985, fig. Ad 433, p. 75

Xenolepidichthys dalgleishi GILCHRIST, 1922
Pl. 5, Fig. 3
NOLF, 1985, fig. 55D, p. 73
OHE, 1985, fig. 111, p. 75
RIVATON & BOURRET, 1999, pl. 144, figs. 14–18
SMALE *et al.*, 1995, pl. 46, figs. E1–3

Otoliths of the Gramicolepididae are characterised by a strong antero-posterior constriction and a sulcus with a hollow ostium and posterior caudal end. Collicula are either lacking or only developed as flat rudimentary structures. The ostium and the posterior end of the ventral area are very salient. There is a marked posterodorsal angle, which is mainly developed backward. This otolith type is very similar to that of cyttids; in fact, the only feature that seems to distinguish them is that in cyttids the posterodorsal angle is more expanded in the dorsal direction. The otolith represented on Pl. 5, Fig. 2 shows a ventral rim with a manifest concave portion just in front of the salient posterior end. Such hollowing is not seen in the smaller otoliths figured by Campana (herein reproduced on Pl. 5, Fig. 1) and by Ohe, and it may be a feature that appears only at a certain size.

ZEIDAE

Zenopsis conchifer (LOWE, 1852)
Pl. 5, Fig. 4
CAMPANA, 2004, p. 277
CHAINE, 1958, pl. p. 237
SCHMIDT, 1968, pl. 5, fig. 59; pl. 18
SMALE *et al.*, 1995, pl. 45, figs. E1–2

Zenopsis nebulosus (Temminck & Schlegel, 1845)
Pl. 5, Figs. 9–12
OHE, 1985, fig. 113, p. 76

Zeus capensis VALENCIENNES, 1835
SMALE *et al.*, 1995, pl. 45, figs. F1–4

Zeus faber LINNAEUS, 1758
Pl. 5, Figs. 5–8
ASSIS, 2004, fig. 56, p. 118
CHAINE, 1958, pl. p. 237, under the names of *Z. faber* and *Z. pungio*
FROST, 1927, pl. 8, figs. 8–9 (sac., utr., lag.)
HÄRKÖNEN, 1986, pl. 41, figs. A–B
NOLF, 1985, fig. 55C, p. 73
SCHMIDT, 1968, pl. 4, fig. 58; pl. 18
SMALE *et al.*, 1995, pl. 45, figs. G1–2

Zeid otoliths, with their tri-lobed outline, can be immediately distinguished from those of any other fish taxon. Other marked features are the protruding collicula that form additional small anterior and posterior lobes, and the rim that is smooth along almost the entire outline of the otolith. In *Zeus*, the lobes of the ventral portion are directed further outward than in *Zenopsis*.

TETRAODONTIFORMES
[PLECTOCRETACICOIDEI, extinct]
[CRETATRIACANTHIDAE, extinct; Upper Campanian-Lower Maastrichtian; Nardò, Puglia, Italy; otoliths unknown]
[PLECTOCRETACICIDAE, extinct; Lower Cenomanian; Hakel, Lebanon; otoliths unknown]
[PROTRIACANTHIDAE, extinct; Upper Cenomanian-Lower Turonian; Comen, Slovenia; otoliths unknown]

TRIACANTHODOIDEI
TRIACANTHODIDAE, Hollardiinae
Available iconography:

Hollardia hollardi POEY, 1861
TYLER, 1968, fig. 31G, p. 102

Parahollardia lineata (LONGLEY, 1935)
TYLER, 1968, fig. 18, p. 79

Parahollardia schmidti WOODS, 1959
TYLER, 1968, fig. 25G, p. 88

Otoliths of hollardiin triacanthodids are known only by the schematic drawings of TYLER (1968), which depicted only the outlines of the otoliths and were figured upside down in all three cases. Unfortunately, our search (mostly at the Academy of Natural Sciences of Philadelphia) for these original otolith materials of cleared and stained specimens was unsuccessful; the otoliths probably have been dissolved or dispersed in the residue of the much dissected alizarine preparation. These outline drawings, however, show a general similarity with the triacanthodid otolith illustrations herein, except that they show a stronger constriction along the antero-posterior midline.

TRIACANTHODIDAE, Triacanthodinae
Available iconography:

Halimochirurgus centriscoides ALCOCK, 1899
TYLER, 1968, fig. 90G, p. 223

Johnsonina eriomma MYERS, 1934
TYLER, 1968, fig. 57G, p. 158

Macrorhamphosodes sp.
SMALE *et al.*, 1995, pl. 147, fig. A1

Macrorhamphosodes platycheilus FOWLER, 1934
TYLER, 1968, fig. 84G, p. 214

Macrorhamphosodes uradoi (KAMOHARA, 1933)
OHE, 1985, fig. 415, p. 173
TYLER, 1968, fig. 78G, p. 202

Paratriacanthodes retrospinis FOWLER, 1934
Pl. 6, Fig. 3
TYLER, 1968, fig. 52G, p. 147

Triacanthodes anomalus TEMMINCK & SCHLEGEL, 1850
OHE, 1985, fig. 414, p. 173
TYLER, 1968, fig. 2B, p. 8; fig. 39G, p. 120

Triacanthodes ethiops ALCOCK, 1894
Pl. 6, Fig. 1
NOLF, 1985, fig. 79A, p. 105
RIVATON & BOURRET, 1999, pl. 83, figs. 1–6
TYLER, 1968, fig. 43G, p. 127

Triacanthodes sp.
RIVATON & BOURRET, 1999, pl. 83, figs. 7–8

Tydemania navigatoris WEBER, 1913
Pl. 6, Fig. 2
RIVATON & BOURRET, 1999, pl. 83, figs. 9–10
TYLER, 1968, fig. 70, p. 187

Otoliths are unknown for the genera *Atrophacanthus, Bathyphylax* and *Halimochirurgus*.
Triacanthodids are characterized by round shaped otoliths with a well-marked antero-posterior constriction. The outer face is slightly concave and nearly flat; the inner face is strongly convex. The sulcus is well incised, and in at least some otoliths, there is a slight to distinct crista superior. The presence of a crista superior is a plesiomorphic feature, as it is lacking in more derived tetraodontiform otolith types.

BALISTOIDEI
TRIACANTHOIDEA
TRIACANTHIDAE
Available iconography:

Pseudotriacanthus strigilifer (CANTOR, 1849)
Pl. 6, Fig. 4
SANTINI & TYLER, 2002, fig. 5B, p. 328
TYLER, 1968, fig. 124G, p. 296

Triacanthus biaculeatus (BLOCH, 1786)
Pl. 6, Fig. 6
OHE, 1985, fig. 413, p. 173, as *T. brevirostris*
SANTINI & TYLER, 2002, fig. 5A, p. 328
TYLER, 1968, fig. 113G, p. 266

Triacanthus nieuhofi BLEEKER, 1852
TYLER, 1968, fig. 117G, p. 278

Tripodichthys angustifrons (HOLLARD, 1854)
TYLER, 1968, fig. 130G, p. 310

Tripodichthys blochii (BLEEKER, 1852)
TYLER, 1968, fig. 2A, p. 8; fig. 128G, p. 304

Tripodichthys oxycephalus (BLEEKER, 1851)
TYLER, 1968, fig. 132G, p. 316

Trixiphichthys weberi (CHAUDHURI, 1910)
Pl. 6, Fig. 5
TYLER, 1968, fig. 121G, p. 288

Triacanthid otoliths are comparable to those of triacanthodids because of their rather deeply incised sulcus, with at least some rudiments of a crista superior, and because of their antero-posterior constriction. Their dorsal area, however, is higher and narrower, and their rostrum is very salient relative to triacanthodids.

[MOCLAYBALISTOIDEA, extinct]
[MOCLAYBALISTIDAE, extinct; late Paleocene, Mo-Clay (Fur) Formation; Jutland, Denmark; otoliths unknown]

[BOLCABALISTOIDEA, extinct]
[BOLCABALISTIDAE, extinct; middle Eocene, Lutetian; Monte Bolca, Italy; otoliths unknown]
[EOSPINIDAE, extinct; late Paleocene, Danatinian Formation; Uylya-Kushlyuk, Turkmenistan; otoliths unknown]

BALISTOIDEA
BALISTIDAE
Available iconography:

Balistapus undulatus (MUNGO PARK, 1797)
Pl. 7, Fig. 4
NOLF, 1985, fig. 79B, p. 105
SMALE *et al.*, 1995, pl. 147, fig. B1

Balistes capriscus GMELIN, 1789
Pl. 8, Figs. 1–6
ASSIS, 2004, fig. 91, p. 161, as *B. carolinensis*
CAMPANA, 2004, p. 273
FROST, 1930, pl. 23, fig. 3

Balistes polylepis STEINDACHNER, 1876
Pl. 8, Figs. 10–11

Balistes vetula LINNAEUS, 1758
Pl. 8, Figs. 7–9

Balistoides viridescens (BLOCH & SCHNEIDER, 1801)
Pl. 8, Fig. 12

Canthidermis maculatus (BLOCH, 1786)
Pl. 8, Fig. 13
OHE, 1985, fig. Ad 448, p. 171
SMALE *et al.*, 1995, pl. 147, fig. C1

Melichthys indicus RANDALL & KLAUSEWITZ, 1973
SMALE *et al.*, 1995, pl. 147, fig. D1

Melichthys niger (BLOCH, 1786)
Pl. 7, Fig. 1

Melichthys vidua (RICHARDSON, 1845)
Pl. 7, Figs. 5–6

Odonus niger (RÜPPELL, 1836)
Pl. 7, Figs. 2-3
RIVATON & BOURRET, 1999, pl. 84, figs. 5–6
SMALE *et al.*, 1995, pl. 147, fig. E1

Pseudobalistes fuscus (BLOCH & SCHNEIDER, 1801)
Pl. 8, Fig. 14

Rhinecanthus aculeatus (LINNAEUS, 1758)
? SMALE *et al.*, 1995, pl. 147, fig. F1: probably a *Sufflamen* otolith
RIVATON & BOURRET, 1999, pl. 84, figs. 7–8 (only utricular)

Rhinecanthus rectangulus (BLOCH & SCHNEIDER, 1801)
Pl. 8, Figs. 15–16

Sufflamen bursa (BLOCH & SCHNEIDER, 1801)
Pl. 9, Fig. 4

Sufflamen chrysopterus (BLOCH & SCHNEIDER, 1801)
Pl. 9, Figs. 1–2
SMALE *et al.*, 1995, pl. 147, fig. G1

Sufflamen fraenatus (LASTRICELLE, 1804)
Pl. 9, Fig. 3
RIVATON & BOURRET, 1999, pl. 84, figs. 1–4
SMALE *et al.*, 1995, pl. 147, fig. H1

Sufflamen verres (GILBERT & STARKS, 1904)
Pl. 9, Fig. 5

Xanthichthys lineopunctatus (HOLLARD, 1854)
OHE, 1985, fig. 408, p. 171

Xanthichthys mento (JORDAN & GILBERT, 1882)
Pl. 7, Figs. 7–8

Otoliths are unknown for the genera *Abalistes* and *Xenobalistes*.

All balistid otoliths are characterized by a strong salient rostrum. The posterior incision is only very weakly incised. Based upon otolith morphology, one can distinguish three easily recognizable groups among balistids. The first group includes the genera *Balistapus, Melichthys, Odonus* and *Xanthichthys*. It is characterized by very thick otoliths with a strongly convex inner face, a very deeply incised sulcus, a salient rostrum and antirostrum, and a rudimentary posterior constriction. The second group includes *Balistes, Balistoides, Canthidermis, Pseudobalistes* and *Rhinecanthus,* which has a very peculiar type of otolith. It is composed of two parts: a main otolith body with a more-or-less typical otolith morphology, and a posteroventral accretional body that is about as large as the main otolith body. An accretional body of that size is unique among all teleosts. The third group is composed of the genus *Sufflamen*. It is characterized by a thick otolith with a strong expansion of the posterodorsal area, a very deeply incised sulcus that is well delimited by a salient crista superior and inferior, and a strongly protruding rostrum and antirostrum.

MONACANTHIDAE

Available iconography:

Aluterus monoceros (LINNAEUS, 1758)
Pl. 10, Figs. 5–6
OHE, 1985, fig. Ad 450, p. 172
SMALE *et al.*, 1995, pl. 147, figs. I1–4

Aluterus schoepfi (WALBAUM, 1792)
Pl. 10, Figs. 1–3

Aluterus scriptus (OSBECK, 1765)
Pl. 10, Fig. 4
RIVATON & BOURRET, 1999, pl. 83, figs. 18–19

Anacanthus barbatus GRAY, 1830
Pl. 10, Figs. 7-8

Brachaluteres ulvarum JORDAN & FOWLER, 1902
OHE, 1985, fig. 410, p. 172

Cantherhines dumerilii (HOLLARD, 1853)
Pl. 11, Fig. 1

Cantherhines macrocerus (HOLLARD, 1853)
Pl. 11, Fig. 2

Cantherhines pardalis (RÜPPELL, 1837)
SMALE *et al.*, 1995, pl. 147, fig. J1

Cantherhines sandwichiensis (QUOY & GAIMARD, 1824)
Pl. 11, Fig. 3

Chaetodermis penicilligerus (CUVIER, 1816)
Pl. 10, Fig. 12
OHE, 1985, fig. Ad 449, p. 172

Meuschenia australis (DONOVAN, 1824)
Pl. 10, Fig. 11
NOLF, 1985, fig. 79C, p. 105, as *Navodon* sp.

Meuschenia scaber (FORSTER, 1801)
Pl. 10, Figs. 9–10

Monacanthus chinensis (OSBECK, 1765)
Pl. 11, Figs. 6–9

Monacanthus tuckeri BEAN, 1906
Pl. 11, Fig. 4

Oxymonacanthus longirostris (BLOCH & SCHNEIDER, 1801)
Pl. 11, Fig. 5

Paraluteres prionurus (BLEEKER, 1851)
Pl. 10, Fig. 13

Paramonacanthus oblongus (TEMMINCK & SCHLEGEL, 1850)
Pl. 12, Figs. 9–12

Pervagor janthinosoma (BLEEKER, 1854)
SMALE *et-al.*, 1995, pl. 148, figs. A1–3

Pervagor melanocephalus (BLEEKER, 1853)
Pl. 11, Fig. 10

Pervagor spilosoma (LAY & BENNETT, 1839)
Pl. 11, Figs. 11–12

Pseudomonacanthus macrurus (BLEEKER, 1857)
Pl. 12, Figs. 2–5

Stephanolepis cirrhifer (TEMMINCK & SCHLEGEL, 1850)
OHE, 1985, fig. 409, p. 172

Stephanolepis hispidus (LINNAEUS, 1766)
Pl. 12, Fig. 1

Thamnaconus fajardoi SMITH, 1953
SMALE *et al.*, 1995, pl. 148, fig. B1

Thamnaconus hypargyreus (COPE, 1873)
Pl. 12, Fig. 6
RIVATON & BOURRET, 1999, pl. 83, figs. 11–17 (sac., utr., lag.)

Thamnaconus modestoides (BARNARD, 1927)
SMALE *et al.*, 1995, pl. 148, fig. C1

Thamnaconus modestus (GÜNTHER, 1877)
Pl. 12, Figs. 7–8
OHE, 1985, fig. 411, p. 172, as *Navodon modestus*

Otolith morphology indicates that monacanthids are a rather homogeneous group. Monacanthid otoliths are characterized by a very strong antero-posterior constriction. The upper portion of the otolith is always much narrower than the lower portion and often shows a well-marked posterodorsal angle. In many species, the lower portion of the otolith is about twice as large as the upper portion, and sometimes it develops anterior, posterior and ventral expansions. Therefore, in several taxa, the anterior and posterior halves of the otolith look almost symmetrical, which, for isolated otoliths, makes it sometimes difficult to judge if a left or a right one is concerned. In such cases, the posterodorsal angle, if sufficiently developed, is often the best criterion to judge. The crista superior is lacking or obsolete in all the examined taxa.

OSTRACIOIDEA

[SPINACANTHIDAE, extinct; middle Eocene, Lutetian; Monte Bolca, Italy; otoliths unknown]

[PROTOBALISTIDAE, extinct; middle Eocene, Lutetian; Monte Bolca, Italy; otoliths unknown]

ARACANIDAE

Available iconography:

Anoplocapros inermis (FRASER-BRUNNER, 1935)
Pl. 13, Figs. 4–5

Anoplocapros robustus (FRASER-BRUNNER, 1941)
Pl. 13, Fig. 3

Aracana ornata (GRAY, 1838)
Pl. 13, Fig. 6

Kentrocapros aculeatus (HOUTTUYN, 1782)
Pl. 13, Fig. 7
OHE, 1985, fig. 412, p. 173

Otoliths are unknown for the genera *Caprichthys, Capropygia, Polyplacapros* and *Strophiurichthys*.
Otoliths of the four taxa of aracanids that we examined are characterized by a globally rounded outline, but with a very strong antero-posterior constriction. The sulcus is rather strongly incised, and both the crista inferior and superior are clearly developed. The presence of a well-developed crista superior can be considered a plesiomorphic feature relative to ostraciid otoliths, in which this crista often tends to become obsolete. In most of the examined aracanid otoliths, the dorsal portion is manifestly narrower than the ventral portion.

OSTRACIIDAE

Available iconography:

Acanthostracion quadricornis (LINNAEUS, 1758)
Pl. 14, Figs. 1–2

Lactophrys trigonus (LINNAEUS, 1758)
Pl. 14, Fig. 3

Lactoria fornasini (BIANCONI, 1846)
Pl. 14, Fig. 4
SMALE *et al.*, 1995, pl. 148, fig. D1

Ostracion cubicus LINNAEUS, 1758
Pl. 14, Figs. 5–6
RIVATON & BOURRET, 1999, pl. 84, fig. 9
SMALE *et al.*, 1995, pl. 148, fig. E1

Ostracion meleagris SHAW, 1796
Pl. 14, Figs. 8–9
NOLF, 1985, fig. 79D, p. 105, as *Ostracion lentiginosum*

Rhinesomus concatenatus (BLOCH, 1785)
OHE, 1985, fig. 419, p. 174

Tetrosomus gibbosus (LINNAEUS, 1758)
Pl. 14, Fig. 7
FROST, 1930, pl. 23, fig. 4, as *Ostracion gibbosus*

Otoliths are unknown for the genera *Lactoria* and *Rhynchostracion*.
Ostraciid otoliths are very similar to those of aracanids. The only observable difference is the crista superior, which is absent or tends to become obsolete in many of the examined ostraciids. In *Acanthostracion,* the otoliths are extremely thick, but all other examined species have a normal thickness. For the rest, we judge the available material insufficient for any further conclusions.

TETRAODONTOIDEI

[EOPLECTOIDEA, extinct]

[EOPLECTIDAE, extinct; middle Eocene, Lutetian; Monte Bolca, Italy; otoliths unknown]

TRIODONTOIDEA

TRIODONTIDAE

Available iconography:

Triodon macropterus LESSON, 1829
Pl. 13, Figs. 1–2
RIVATON & BOURRET, 1999, pl. 84, figs. 14–15

The otoliths of the single extant species of this family are characterized by a high dorsal portion, a strong antero-posterior constriction along the midline, and a ventral portion with a long prominent rostrum, a moderate posterior expansion, and an extremely reduced ventral area, which makes up a concave ventral rim.

TETRAODONTOIDEA

TETRAODONTIDAE

Available iconography:

Amblyrhynchotes honkenii (BLOCH, 1795)
Pl. 15, Fig. 7, redrawn after SMALE *et al.*, 1995
SMALE *et al.*, 1995, pl. 148, figs. F1–5 (series of variability)

Arothron hispidus (LINNAEUS, 1758)
Pl. 15, Fig. 1

RIVATON & BOURRET, 1999, pl. 84, figs. 16–17
SMALE *et al.*, 1995, pl. 148, fig. G1

Arothron immaculatus (BLOCH & SCHNEIDER, 1801)
Pl. 15, Fig. 2

Arothron mappa (LESSON, 1831)
Pl. 15, Fig. 3

Arothron stellatus (BLOCH & SCHNEIDER, 1801)
SMALE *et al.*, 1995, pl. 149, fig. A1

Canthigaster amboinensis (BLEEKER, 1865)
Pl. 16, Fig. 3

Canthigaster coronata (VAILLANT & SAUVAGE, 1875)
Pl. 16, Fig. 2

Canthigaster jactator (JENKINS, 1901)
Pl. 16, Fig. 1

Canthigaster margaritata (RÜPPELL, 1829)
Pl. 16, Fig. 6

Canthigaster punctatissimus (GÜNTHER, 1870)
Pl. 16, Fig. 4

Canthigaster rivulatus (TEMMINCK & SCHLEGEL, 1850)
Pl. 16, Fig. 5
OHE, 1985, fig. 418, p. 174

Canthigaster solandri (RICHARDSON, 1845)
Pl. 16, Fig. 7
SMALE *et al.*, 1995, pl. 149, fig. B1

Canthigaster valentini (BLEEKER, 1853)
RIVATON & BOURRET, 1999, pl. 84, fig. 13

Contusus richei (FREMINVILLE, 1813)
Pl. 15, Figs. 10–12

Lagocephalus ?guentheri RIBEIRO, 1915
SMALE *et al.*, 1995, pl. 149, figs. C1–2 (growth series)

Lagocephalus inermis (SCHLEGEL, 1850)
SMALE *et al.*, 1995, pl. 149, figs. D1–2

Lagocephalus lunaris (BLOCH & SCHNEIDER, 1801)
Pl. 15, Figs. 8–9
OHE, 1985, fig. 416, p. 174

Lagocephalus scleratus (GMELIN, 1789)
Pl. 15, Figs. 4–6
RIVATON & BOURRET, 1999, pl. 84, figs. 18–22
SMALE *et al.*, 1995, pl. 149, figs. E1–3

Liosaccus cutaneus (Günther, 1870)
OHE, 1985, fig. 417, p. 174

Sphoeroides lobatus (STEINDACHNER, 1870)
Pl. 16, Fig. 8

Sphoeroides maculatus (BLOCH & SCHNEIDER, 1801)
CAMPANA, 2004, p. 275

Sphoeroides nephelus (GOODE & BEAN, 1882)
Pl. 16, Figs. 10–11

Sphoeroides pachygaster (MULLER & TROSCHEL, 1848)
SMALE *et al.*, 1995, pl. 149, figs. F1–3

Sphoeroides spengleri (BLOCH, 1785)
Pl. 16, Fig. 9

Sphoeroides testudineus (LINNAEUS, 1758)
Pl. 16, Fig. 12

NOLF, 1985, fig. 79E, p. 105

Takifugu niphobles (JORDAN & SNYDER, 1901)
OHE, 1985, fig. 421, p. 174

Takifugu oblongus (BLOCH, 1786)
Pl. 17, Figs. 1–5

Takifugu porphyreus (TEMMINCK & SCHLEGEL, 1850)
Pl. 17, Fig. 6

Takifugu rubripes (TEMMINCK & SCHLEGEL, 1850)
OHE, 1985, fig. 420, p. 174

Takifugu xanthopterus (TEMMINCK & SCHLEGEL, 1850)
Pl. 17, Figs. 7–8

Tetraodon fluviatilis HAMILTON, 1822
Pl. 17, Fig. 11

Tetraodon lineatus LINNAEUS, 1758
FROST, 1930, pl. 23, fig. 5, as *Tetrodon fahaka*

Tetraodon palembangensis BLEEKER, 1852
Pl. 17, Fig. 9

Tylerius spinosissimus (REGAN, 1908)
Pl. 17, Fig. 10

Otoliths are unknown for the genera *Carinotetraodon, Colomesus, Feroxodon, Javichthys* and *Omegophora.*
Otoliths of tetraodontids show a considerable diversity. The crista superior is always lacking or obsolete. The central part of the crista inferior is always very salient. Although only a limited number of specimens was examined (and in some cases, the various specimens of the species examined showed considerable differences in size), some characteristic clusters could be determined. The outlines of the otoliths of *Amblyrhynchotes, Contusus, Sphoeroides* and *Takifugu* are similar to those of monacanthid otoliths, but they differ from monacanthids by having an extremely salient crista inferior. The outline and the very salient rostrum of *Lagocephalus* resemble that of *Triodon.* In *Tetraodon,* the crista inferior and associated upper part of the ventral area becomes extremely distended, and the ventral part of the sulcus is deeply incised, which has similarities to the morphology of the funnel-like sulcus of diodontids. A straight forward, recognizable morphology is also present in *Canthigaster.* It has a strong antero-posterior constriction, a very narrow and angular dorsal portion, a widely extended ventral portion with a very salient rostrum and a round, thickened posterior end. *Arothron* is only documented by very small otoliths, but these exhibit some similarity to those of *Canthigaster.*

DIODONTIDAE
Available iconography:

Allomycterus whitleyi PHILLIPPS, 1932
Pl. 18, Fig. 1

Chilomycterus affinis GÜNTHER, 1870
Pl. 18, Fig. 3

Chilomycterus schoepfii (WALBAUM, 1792)
Pl. 18, Fig. 2
CAMPANA, 2004, pl. on p. 274

Cyclichthys orbicularis (BLOCH, 1785)
Pl. 18, Fig. 4

Dicotylichthys punctulatus KAUP, 1855
Pl. 18, Fig. 5

Diodon holocanthus LINNAEUS, 1758
Pl. 18, Figs. 8–9

Diodon hystrix LINNAEUS, 1758
Pl. 18, Fig. 6
RIVATON & BOURRET, 1999, pl. 84, figs. 10–12
SMALE *et al.*, 1995, pl. 149, figs. G1–3

Diodon nicthemerus CUVIER, 1818
Pl. 18, Fig. 7

Otoliths are unknown for the genera *Lophodiodon* and *Tragulichthys*.
Diodontid otoliths, with their crystal-like salient needles and their horn-like appearance, are among the strangest otoliths known among fishes. Their morphology can only be understood if one considers them to be highly modified derivatives of the type observed in tetraodontids, such as *Tetraodon*. In diodontid otoliths, the salient central part of the crista inferior is extremely protruding, and the ventral part of the sulcus sinks deeply, which together form a funnel-like structure. In *Diodon holocanthus,* the homology with *Tetraodon* otoliths is still visible. Only by comparison with the transitional otolith morphologies from *Tetraodon* to *Diodon* can the structure of the otolith in *Allomycterus* be understood.

MOLOIDEA
MOLIDAE
Available iconography:

Mola mola (LINNAEUS, 1758)
NOLF, 1985, fig. 79F, p. 105

Ranzania laevis (PENNANT, 1776)
Pl. 18, Fig. 10

In the labyrinth of *Mola mola,* a fish with very poor ossification of the skeleton, only some chalk dust has been collected (figured by NOLF, 1985), which is not amenable to morphological interpretation. For *Ranzania laevis,* a single very fragile small otolith is available, which shows some spine-like crystal extrusions, as in diodontids. On the basis of homologies with other tetraodontiform otoliths, the small *Ranzania* otolith can be interpreted as having an elongate ventral portion, a strong but structureless crista inferior accentuated by a deep ventral portion of the sulcus, and a very narrow, strongly salient dorsal area. We presume that the spine-like crystal extrusions of the *Ranzania* otolith are related to the crystalline needles of diodontids.

Examined out-group taxa

PERCIFORMES
CAPROIDAE
CAPROIDAE, Antigoniinae
Available iconography:

Antigonia capros LOWE, 1843
Fig. 6
HUYGHEBAERT & NOLF, 1979, pl. 4, figs. 11–12
KOTLYAR & PARIN, 1990, fig. 5, p. 110
OHE, 1985, fig. 110, p. 74
RIVATON & BOURRET, 1999, pl. 145, figs. 1–4
SCHMIDT, 1968, pl. 5, fig. 60; pl. 18
SCHWARZHANS, 1980, fig. 376, p. 114
STEURBAUT, 1979, pl. 6, figs. 12–13
STINTON, 1978, fig. 26g, p. 136

Antigonia eos GILBERT, 1905
NOLF, 1993, fig. 3N, p. 228

Antigonia malayana WEBER, 1913
Fig. 7
RIVATON & BOURRET, 1999, pl. 145, figs. 5–9

Antigonia rubescens (GÜNTHER, 1860)
RIVATON & BOURRET, 1999, pl. 145, figs. 10–15
SMALE *et al.*, 1995, pl. 47, figs. A1–3

CAPROIDAE, Caproinae

Capros aper LINNAEUS, 1758
Fig. 6
ASSIS, 2004, fig. 57, p. 119
CHAINE, 1958, pl. p. 236
FROST, 1927, pl. 8, figs. 11–13 (sac., lag., utr.)
NOLF, 1985, fig. 55F, p. 73
NOLF, 1993, fig. 3, O, p. 228
NOLF & LAPIERRE, 1979, pl. 3, fig. 2
STINTON, 1978, fig. 27d, p. 145

Otolith-based fossil record of caproid, zeiform and tetraodontiform fishes

CAPROIDAE
- ***Antigonia angusta*** STINTON & NOLF, 1970: middle Eocene, Lutetian; Belgium.
- ***Antigonia capros*** LOWE, 1843: early Miocene, Burdigalian; Aquitaine, France (NOLF & BRZOBOHATY, 2002).
- ***Capros parvus*** (MENZEL, 1986): middle Miocene; Germany.
- "**genus Caproidarum**" ***exiguus*** (STINTON, 1978): middle Eocene, Lutetian; southern England.
- "**genus Caproidarum**" ***sonodae*** NOLF & LAPIERRE, 1979): middle Eocene, Lutetian; Paris Basin.

Zeiformes *incertae sedis*
- "**genus Zeiformorum**" ***janni*** SCHWARZHANS, 2003: Middle Paleocene, Selandian; Denmark
- "**genus Zeiformorum**" ***tyleri*** NOLF, 2003: late Cretaceous, Santonian, Pyrenees, France (Pl. 4, Figs. 11-12).
- "**Bavarian zeiforms**" ("Isozen" sp. and "Isozen beatae," invalid names, see NOLF, 2003): Paleocene (Pl. 4, Fig. 5) and Maastrichtian (Pl. 4, Fig. 4); Bavaria (SCHWARZHANS, 1996).

ZENIONTIDAE
- *Zenion hololepis* GOODE & BEAN, 1896: early Pliocene, Zanclian, SE France (NOLF & CAPPETTA, 1989, pl. 14, figs. 13-14).

- "**genus aff. *Zenion***" sp. n.: early Eocene, Ypresian (Gan Clay) (Pl. 4, Figs. 2-3) and middle Eocene, Lutetian (Miretrain marls); Aquitaine, France.
- ***Zenion*** sp.: early Oligocene, Rupelian; Piemonte, Italy (NOLF & STEURBAUT, 2004, pl. 9, fig. 2: an eroded *Zenion* otolith, not identifiable at species level).
"**genus Zeniontidarum**" ***sulcifer*** (STINTON, 1966): early Eocene, Ypresian, London Clay; southern England (Pl. 4, Figs. 9-10).

TRIACANTHIDAE
- ***Triacanthus*** sp.: early Eocene, Ypresian (London Clay) (Pl. 6, Fig. 7) (Coll. Rundle, new fossil record).

OSTRACIIDAE
- ***Ostracion pergravis*** SCHWARZHANS, 2003: Paleocene, Selandien ; Denmark (Pl. 14, Fig. 10–11).

Discussion

Characterization of otoliths in caproid, zeiform and tetraodontiform fishes

1. Plesiomorphic otoliths and the plesiomorphic configuration of generalized perciform otoliths.

Before proceeding with the morphological analysis of zeiform and tetraodontiform otoliths, it is important to bear in mind the configuration of plesiomorphic otoliths of acanthopterygian fishes in general, and especially of those of generalized perciforms. In Fig. 4, various types of acanthopterygian otoliths (holocentids, atherinids, mugilids, polynemids) are compared with a number of other taxa, including primitive teleosts, such as osteoglossids and elopids, and selected euteleosteans, such as salmonids, aulopids, synodontids and polymixiids. A first conclusion to be drawn from this comparison is that generalized acanthopterygian (and percoid) otoliths exhibit a Bauplan that can be traced back as far as the elopids; even osteoglossids are not incompatible as an ancestral percoid otolith type. At the level of synodontids, it is even difficult to define, for that group, otolith features that are fundamentally different from those of percoids. If the series from Fig. 4 were presented in a cladogram, with osteoglossids as the most plesiomorphic group and the acanthopterygians as the most apomorphic, the cladogram probably would meet with general agreement among fish phylogenists, but it also would contain extremely important lacunae.

2. Polarity of the sulcus morphology in holocentrid and berycid otoliths. Importance of the Santonian *Centroberyx antiquus*.

Round and deep-bodied otoliths with a broad sulcus consisting of a rather long ostium and a straight, relatively wide cauda, are considered to be derived; however, this type of otolith apparently evolved independently in several taxonomic groups that are not closely related. This feature is observed mainly in fishes with a mesopelagic or benthopelagic habitat, and it must be considered a homoplasy. See Nolf, 1993, fig. 3, p. 228, for illustrations of this type of otolith in myctophids, neoscopelids, five families of beryciforms and caproids. In Fig. 5, *Polymixia* and *Sargocentron* represent the plesiomorphic condition, and *Centroberyx affinis* and *Beryx* represent the homoplasic apomorphic conditions. The Santonian (Upper Cretaceous) *Centroberyx antiquus* exhibits a more plesiomorphic level than in berycoid otoliths: this species already has the round, rather deep-bodied form and the wide ostium, but it still has a narrow cauda, as in perciforms, holocentrids and *Polymixia*. Both by its ancient age and morphology, the otolith of *Centroberyx* indicates a more plesiomorphic condition than in Recent berycids, and it helps to determine the polarity of otolith features.

3. Caproid otoliths and the "berycid" aspect of those of Antigonia.

Fig. 6 shows the plesiomorphic versus derived morphology for, respectively, berycoids, caproids and percoids. In berycoids, the plesiomorphic condition is demonstrated by the holocentrid *Sargocentron,* and the derived condition is represented by *Beryx decadactylus*. Percoids, such as *Morone*, demonstrate the plesiomorphic condition, which is very similar to that of *Sargocentron,* whereas the derived condition is exhibited by *Kurtus* or *Apogon*. Both the plesiomorphic and derived conditions also exist in caproids, a family that has been included in the Zeiformes in many classifications, and STINTON (1967) even suggested that *Antigonia* is a berycoid on the basis of its otolith morphology. Considering the deep-bodied otoliths with a straight sulcus as a homoplasic feature that has evolved independently in many groups, our interpretation is that in caproids the plesiomorphic sulcus condition is found in *Capros,* whereas the derived "berycid"-like otolith is found in *Antigonia*. The antero-posterior constriction seen in *Capros,* however, is a synapomorphy shared with zeiforms and tetraodontiforms.

4. Characterization of caproid, zeiform and tetraodontiform otoliths.

In *Capros,* the otolith is deep-bodied, but the sulcus pattern is more like that of *Sargocentron* and *Morone* (Fig. 6), with a short ostium and with a long cauda that is slightly bent ventrally in its posterior portion. The otolith of *Capros* is interesting in the sense that it already has a feature that can be taken as a synapomorphy for zeiform and tetraodontiform otoliths, which consists of a marked antero-posterior constriction along the horizontal midline of the otolith.
Both zeiform and tetraodontiform otoliths belong to the deep-bodied otolith type, but because this feature appears independently many times in the otoliths of unrelated groups of fishes, it cannot be utilized as a synapomorphy.
Zeiform and tetraodontiform otoliths, however, are united by a synapomorphy that consists of a swelling of the upper part

of the ventral area, just below the caudal crista inferior. This feature is lacking in caproid otoliths. Because in all taxa of zeiforms and tetraodontiforms the cauda is markedly longer than the ostium, this swelling occupies a central position.

5. Polarity in zeiform otoliths.

In Fig. 7, a series of beryciform (*Monocentris* and *Diretmus*), caproid (*Antigonia*) and zeiform (*Cyttus* and *Zeus*) otoliths are compared. The zeiforms *Cyttus* and *Zeus* represent, respectively, a plesiomorphic and the most derived otolith types among zeiforms. Both of these zeiforms have the constriction along the midline and the swollen upper central part of the ventral area. Except for the constriction, the general outline of the otolith in *Cyttus* still presents a berycid-like appearance. In *Zeus,* the lower portion of the otolith has strongly modified anterior and posterior lobiform expansions, but the upper portion remains comparable to that of *Cyttus,* and it still shows the development of a strong posterodorsal angle, as in *Cyttus* and *Diretmus*.

6. Polarity in tetraodontiform otoliths.

In Fig. 8, the otoliths from two taxa of the most phylogenetically basal family (Triacanthodidae) of extant tetraodontiforms, and of a representative of each of three more derived families (Monacanthidae, Tetraodontidae, Diodontidae) of that order are compared with the otolith of a caproid; all have a reasonable similarity. The tetraodontiforms, however, have a derived condition: the swollen upper central part of the ventral area. Monacanthids, diodontids and tetraodontids have even more strongly derived otoliths: monacanthids such as *Chaetodermis* and *Pervagor* exhibit an extreme antero-posterior otolith constriction; diodontids and tetraodontids have a funnel-like sulcus. Among other tetraodontiform otoliths, very highly derived types can be found, showing essentially autapomorphic features, which are discussed in the next section.

Phylogenetic evaluation of otolith features of zeiform and tetraodontiform fishes

In the following section, otolith-based data are compared with osteological data from osteologically based phylogenetic studies of zeiform (TYLER *et al.*, 2003) (Fig. 9) and tetraodontiform (TYLER, 1980, and SANTINI & TYLER, 2003) (Fig. 10) fishes.

In zeiforms, the otolith data seem to support reasonably well the homogeneity of the six defined families, but they are of little use in interpreting the interrelationships among these families.

In cyttids, the otoliths suggest a very homogeneous cluster, with all species showing deep-bodied otoliths with a strong posterodorsal angle, a strong antero-posterior constriction, and a hollow sulcus with no, or only rudimentary, collicular formations. A similar otolith type is found in **grammicolepidids**, among which the grammicolepidine subfamily also constitutes a very homogeneous cluster, differing from cyttids only by their less upward-protruding posterodorsal angle. Based only upon otolith morphology, one would tend to group these two families closely together and also to relate the very homogeneous cluster of **oreosomatids** to them, as an apomorphic group, characterized by a ventral expansion of the anterior and posterior end of the sulcus and by hypertrophy of the collicula, but otherwise showing a very similar otolith type.

The parazenids clearly split into two clusters: *Parazen,* with a very plesiomorphic otolith type, and the Cyttopsinae (*Cyttopsis* + *Stethopristes*), which, based only upon otolith morphology, can be integrated perfectly in the cyttid-grammicolepidid-oreosomatid group.

In zeniontids, the situation is even more complicated. *Zenion* exhibits a plesiomorphic otolith type, whereas the [*Capromimus* + *Cyttomimus*] cluster can be defined as an apomorphic relative (characterized by reduction of the collicula toward the anterior and posterior marginal zones) of the cyttid-grammicolepidid-oreosomatid group. The situation becomes even more complex because the otolith of *Cyttomimus* could function perfectly as a plesiomorphic sister group for the zeid family. The protruding collicula, the dorsal area and the swollen upper central part of the ventral area are almost identical in both groups. Moreover, the anterior and posterior constrictions in the ventral margin of *Cyttomimus* strongly appear to be precursors of the ventral lobe-like expansions of zeid otoliths.

In zeids, the otoliths of *Zeus* and *Zenopsis,* based upon their tri-lobed shape, comprise an unambiguous homogeneous group, which is incontestably the most apomorphic zeiform clade.

The most problematic cases are clearly the plesiomorphic otoliths of the genera *Parazen* and *Zenion*. Both of these genera were separately and relatively deeply nested in the osteology-based phylogeny of zeiforms by TYLER *et al.* (2003). SCHWARZHANS (1996), using otolith information, proposed a cladogram in which he grouped *Parazen* and *Zenion* as the plesiomorphic sister group of all other zeiforms. Johnson and PATTERSON (1993) previously had suggested that *Zenion* and *Parazen* might be the more morphologically primitive zeiform taxa; the otolith data presented herein are in agreement with that proposal.

The phylogenetic placement of *Parazen* as sister to [*Cyttopsis* + *Stethopristis*] in parazenids and *Zenion* as sister to [*Capromimus* + *Cytomimus*] in zeniontids, however, is logically consistent within both families. A plausible explanation is that in both of these families the genera with a plesiomorphic otolith type represent independent retention of the ancestral condition: they may be surviving taxa with the plesiomorphic otolith type, whereas in other zeiform families, such forms are extinct, or not yet discovered. We note that TYLER and SANTINI (2005) analyzed all of the fossil and extant zeiform and zeomorph-like fishes (dating to the Upper Cretaceous) using a large osteological data set. That study also called into question several aspects of the monophyly and inclusiveness of the Parazenidae and Zeniontidae. Additional study is necessary to resolve these issues.

In tetraodontiforms, the otoliths exhibit a broad scope of

very different morphologies. The most characteristic types are herein (Fig. 10) placed beside the phylogenetic hypothesis of SANTINI & TYLER (2003) for ease of comparison.

All tetraodontiform otoliths have, at least in some measure, an antero-posterior constriction along the midline of the otoliths, a synapomorphy shared with *Capros* and with zeiforms.

The position of **triacanthodids** and **triacanthids** as the most plesiomorphic families of tetraodontiforms is confirmed by their otolith morphology. Triacanthodid and triacanthid otoliths exhibit a round, deep body with a sulcus delimited by well-structured cristae, which are also found in many beryciforms and caproids.

In **balistids**, three different clusters can easily be recognized by otolith morphology (see descriptive section): (1) *Balistapus, Melichthys, Odonus* and *Xanthichthys*; (2) *Balistes, Balistoides, Canthidermis, Pseudobalistes* and *Rhinecanthus*; and (3) *Sufflamen*. Among these, the "*Balistapus* group" apparently is the most plesiomorphic because of their regular outline and their well-marked cristae; however, the extreme thickening of their otoliths is an apomorphic condition. The other two groups have only very marked autapomorphic features.

We have more confidence in the phylogenetic validity of these three groups than in the groups hypothesized with uncertainty by TYLER (1980, p. 121), who stated that the generic relationships of balistids were not especially clear on the basis of his osteological analysis. The otolith data also conflicts with the composition of the three groups into which MATSUURA (1979) divided the balistids.

Monacanthid otoliths seem to indicate that this is a very homogeneous group. For example, otolith morphologies like that of *Anacanthus* can be considered to be plesiomorphic, whereas extremely slender otoliths, such as in *Chaetodermis* (Pl. 10, Fig. 12) and *Stephanolepis* (Pl. 12, Fig. 1), are considered to be the most derived. The available otolith material does not allow for a detailed analysis that would lead to a clustering of taxa within this large family (about 107 species).

Similarities among **aracanid** and **ostraciid** otoliths indicate these taxa form a homogeneous group, but the material available to us does not allow for a detailed analysis. The two families may be distinguished, however, by the presence of a well-developed crista superior in all of the examined aracanids. This feature is considered to be plesiomorphic relative to ostraciids, in which the crista tends to become obsolete.

The single extant species of **triodontid** is characterized only by autapomorphic otolith features. One should note, however, the considerable similarity in outline of *Triodon* otoliths and those of tetraodontids, such as *Lagocephalus* (Pl. 15, Figs. 4–6 and Figs. 8–9). The otolith similarities agree with their placement in the cladogram.

Tetraodontid otoliths, although united by a synapomorphy (the presence of a very salient crista inferior) with diodontids, exhibit considerable diversity. On the basis of the limited number of species examined (the family has about 185 species), at least three clusters can be recognized: relatively plesiomorphic tetraodontid otoliths are found in *Amblyrhynchotes, Contusus, Sphoeroides* and *Takifugu*, whereas *Tetraodon* and *Canthigaster* represent two different groups that are easily distinguished by their otoliths.

Diodontid otoliths, with their deep funnel-like sulcus and their salient crystal needles, represent an extremely derived apomorphic otolith type that is easy to recognize but is not easy to interpret. The diodontid condition can be best understood by comparison with otoliths of the tetraodontid genus *Tetraodon*, which can be considered to be their plesiomorphic counterpart. This confirms their position in the cladogram, where tetraodontids and diodontids appear as, respectively, plesiomorphic and apomorphic sister groups.

Molids are known only by the chalky dust in the *Mola* labyrinth and by a single *Ranzania* otolith; thus, one can only comment that it is highly modified but compatible with tetraodontiform otolith morphology, with similarities to diodontids in their crystalline needle-like extrusions.

Otolith-based evaluation of the affinities of the zeiform-tetraodontiform group to other fish taxa

As previously stated under the heading "Characterization of caproid, zeiform and tetraodontiform otoliths," caproids (and especially *Capros*) appear to be the best candidate for a plesiomorphic sister group of the zeiforms and tetraodontiforms, with which they share the synapomorphy of antero-posterior constriction of the otoliths. In addition to this, both groups share various similarities in their overall appearance, such as the very high bodies of their otoliths, and the often strongly developed posterodorsal angle, but such features cannot be considered to be synapomorphies.

Various other groups have also been suggested as relatives of zeiforms or tetraodontiforms. For example, HOLT (1894), THILO (1901) and BOULENGER (1902) suggested that flatfishes were related to zeiforms. NORMAN (1934) rejected such a relationship, and furthermore the otolith morphology does not provide any evidence for such a relationship.

REGAN (1910) proposed a close relationship between zeiforms (his Zeidae) and caproids (his Caproidae), recognized them as the order Zeomorphi, and related them to berycoids. PATTERSON (1968) regarded zeiforms (including caproids) as the apomorphic sister group to berycoids (including stephanoberyciforms). WINTERBOTTOM (1974) suggested a possible zeiform-tetraodontiform relationship. ROSEN (1984) provided evidence for a group comprising caproids, tetraodontiforms and zeiforms, with the latter two being sister groups. JOHNSON AND PATTERSON (1993) suggested that zeiforms (excluding caproids) are the sister group of beryciforms (excluding stephanoberyciforms) plus percomorphs.

The recognition of caproids as the plesiomorphic sister group of zeiforms + tetraodontiforms is supported by their otolith morphology.

Concerning tetraodontiforms, the perciform acanthuroid fishes often have been considered to be likely relatives of tetraodontiforms (e.g., WINTERBOTTOM, 1974, TYLER, 1968 and 1980). Because there is no single reference for acanthuroid otoliths, we provide figures of some in Pl. 19 and Pl. 20. A glance at these plates indicates that acanthuroids have a rather conservative, plesiomorphic percoid otolith

type; compare these, for example, with *Morone* in Fig. 6. This is especially true for the genera *Acanthurus, Ctenochaetus, Zebrasoma* and *Paracanthurus*. The acanthurid genus *Naso* (a phylogenetically basal lineage) and the siganids have a more specialized otolith type, but basically such otoliths remain of the percoid type. The acanthuroid *Zanclus* (Pl. 20, Fig. 6) has a highly derived otolith, but it still agrees with a modified percoid type. All this indicates that, based upon otolith morphology, acanthuroids are very poor candidates as tetraodontiform relatives. We note in passing that NOLF (1985, fig. 75, p. 100) erroneously figured a *Heniochus* (Chaetodontidae) otolith under the name of *Zanclus* (Zanclidae).

This otolith-based search for close relatives of zeiforms and tetraodontiforms is concluded with a figure (Fig. 11) representing otoliths of two taxa, *Macrorhamphosus* (Gasterosteiformes, Syngnathoidei) and *Caristius* (Percoidei), that have never been suggested as possible candidates for such a relationship. Nonetheless, the otoliths of these two taxa are much more similar to those of zeiforms and tetraodontiforms than they are to those of other fishes in the orders in which they are currently placed. They should be considered in future morphological studies of the higher relationships of these groups.

Acknowledgments

The present paper could only be accomplished in a reasonable amount of time because of the existence of a large collection of otoliths of Recent fishes at the Institut royal des Sciences naturelles de Belgique (IRSNB). This collection was amassed during the last forty years, with the collaboration of many people who sent material to the first-listed author or who allowed for the dissection of otoliths from their museum specimens. In obtaining the material used for the present study, we especially appreciate the help of the following people: John E. Fitch (California), Keiki Iizuka (Japan), A. Johnston (New Zealand), Tomasz Linkowski (Poland), Nathalie Mémoire (Bordeaux), Nigel R. Merrett (England), Filip Moreaux (Ronse), Alain Philippart and Christian Willig (Aquarium Nancy), Bob Shipp (Alabama), Werner Schwarzhans (Hamburg), Bernard Séret (Paris), Fred Stinton (Bournemouth).

An important series of additional otolith material from the collection of the late John Fitch, presently in the collections of the Los Angeles County Museum (LACM), was sent on loan to IRSNB by Jeffrey Seigel, and some interesting London Clay fossils were brought to our attention by Adrian Rundle (London).

We also thank Diane M. Tyler for editorial help with several drafts of this manuscript; John Lundberg and Mark Sabaj for help in examining specimens at the Academy of Natural Sciences of Philadelphia; James DiLoreto, Smithsonian Institution, for help with transmitting and printing electronic illustrations and Anne Wauters (IRSNB), who helped in preparing the drawings..

The first author thanks the Smithsonian Institution, Washington, D.C., for two short-term visitor grants (in 1997 and 2000), during which stays the present study was initiated.

Literature Cited

ASSIS, C.A., 2003. The lagenar otoliths of teleosts: their morphology and its application in species identification, phylogeny and systematics. *Journal of Fish Biology*, 2003 (3): 1268-1295.

ASSIS, C.A., 2004. Guia para a identificaçao de algumas familias de peixes osseos de Portugal continental, através da morfologia dos seus otolitos sagitta. Camara Municipal de Cascais, Museu do Mare Rei D. Carlos, 190 pp.

ASSIS, C.A., 2005. The utricular otoliths, lapili, of teleosts: their morphology and relevance for species identification and systematic studies. *Scientia Marina*, 69 (2): 259-273.

BOULENGER, G.A., 1902. Notes on the classification of teleostean fishes, IV: On the systematic position of the Pleuronectidae. *Annals and Magazine of Natural History*, series 7, 16: 295-304.

CAMPANA, S.E., 2004. Photographic atlas of fish otoliths of the northwest Atlantic Ocean. *Canadian Special Publication of Fisheries and Aquatic Sciences,* 133: 1–284.

CHAINE, J. 1956. Recherches sur les otolithes des poissons. Etude descriptive et comparative de la sagitta des téléostéens (suite). *Bulletin du Centre d'Etudes et de Recherches Scientifiques Biarritz,* 1 (2): 159–275.

CHAINE, J. 1958. Recherches sur les otolithes des poissons. Etude descriptive et comparative de la sagitta des téléostéens (suite). *Bulletin du Centre d'Etudes et de Recherches Scientifiques Biarritz,* 2 (2): 141–241.

CHAINE, J. & DUVERGIER, J., 1934. Recherches sur les otolithes des poisssons. Etude descriptive et comparative de la sagitta des téléostéens. *Actes de la Société Linnéenne de Bordeaux,* 86: 1–254.

FROST, G.A., 1927. A comparative study of the otoliths of the neopterygian fishes, pt. VII. *Annals and Magazine of Natural History,* (9) 19: 439–445.

FROST, G.A., 1930. A comparative study of the otoliths of the neopterygian fishes, pt. XIII. *Annals and Magazine of Natural History,* (10) 5: 231–239.

GON, O. & HEEMSTRA, P.C. (Editors), 1990. Fishes of the Southern Ocean. J.L.B. Smith Institute of Ichthyology, Grahamstown, 462 pp.

HÄRKÖNEN, T., 1986. Guide to the otoliths of the bony fishes of the northeast Atlantic. Danbiu ApS. Biological Consultants, Hellrup, Denmark, xi + 256 pp.

HOLT, E.W.L., 1894. Studies in teleostean morphology from the Marine Laboratory at Cleethorpes. *Proceedings of the Zoological Society of London*, 1894 (3): 413-446.

HUYGHEBAERT, B. & NOLF, D., 1979. Otolithes de téléostéens et biostratigraphie des Sables de Zonderschot (Miocène moyen) de la Belgique. *Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie,* 16 (2): 59–100.

JOHNSON, G.D. & PATTERSON, C., 1993. Percomorph phylogeny: A survey of acanthomorphs and a new proposal. *Bulletin of Marine Science*, 52 (1): 554–626.

KOTLYAR, A.N., 2001. A rare zeid species - *Parazen pacificus:* osteology, systematics, and distribution (Parazenidae, Zeiformes). *Journal of Ichthyology,* 41 (9): 687–697.

KOTLYAR, A.N. & PARIN, N.V., 1990. Otoliths and age of bottom and near bottom fishes of the Nazca and Sala y Comez submarine ridges. *Akademia Nauk SSSR, Trudy Institut Okeanol.*, **125**: 97–126. (in Russian).

MATSUURA, K., 1979. Phylogeny of the superfamily Balistoidea (Pisces: Tetraodontiformes). *Memoirs of the Faculty of Fisheries, Hokkaido University*, 26 (1-2): 49-169.

NELSON, J.S., 2006. Fishes of the world, Fourth edition. John Wiley & Sons, USA, 601 pp.

NOLF, D., 1985. Otolithi Piscium. *In*: H.P. Schultze (ed.). Handbook of Paleoichthyology, 10. Fischer, Stuttgart and New York, pp. 1–145.

NOLF, D., 1993. A survey of perciform otoliths and their interest for phylogenetic analysis, with an iconographical synopsis of the Percoidei. *Bulletin of Marine Science,* 52 (1): 220–239.

NOLF, D., 2003. Fish otoliths from the Santonian of the Pyrenean realm, and an overview of all otolith-documented North Atlantic Late Cretaceous teleosts. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, 73: 155-173.

NOLF, D. & CAPPETTA, H., 1989. Otolithes de poissons pliocènes du Sud-Est de la France. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre,* 58 (1988): 209–271.

NOLF, D. & LAPIERRE, H. 1979. Otolithes de poissons nouveaux ou peu connus du Calcaire Grossier et de la Formation d'Auvers (Eocène du Bassin parisien). *Bulletin du Museum National d'Histoire Naturelle, Paris*, 4, 1, C, 2: 79-125.

NOLF, D. & BRZOBOHATY, R., 2002 . Otolithes de poissons du Paléocanyon de Saubrigues (Chattien à Langhien), Aquitaine méridionale, France. *Revue de Micropaléontologie*, 45 (4): 261-296.

NOLF, D. & STEURBAUT, E., 2004. Otolithes de poissons de l'Oligocène inférieur du Bassin liguro-piémontais oriental, Italie. *Rivista Piemontese di Storia naturale*, 25: 21-68.

NORMAN, J.R., 1934. A systematic monograph of the flatfishes (Heterosomata), vol. 1: Psettodidae, Bothidae, Pleuronectidae. The Trustees of the British Museum, London, 459 pp.

OHE, F., 1985. Marine fish-otoliths of Japan. *Special Volume of Bulletin (Earth-Science), The Senior High School Attached to the Aichi University of Education,* 184 pp.

PATTERSON, C., 1968. The caudal skeleton in Mesozoic acanthopterygian fishes. *Bulletin of the British Museum (Natural History), Geology,* 17 (2): 47–102.

PATTERSON, 1993. An overview of the early fossil record of acanthomorphs. Bulletin of Marine Science, 52 (1): 29-59.

QUERO, J.C., PORCHE, P. & VAYNE, J.J., 2003. Guide des poissons de l'Atlantique européen. Delachaux et Nestlé, Lonay (Suisse), 465 pp.

REGAN, C.T., 1910. The anatomy and classification of the teleostean fishes of the order Zeomorphi. *Annals and Magazine of Natural History*, series 8, 6: 481-484.

RIVATON, J. & BOURRET, P., 1999. Les otolithes des poissons de l'Indo-Pacifique. *Documents scientifiques et techniques, Institut de recherche pour le développement, Nouméa,* 2 (2): 1–378.

ROSEN, D.E., 1984. Zeiforms as primitive plectognath fishes. *American Museum Novitates,* 2782: 1–38.

SANTINI, F. & TYLER, J., 2002. Phylogeny and biogeography of the extant species of triplespine fishes (Triacanthidae, Tetraodontiformes). *Zoologica Scripta,* 31 (4): 321–330.

SANTINI, F. & TYLER, J.C., 2003. A phylogeny of the families of fossil and extant tetraodontiform fishes (Acanthomorpha, Tetraodontiformes), Upper Cretaceous to Recent. *Zoological Journal of the Linnean Society,* 139: 565–617.

SCHMIDT, W., 1968. Vergleichend morphologische Studie über die Otolithen mariner Knochenfische. *Archiv für Fischereiwissenschaft,* 19 (1): 1–96.

SCHWARZHANS, W., 1980. Die tertiäre Teleosteer-Fauna Neuseelands, rekonstruiert anhand von Otolithen. *Berliner geowissenschaftliche Abhandlungen,* A, 26: 1–211.

SCHWARZHANS, W., 1996. Otoliths from the Maastrichtian of Bavaria and their evolutionary significance. *In* Aratia, G. & Viohl, G. (editors): Mesozoic Fishes - Systematics & Paleoecology, pp. 433–459. Verlag Pfeil, München.

SMALE, M.J., WATSON, G. & HECHT, T., 1995. Otolith atlas of South African marine fishes. *Ichthyological Monographs,* 1: 1–253.

STEURBAUT, E.,1979. Les otolithes de Téléostéens des Marnes de Saubrigues (Miocéne d'Aquitaine méridionale, France). *Palaeontographica*, A, 166: 50-91.

STINTON, F.C., 1967. The otoliths of the teleostean fish *Antigonia capros* and their taxonomic significance. *Bocagiana, Museu Municipal do Funchal,* 8: 1–7.

STINTON, F.C., 1978. Fish otoliths from the English Eocene, III. *Palaeontographical Society Monographs*, 555: 127-189.

THILO, O., 1901. Die Vorfahren der Schollen. *Bulletin de l'Académie Impériale des Sciences de St. Pétersbourg*, series 5, 14 (3): 315-350.

TYLER, J.C., 1968. A monograph on plectognath fishes of the superfamily Triacanthoidea. *The Academy of Natural Sciences of Philadelphia, Monograph,* 16:1–364.

TYLER, J.C., 1980. Osteology, phylogeny and higher classification of the fishes of the order Plectognathi (Tetraodontiformes). *NOAA Technical Report, National Marine Fisheries Circular,* 434: 1–422.

TYLER, J.C., O'TOOLE, B. & WINTERBOTTOM, R., 2003. Phylogeny of the genera and families of Zeiform fishes, with comments on their relationships with tetraodontiforms and caproids. *Smithsonian Contributions to Zoology,* 618: 1–110.

TYLER, J.C. & SANTINI, F., 2005. A phylogeny of the fossil and extant zeiform-like fishes, Upper Cretaceous to Recent, with comments on the putative zeomorph clade (Acanthomorpha). *Zoologica Scripta,* 34 (2): 157–175.

WINTERBOTTOM, R., 1974. The familial phylogeny of the Tetraodontiformes (Acanthopterygii: Pisces) as evidenced by their comparative myology. *Smithsonian Contributions to Zoology,* 155: 1–201.

Dirk NOLF
Koninklijk Belgisch Instituut voor Natuurwetenschappen
Vautierstraat 29, B 1000 Brussel, België
email: dirk.nolf@natuurwetenschappen.be

James C. TYLER
National Museum of Natural History, Smithsonian Institution (MRC-106), Washington D.C. 20560, USA
email: tylerj@si.edu

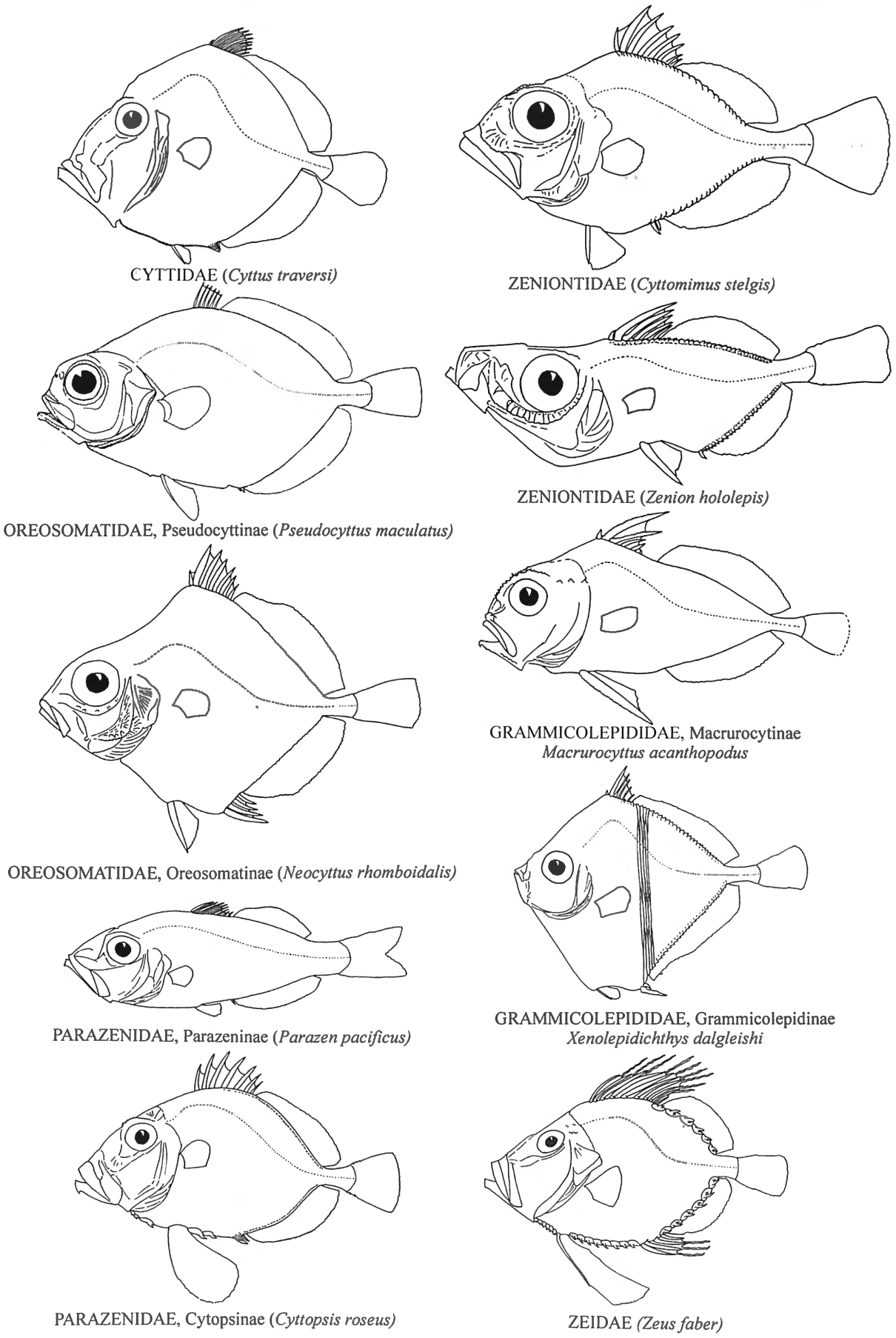


Fig. 1. A pictorial overview of fishes in the Recent families and subfamilies of zeiform fishes (after TYLER *et al.*, 2003).

T 2 Tetraodontiformes

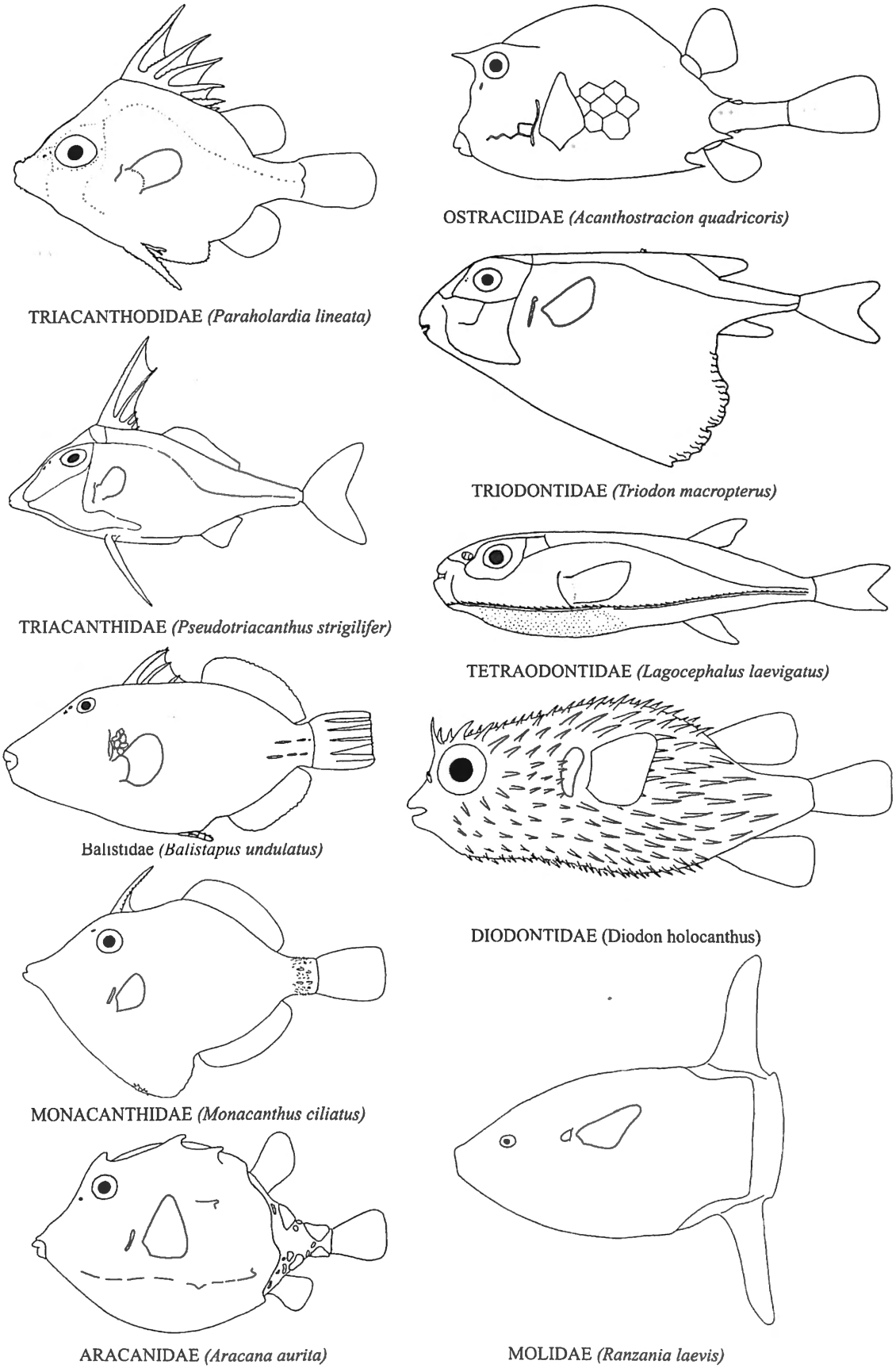


Fig. 2. A pictorial overview of fishes in the Recent families of tetraodontiform fishes (after TYLER, 1980).

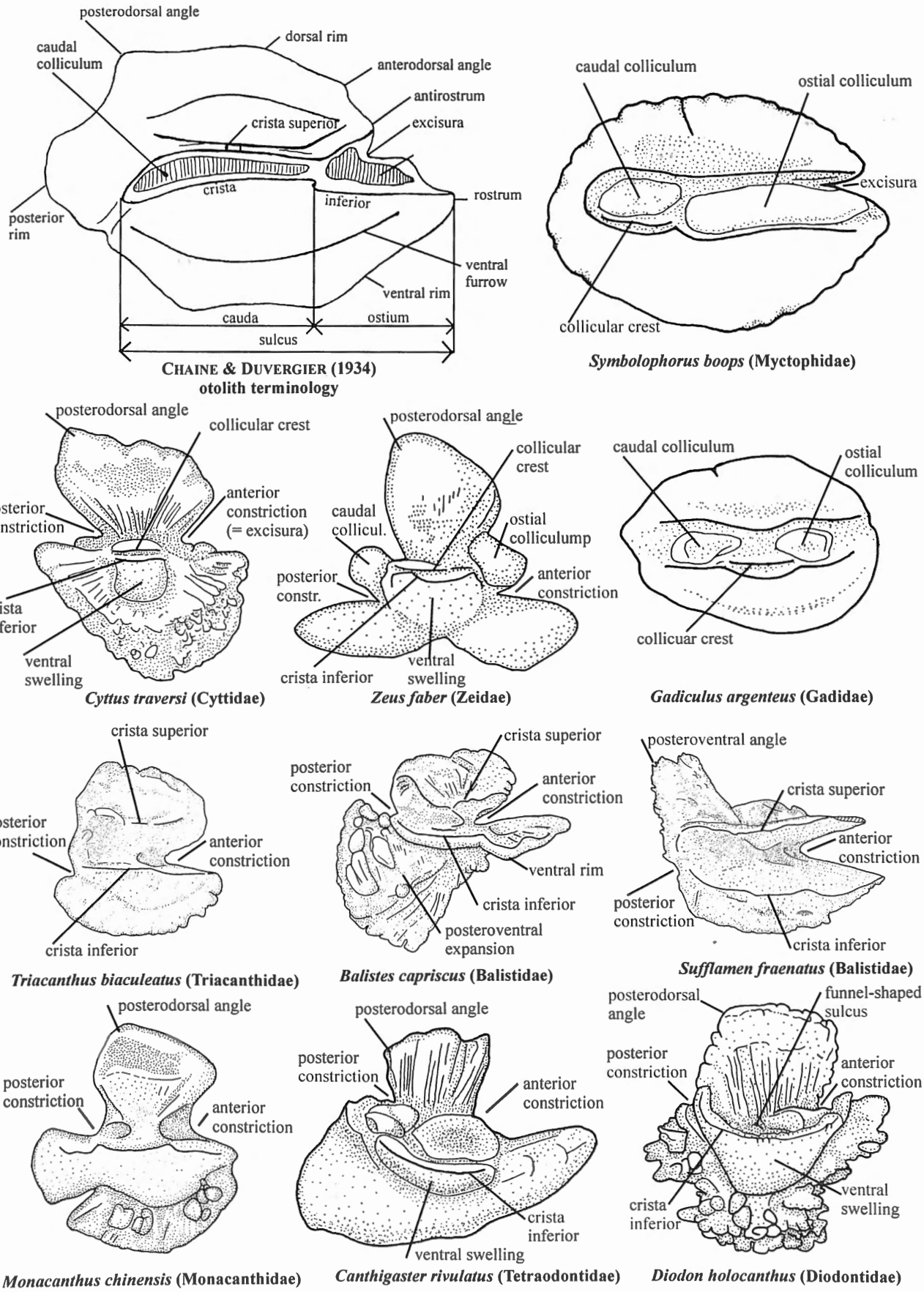


Fig. 3. Morphological nomenclature of otoliths, with examples in zeiforms, tetraodontiforms, myctophids and gadids.

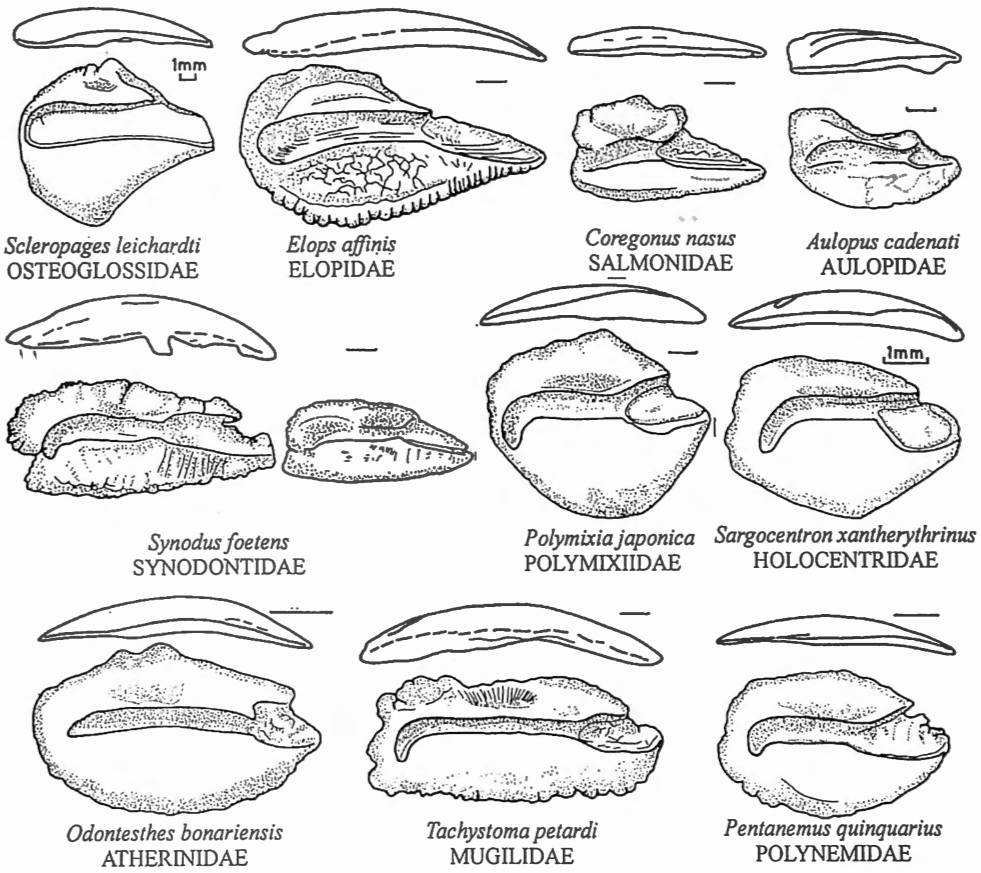


Fig. 4. Various types of relatively plesiomorphic teleostean otoliths.

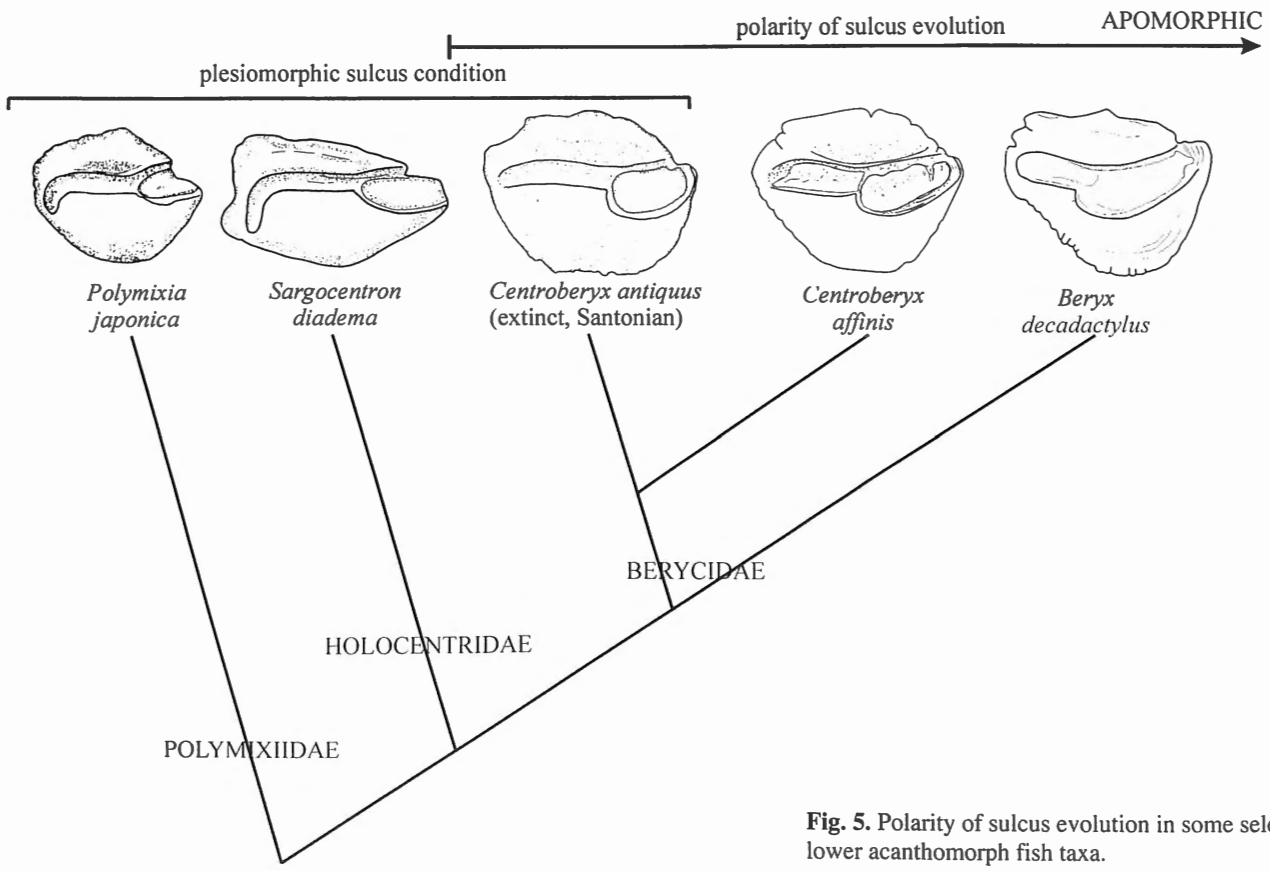


Fig. 5. Polarity of sulcus evolution in some selected lower acanthomorph fish taxa.

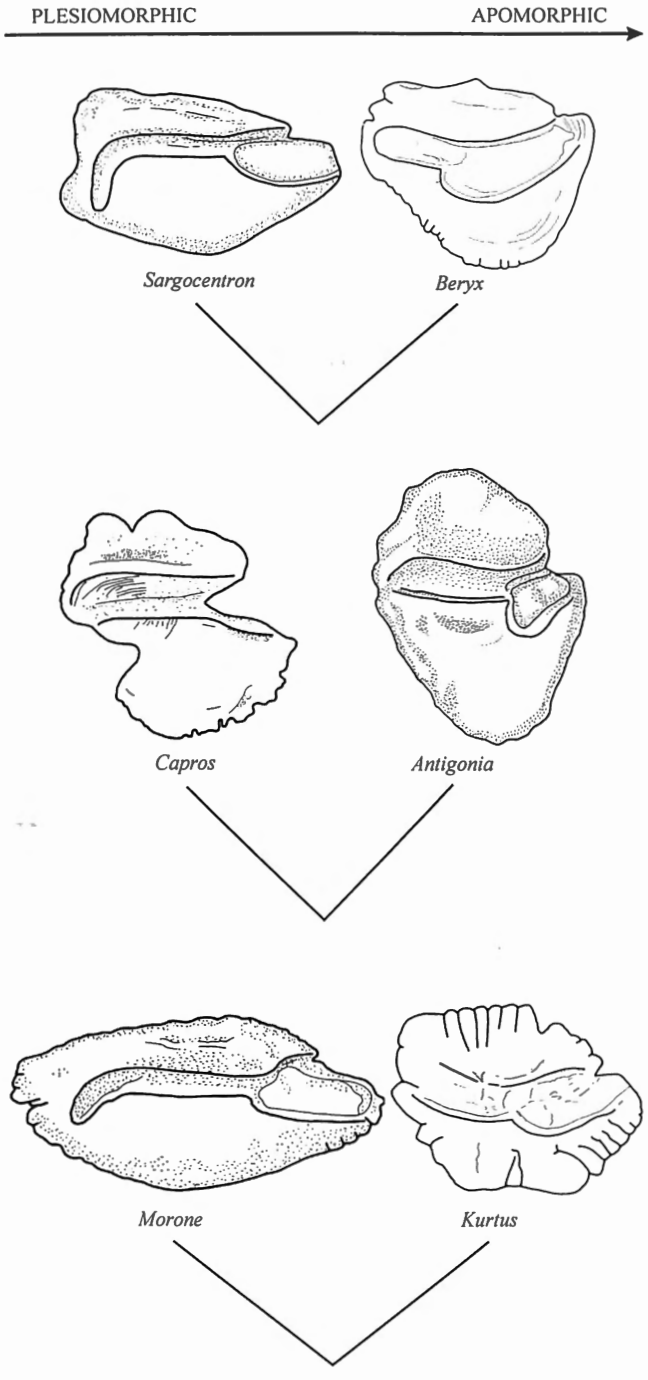


Fig. 6. Plesiomorphic (to left) versus derived (to right) morphology for, respectively from top to bottom, beryciforms, caproids and percoids.

Appendix: Geographic origin and depository of the figured specimens

Institutional abbreviations:
ANSP = Academy of Natural Sciences of Philadelphia;
IRSNB = Institut royal des Sciences naturelles de Belgique;
MGUH = Geological Museum, University of Copenhagen;
MHNB = Musée d'Histoire naturelle, Bordeaux;
USNM = National Museum of Natural History, Smithsonian Institution.

Perusing the following list, one may be surprised that much of the locality data is vague. As previously mentioned, otolith dissection in tetraodontiforms causes severe external damage to the specimens; thus, it is rarely performed on museum materials. Consequently, almost all of the tetraodontiform otoliths for this study were obtained from preserved fishes from the aquarium trade, where usually no trustworthy locality data are available. In such cases, the general distribution of the species is provided in parentheses.

Acanthostracion quadricornis, no locality data, Aquarium? (tropical W Atlantic and Caribbean), coll. LACM.
Acanthurus monroviae, W Africa, coll. IRSNB, leg. Stinton.
Acanthurus nigrofuscus, New Caledonia, coll. IRSNB, leg. Séret.
Allocyttus folletti, off California, coll. IRSNB, leg. Fitch.
Allocyttus niger, off New Zealand, coll. IRSNB, leg. Linkowski.
Allocyttus verrucosus, SW Atlantic, coll. IRSNB, leg. Karrer, via Fitch.
Allomycterus whitleyi, off New Zealand, coll. IRSNB, leg. Johnston.
Aluterus monoceros, no locality data (circumtropical), coll. LACM 56211.001, leg. Fitch.
Aluterus schoepfi, no locality data (W Atlantic, from Nova Scotia to Brazil), coll. LACM 56211.002, leg. Berry.
Aluterus scriptus, Aquarium Nouméa, New Caledonia, coll. IRSNB, leg. Séret.
Amblyrhynchotes honckenii, off South Africa, redrawn after SMALE *et al.*, 1995.
Anacanthus barbatus, off Australia, coll. LACM 56211.003, leg. Coates.
Anoplocapros inermis, off Australia, coll. LACM 56233.001, leg. Lavenberg.
Anoplocapros robustus, off Sydney, Australia, coll. LACM 56233.002, leg. Fitch.
Antigonia capros, off New Caledonia, coll. IRSNB, leg. Séret
Antigonia malayana, off New Caledonia, coll. IRSNB, leg. Séret.
Aracana ornata, off Adelaide, Australia, coll. LACM.
Arothron hispidus, Aquarium Nouméa, New Caledonia, coll. IRSNB, leg. Séret.
Arothron immaculatus, Taiwan, coll. IRSNB, leg. Stinton.
Arothron mappa, Aquarium Nancy (Indo-W Pacific), coll. IRSNB.
Aulopus cadenati, off Congo, coll. IRSNB.
Balistapus undulatus, Aquarium (Indo-W Pacific), coll. IRSNB.
Balistes capriscus, off Dauphin Island, Alabama, coll. IRSNB, leg. Shipp.
Balistes polylepis, off California, coll. LACM 56211.004, leg. Fitch.
Balistes vetula, Caribbean, locality unknown (Caribbean), coll. LACM 56211.005 (Pl. 8, Figs 7 and 9) and aquarium, coll. IRSNB (Pl. 8, Fig. 8).
Balistoides viridescens, E Africa, coll. IRSNB.
Beryx decadactylus (Fig. 6), Madeira, coll. IRSNB.
Cantherhines dumerilii, locality unknown (from E Africa to Mexico; W Pacific), LACM 56211.006.
Cantherhines macrocerus, locality unknown: «tropical W Atlantic», coll. LACM 56211.007.
Cantherhines sandwichiensis, off Philippines, coll. IRSNB, leg. Stinton.
Canthidermis maculatus, off California, coll. LACM 56211.016, leg. Fitch.
Canthigaster amboinensis, East Indies, coll. IRSNB, leg. Stinton.
Canthigaster coronata, off Hawaii, coll. IRSNB, leg. Stinton.
Canthigaster jactator, off Hawaii, coll. LACM 56226.001, leg. Baldwin.
Canthigaster margaritata, Aquarium (Indo-W Pacific), coll. IRSNB, leg. Stinton.
Canthigaster punctatissimus, Pacific coast of Mexico, coll. LACM 56211.008, leg. Fitch.
Canthigaster rivulatus, Hong Kong fish market, coll. IRSNB, leg. Stinton.
Canthigaster solandri, Aquarium (Micronesia), coll. IRSNB.
Capromimus abbreviatus, off Mahia Peninsula, New Zealand, coll. IRSNB, leg. Johnston.
Capros aper, locality unknown (Gulf of Biscaye?), coll. Chaine in IRSNB.

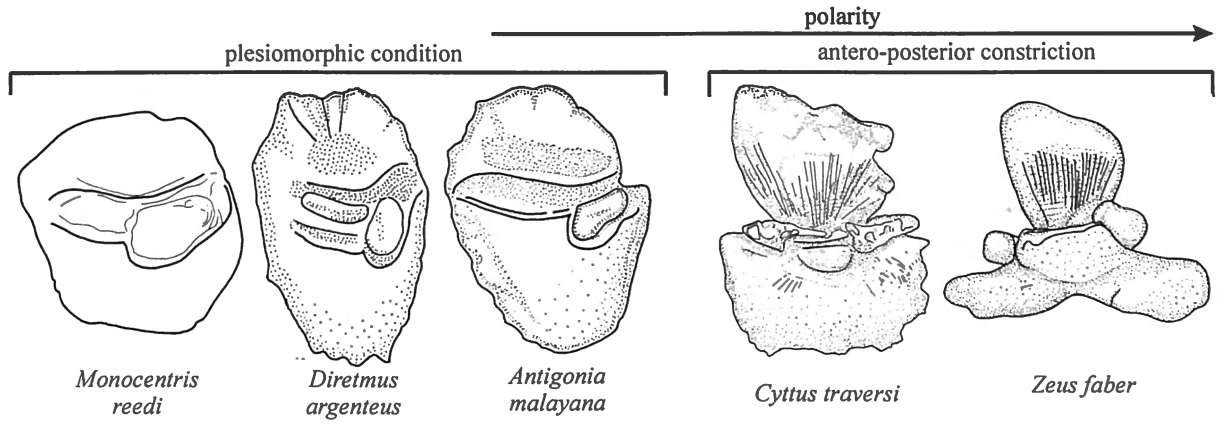


Fig. 7. Comparison of beryciform and zeiform otoliths and illustration of zeiform synapomorphies: antero-posterior constriction along the midline and swelling of the central upper portion of the ventral area.

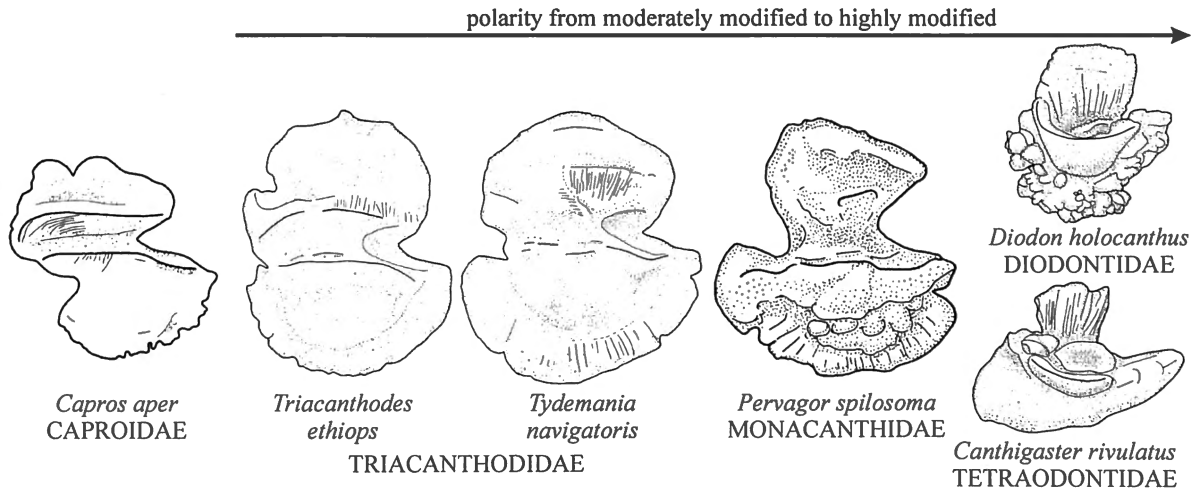


Fig. 8. Polarity from moderately modified to highly modified otolith morphology in *Capros* and selected tetraodontiforms.

Caristius macropus, Atlantic, 45°16'N 48°08'W, coll. Schwarzhans.
Centroberyx affinis, off New Zealand, coll. IRSNB.
Centroberyx antiquus, extinct, Upper Cretaceous, Santonian, S of Tremp, Spain.
Chaetodermis penicilligerus, Aquarium Nancy (Malaysia, Indonesia, Australia), coll. IRSNB.
Chilomycterus affinis, Philippines, coll. IRSNB, leg. Stinton.
Chilomycterus schoepfii, locality unknown (Florida?), LACM 56211.009, leg. Berry.
Contusus richei, off Gisborne, New Zealand, coll. IRSNB, leg. Johnston.
Coregonus nasus, N Canada, freshwater, coll. IRSNB.
Ctaenochaetus strigosus, off Gisborne, New Zealand, coll. IRSNB, leg. Stinton.
Cyclichthys orbicularis, off Hawaii, coll. IRSNB, leg. Stinton.
Cyttomimus stelgis, of Ile des Pins, New Caledonia, coll. IRSNB, leg. Séret.
Cyttopsis cypho, off NW Australia, coll. IRSNB, leg. Séret.
Cyttopsis roseus, locality unknown (Gulf of Biscaye?), coll. Chaine in MHNB.
Cyttus australis, off Aukland, new Zealand, coll. IRSNB, from USNM 177 084.
Cyttus novaezelandiae, off Mahia Peninsula, New Zealand, coll. IRSNB, leg. Johnston.
Cyttus traversi, off New Zealand, coll. IRSNB.
Elops affinis, off California, coll. IRSNB, leg. Fitch.
Dicotylichthys punctulatus, Aquarium (Indian Ocean), coll. IRSNB, leg. Stinton.
Diodon holocanthus, Hong Kong fish market, coll. IRSNB, leg. Stinton.
Diodon hystrix, off New Caledonia, coll. IRSNB, leg. Séret
Diodon nicthemerus, off Adelaide, S Australia, coll. LACM 26225.001, leg. Fitch
Diretmus argenteus, Indian Ocean, 9°34'S 59°55'E, coll. IRSNB from USNM 308026
Grammicolepis brachiusculus, off New Caledonia, coll. IRSNB, leg. Merrett.
Kentrocapros aculeatus, Sagami Bay, Japan, coll. IRSNB, leg. Stinton.
Kurtus guliveri, off Bivak Island, coll. IRSNB.
Lactophrys trigonus, locality unknown (tropical W Atlantic), coll. LACM 56211.012, leg. Fitch.
Lactoria fornasini, off south Africa, coll. IRSNB, leg. Stinton.
Lagocephalus lunaris, Hong Kong fish market, coll. IRSNB, leg. Stinton.
Lagocephalus scleratus, off New Caledonia, coll. IRSNB, leg. Séret.
Macrorhamphosus scopelax, off California, coll. IRSNB, leg. Fitch.
Melichthys niger, Pacific, off Socorro, Mexico, coll. LACM 56229.011, leg. Fitch.

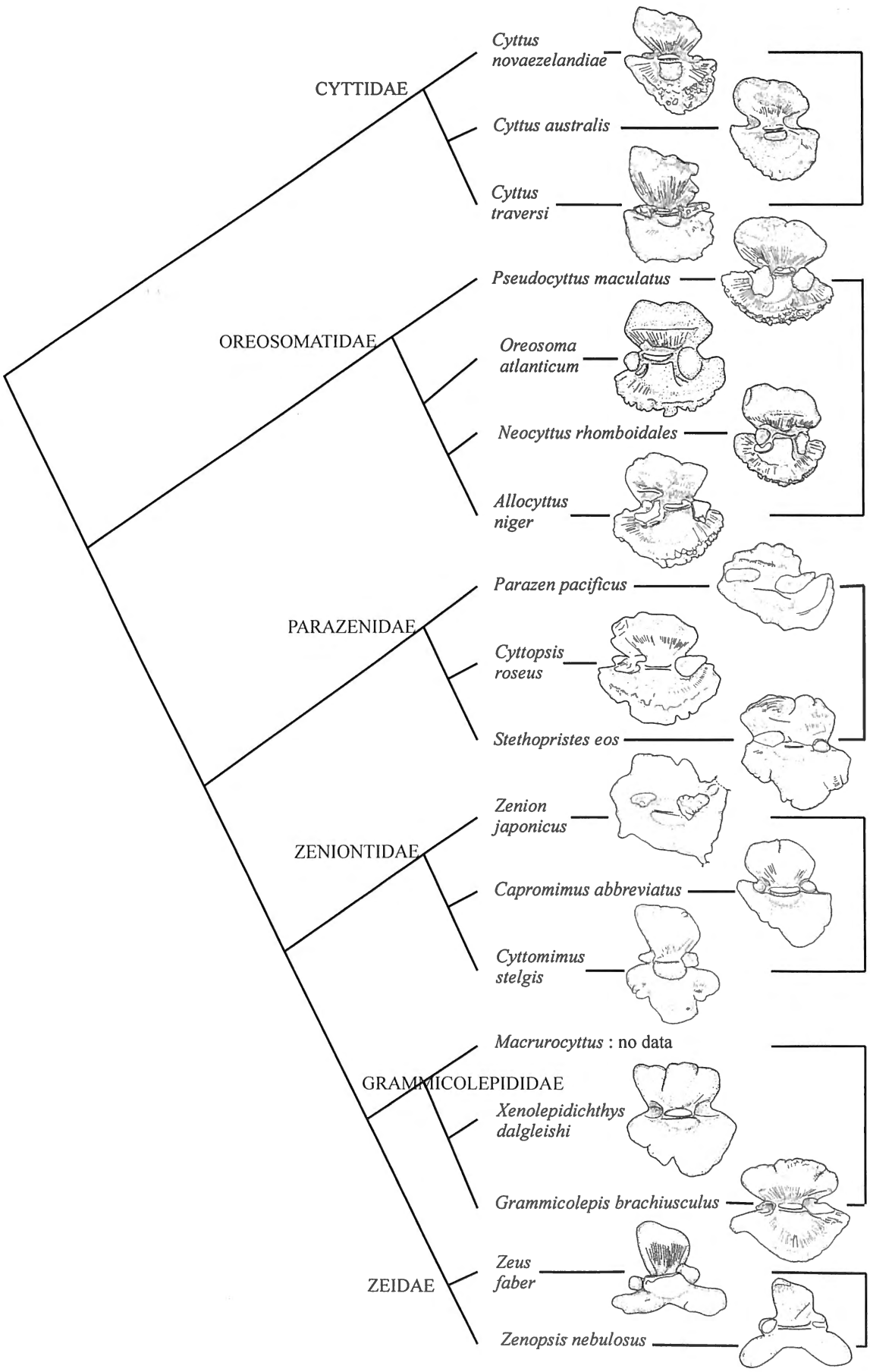


Fig. 9. Otolith-based testing of TYLER, O'TOOLE & WINTERBOTTOM's (2003) cladogram of zeiform interrelationships (their fig. 4).

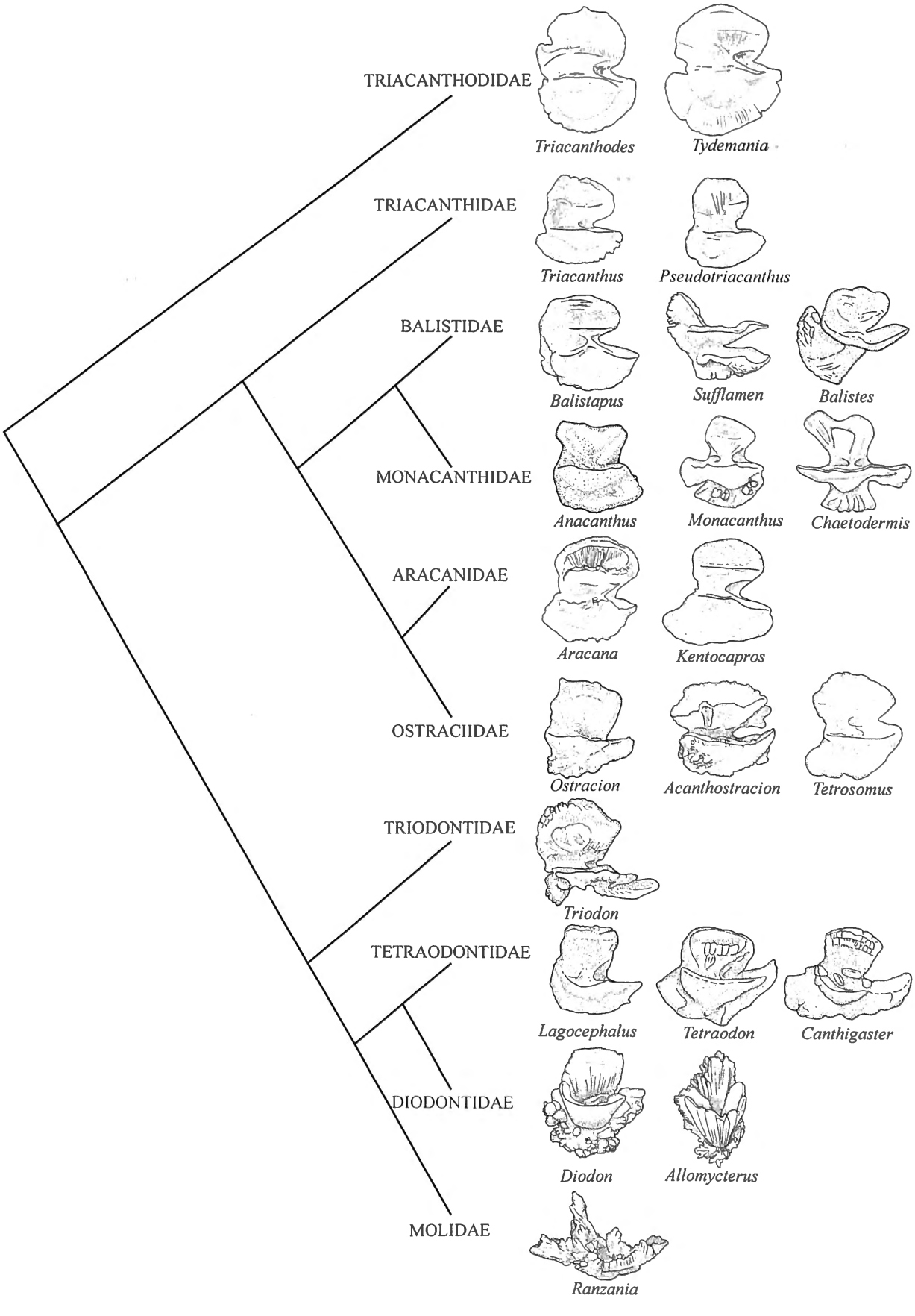
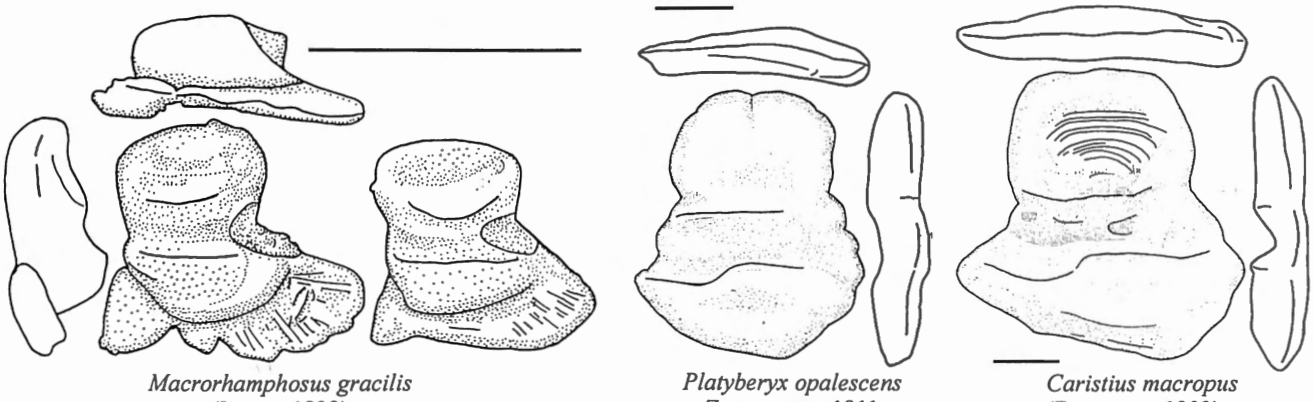


Fig. 10. Otolith-based testing of SANTINI & TYLER's (2003) cladogram of Recent tetraodontiform interrelationships (their fig. 5, only extant taxa shown here).



Macrorhamphosus gracilis (LOWE, 1839) MACRORHAMPHOSIDAE

Platyberyx opalescens ZUGMAYER, 1911

Caristius macropus (BELLOTTI, 1903) CARISTIIDAE

Fig. 11. Otoliths of Macrorhamphosidae (Gasterosteiformes, Syngnathoidei) and Caristiidae (Percoidei).

Melichthys vidua, off Philippine islands (Pl. 7, Fig. 5), coll. IRSNB and off Johnston Island (Pl. 7, Fig. 6), coll. LACM 56230.001, leg. Baldwin.
Meuschenia australis, off New Zealand, coll. IRSNB.
Meuschenia scaber, Tasman Bay, New Zealand, coll. IRSNB.
Monacanthus chinensis, off Australia, LACM 56212.005, leg. Coates.
Monacanthus tuckeri, Aquarium (West Indies), coll. IRSNB, leg. Stinton.
Monocentris reedi, off San Felix Island (Chile), coll. IRSNB, leg. Fitch.
Morone labrax, loc. unknown (Gulf of Biscaye?), coll. Chaine in IRSNB.
Naso unicornis, off New Caledonia, coll. IRSNB, leg. Séret.
Naso vlamingii, Aquarium Nancy (Indo-W Pacific), coll. IRSNB.
Neocyttus helgae, North atlantic, coll. Schwarzhans
Neocyttus rhomboidalis, off South Africa, redrawn after SMALE *et al.*, 1995.
Odontesthes bonariensis, off Uruguay, coll. IRSNB.
Odonus niger, aquarium Nouméa, New Caledonia; coll. IRSNB, leg. Séret.
Oreosoma atlanticum, off South Africa, redrawn after SMALE *et al.*, 1995.
Ostracion cubicus, Aquarium Nouméa, New Caledonia (Pl. 14, Fig. 5), aquarium, leg. Stinton (Pl. 14, Fig. 6), coll. IRSNB.
Ostracion meleagris, Aquarium, E Africa (Pl. 14, Fig. 8), Hawaii (Pl. 14, Fig. 9), coll. IRSNB, leg. Stinton.
Ostracion pergravis, Paleocene, Selandien, Denmark, coll. MGUH 26232 and 26233.
Oxymonacanthus longirostris, Aquarium (Indo-Pacific), coll. IRSNB, leg. Stinton.
Paracanthurus hepatus, Aquarium (Indo-W Pacific), coll. IRSNB.
Paraluteres prionurus, Aquarium, E Africa, coll. IRSNB, leg. Stinton.
Paramonacanthus oblongus, off Australia, coll. LACM 56212.002, leg. Coates.
Paratriacanthodes retrospinis, off Mozambique, coll. ANSP 103285.
Parazen pacificus, off Miami, Florida, coll. IRSNB.
Pentanemus quinquarius, off W Africa, coll. IRSNB.
Pervagor melanocephalus, Aquarium, E Africa, coll. IRSNB, leg. Stinton.
Pervagor spilosoma, Hawaii, coll. IRSNB, leg. Stinton.
Platyberyx opalescens, Atlantic, 65°N 32°50'W, coll. Schwarzhans.
Polymixia japonica, off Japan, coll. IRSNB.
Pseudobalistes fuscus, Philippines, coll. IRSNB, leg. Stinton.
Pseudocyttus maculatus, off New Zealand, leg. Linkowski (Pl. 1, Figs. 7-8) and Antartica, Eltanin station 1679 (Pl. 1, Fig. 9), coll. IRSNB.
Pseudomonacanthus macrurus, off Australia, coll. LACM 56212.003, leg. Coates.
Pseudotriacanthus strigilifer, off Bangkok, coll. LACM 56231.001, leg. Lavenberg.
Ranzania laevis, off New Caledonia, coll. IRSNB, leg. Séret.
Rhinecanthus rectangulus, Aquarium, (Indo-Pacific), coll. IRSNB, leg. Stinton.
Sargocentron diadema (Fig. 6), Aquarium (Red Sea to China), coll. IRSNB, leg. Stinton.
Sargocentron xantherythrinus, off Hawaii, coll. IRSNB, leg. Stinton.
Scleropages leichardti, Australia, freshwater, coll. IRSNB, leg. Fitch.
Siganus doliatus, off New Caledonia, coll. IRSNB, leg. Séret.
Siganus virgatus, Hong Kong fish market, coll. IRSNB, leg. Stinton.
Siganus vulpinus, Aquarium (Indo-W Pacific), coll. IRSNB.
Sphoeroides lobatus, tropical E Pacific, coll. LACM 56211.013, leg. Fitch.
Sphoeroides nephelus, off Louisiana, coll. LACM 56232.001, leg. Fitch.
Sphoeroides spengleri, locality unknown (tropical W Atlantic), coll. LACM 56211.014, leg. Berry.
Sphoeroides testudineus, off Haiti, coll. IRSNB, leg. Moreaux.
Stephanolepis hispidus, off Lanzarote, coll. IRSNB.
Stethopristes eos, off Papua New Guinea, coll. IRSNB, leg. Séret.
Sufflamen bursa, Aquarium, (E Africa), coll. IRSNB, leg. Stinton.
Sufflamen chrysopterus, Aquarium (Red Sea to Philippines), coll. IRSNB, leg. Stinton.
Sufflamen fraenatus, off New Caledonia, coll. IRSNB, leg. Séret.
Sufflamen verres, Pacific coast of Mexico, coll. LACM 56211.015, leg. Fitch.
Synodus foetens, off Georgia (Fig. 4e) and off Texas (Fig. 4f), coll. IRSNB.
Takifugu oblongus, Australia, coll. LACM 56212.004, leg. Coates.
Takifugu porphyreus, off Japan, coll. IRSNB, leg. Iizuka.
Takifugu xanthopterus, Hong Kong fish market, coll. IRSNB, leg. Stinton.
Tetraodon fluviatilis, Aquarium (freshwater, South Asia), coll IRSNB.
Tetraodon palembangensis, Thailand, coll. IRSNB, leg. Stinton.
Tetrosomus gibbosus, Aquarium (Indo-Pacific), coll. IRSNB, leg. Stinton.
Thamnaconus hypargyreus, NW Australia, coll. IRSNB, leg. Séret.
Thamnaconus modestus, Hong Kong fish market, coll. IRSNB, leg. Stinton.
Trachystoma petardi, off Townsville, Australia, coll. IRSNB, leg. Fitch.
Triacanthodes ethiops, off Madagascar, coll. IRSNB, leg. Schwarzhans.
Triacanthus biaculeatus, Hong Kong fish market, coll. IRSNB, leg. Stinton.
Triacanthus sp., Ypresian, London Clay, coll. Rundle, new fossil record.
Triodon macropterus, off New Caledonia, coll. IRSNB, leg. Séret.
Trixiphichthys weberi, Andaman Sea, Thailand, coll. ANSP 102136.
Tydemania navigatoris, NW Australia, coll. IRSNB, leg. Séret.
Tylerius spinosissimus, Hong Kong fish market, coll. IRSNB, leg. Stinton.
Xanthichthys mento, Socorro Islands, coll. LACM 56234.001, leg. Fitch.
Xenolepidichthys dalgleishi, W Africa, coll. IRSNB, leg. Fitch.
Zanclus cornutus, Aquarium Nancy (Atlantic, from E Africa till Mexico; W Pacific), Coll. IRSNB.
Zebrasoma flavescens, Aquarium (Indo-Pacific), coll. IRSNB.
Zenion hololepis, Caribbean, coll. IRSNB, leg. Fitch.
Zenion japonicus, off Queensland, Australia, coll. IRSNB, leg. Schwarzhans.
Zenion longipinnis, off New Caledonia, coll. IRSNB, leg. Séret.
Zenopsis conchifer, locality unknown (Gulf of Biscaye?), coll. Chaine in MHNB.
Zenopsis nebulosus, off Mahia Peninsula, New Zealand, coll. IRSNB, leg. Johnston.
Zeus faber, loc. unknown (Gulf of Biscaye?), coll. Chaine in IRSNB.

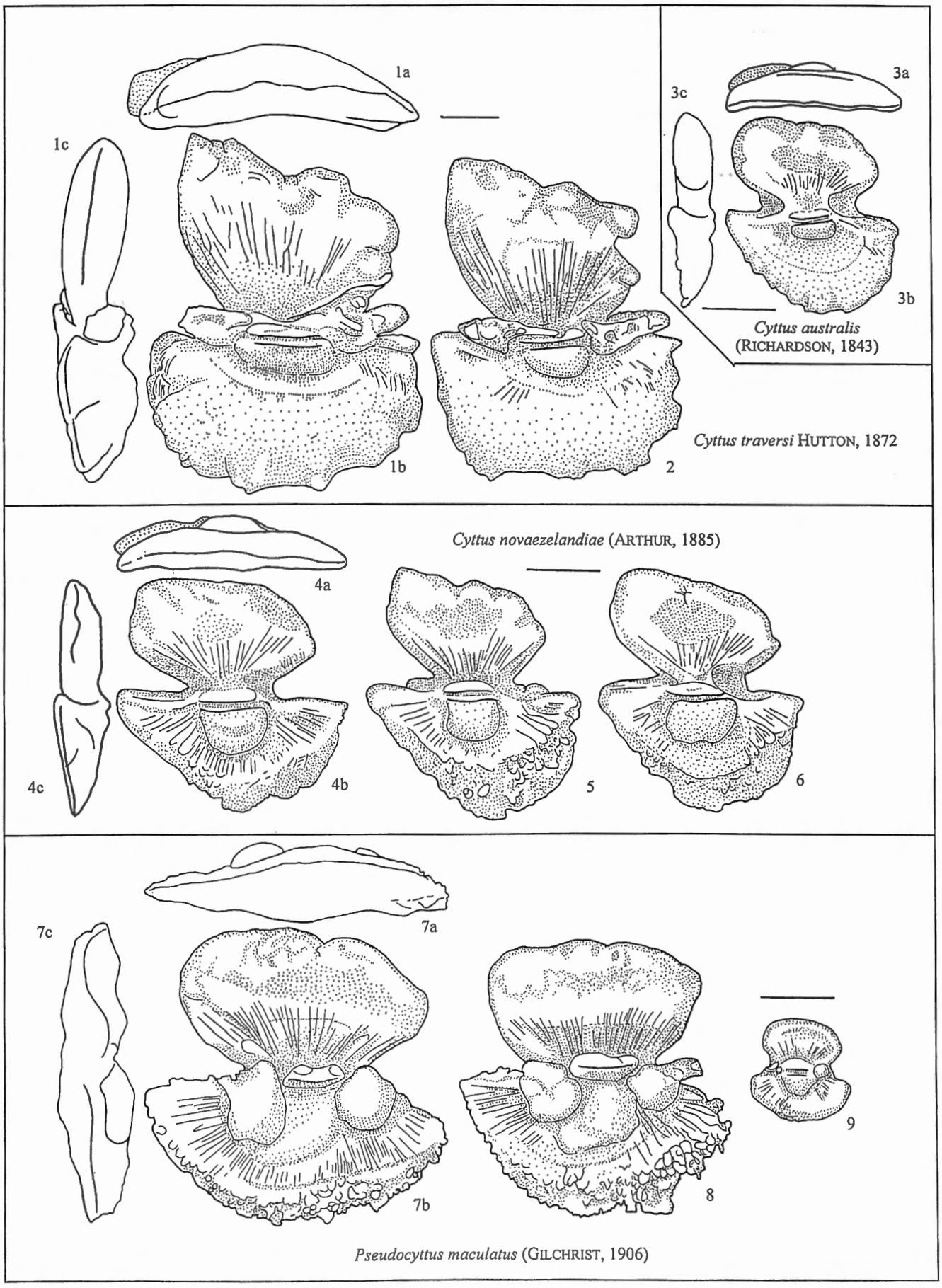


Plate 1. Otoliths of Cyttidae and Oreosomatidae (partim) Pseudocyttinae

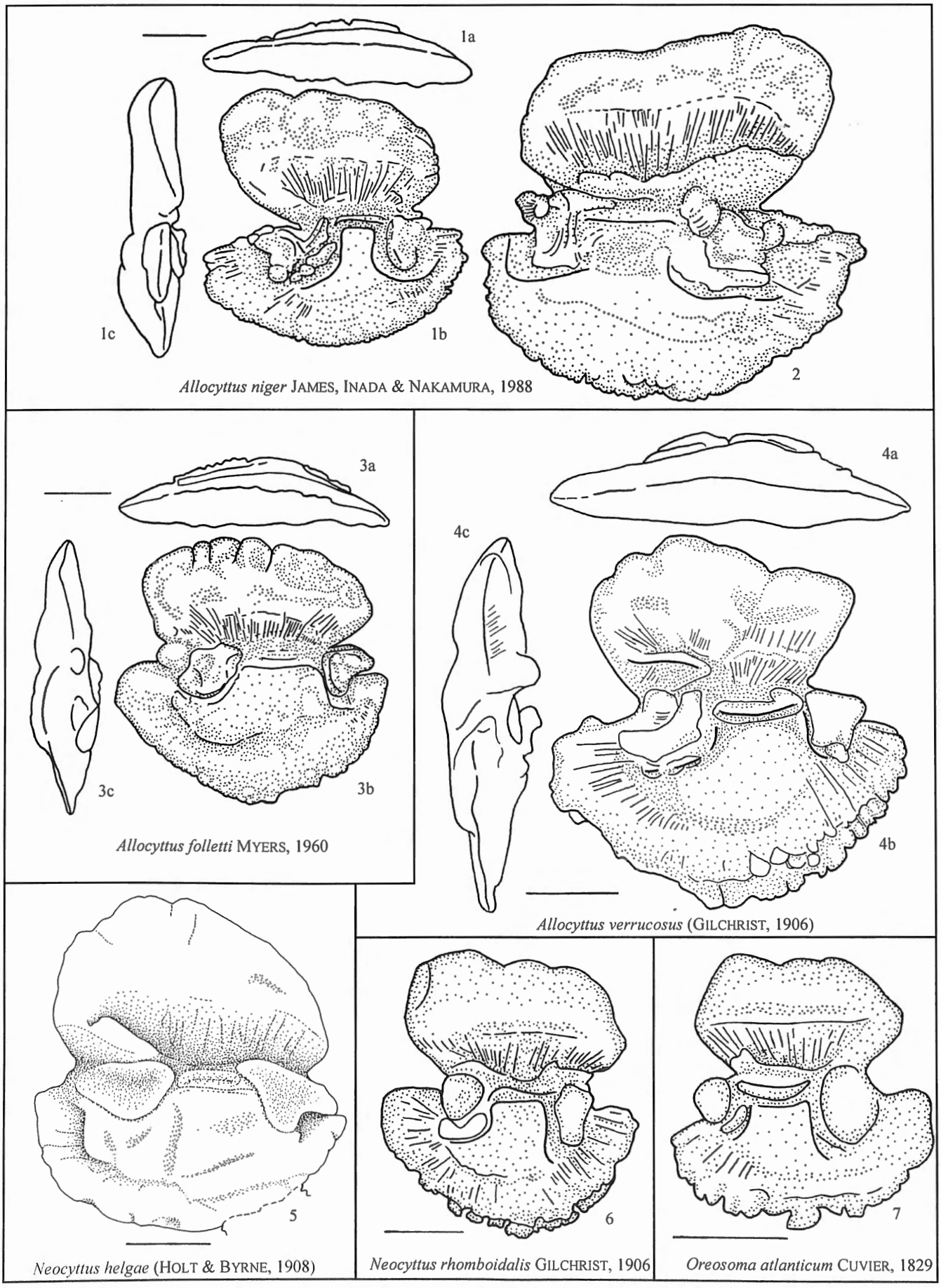
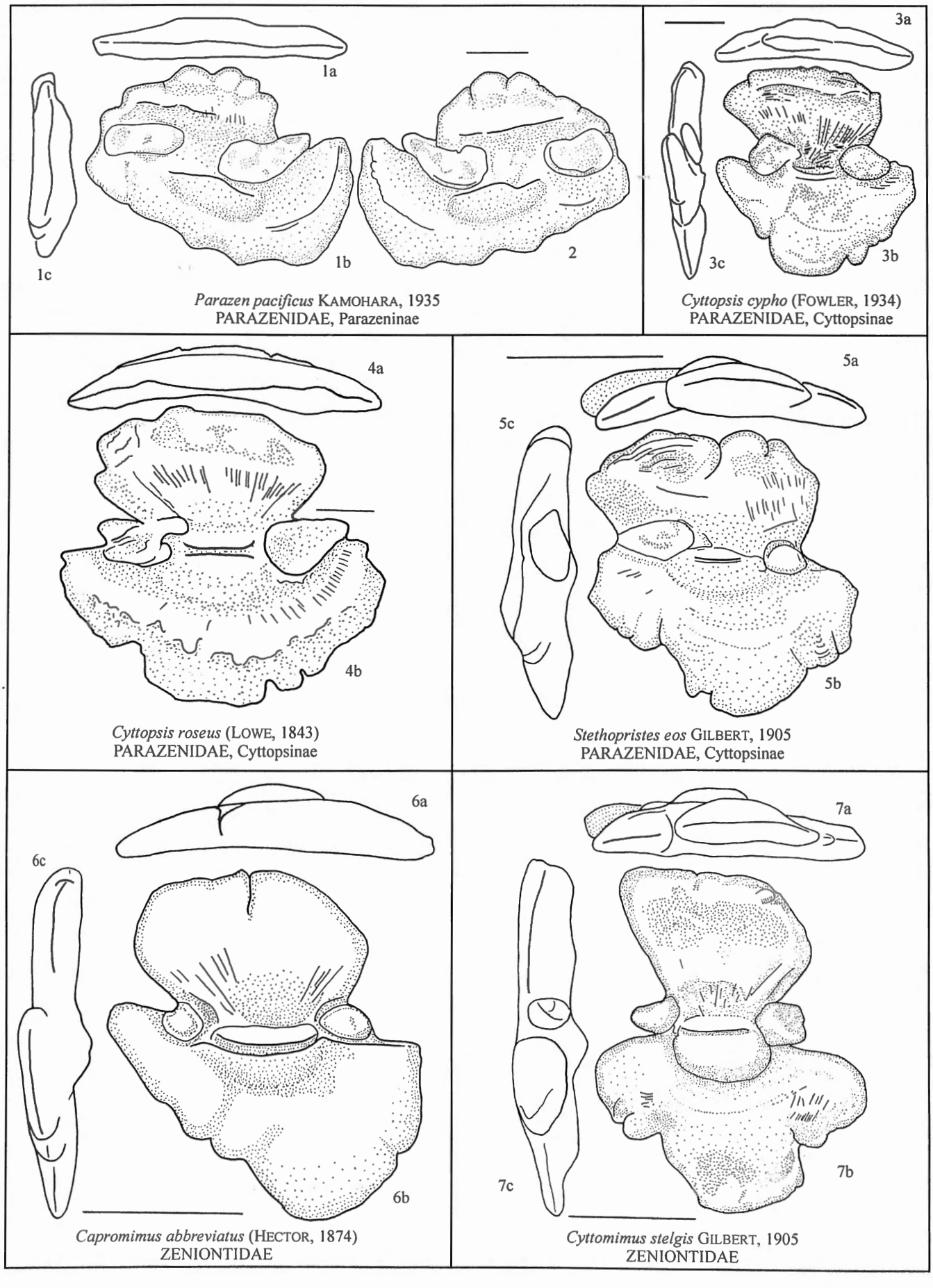


Plate 2. Otoliths of Oreosomatidae. Oresomatinae



Parazen pacificus KAMOHARA, 1935
PARAZENIDAE, Parazeninae

Cyttopsis cypho (FOWLER, 1934)
PARAZENIDAE, Cyttopsinae

Cyttopsis roseus (LOWE, 1843)
PARAZENIDAE, Cyttopsinae

Stethopristes eos GILBERT, 1905
PARAZENIDAE, Cyttopsinae

Capromimus abbreviatus (HECTOR, 1874)
ZENIONTIDAE

Cyttomimus stelgis GILBERT, 1905
ZENIONTIDAE

Plate 3. Otoliths of Parazenidae and Zeniontidae (partim): *Capromimus* and *Cyttomimus*

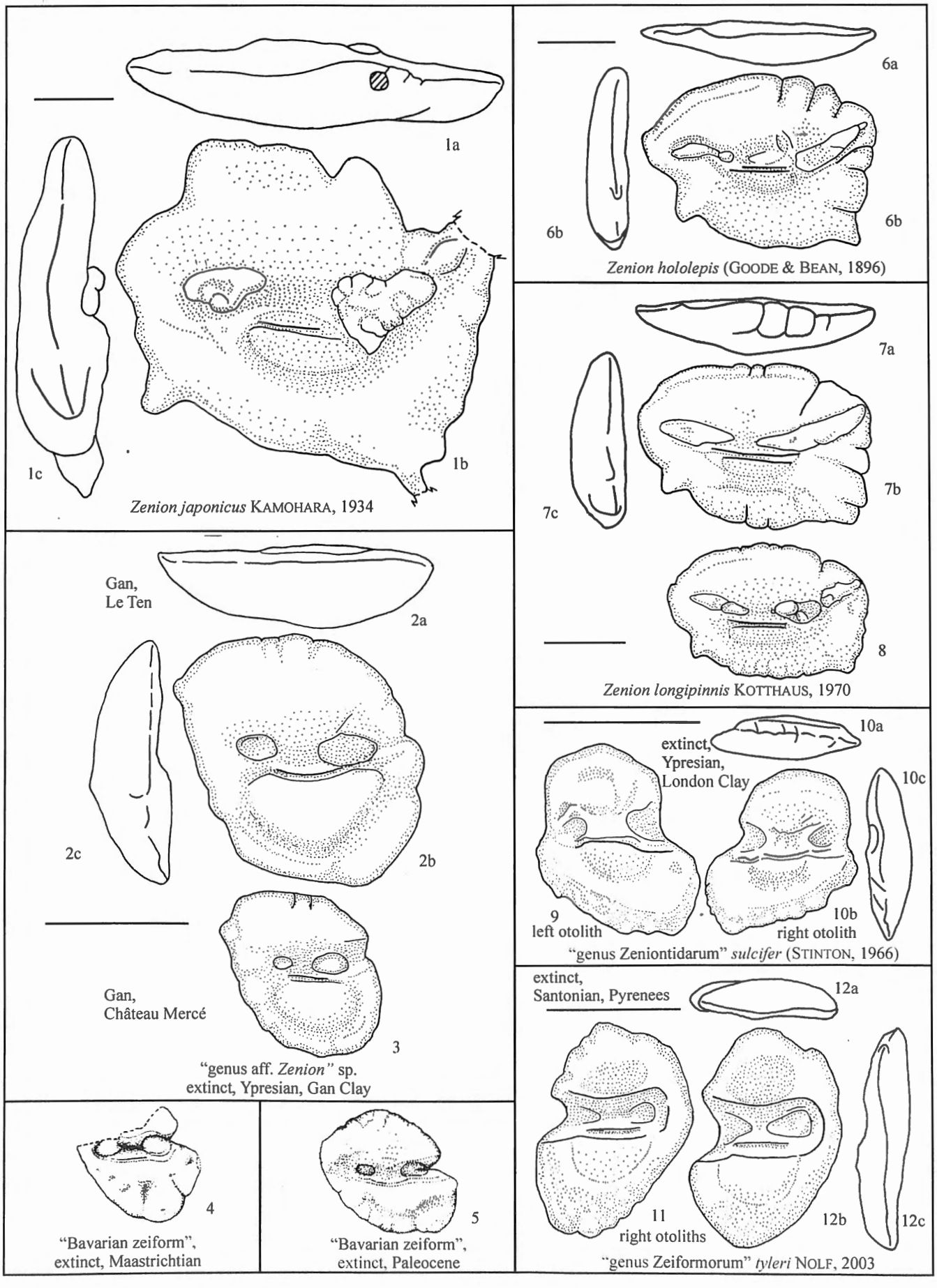


Plate 4. Otoliths of Zeniontidae, *Zenion* and fossil relatives + incertae sedis fossil zeiforms

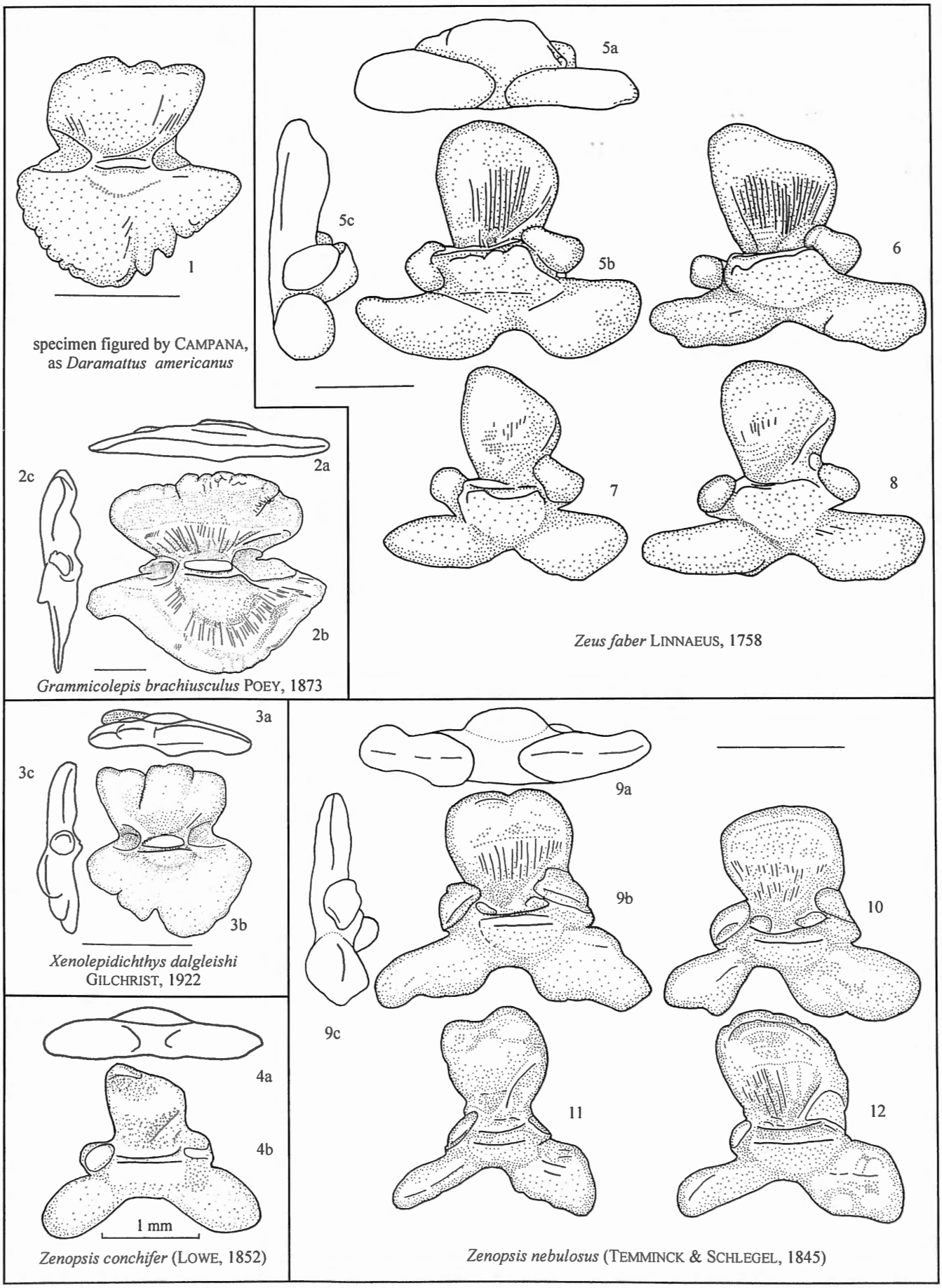


Plate 5. Otoliths of Grammicolepididae and Zeidae

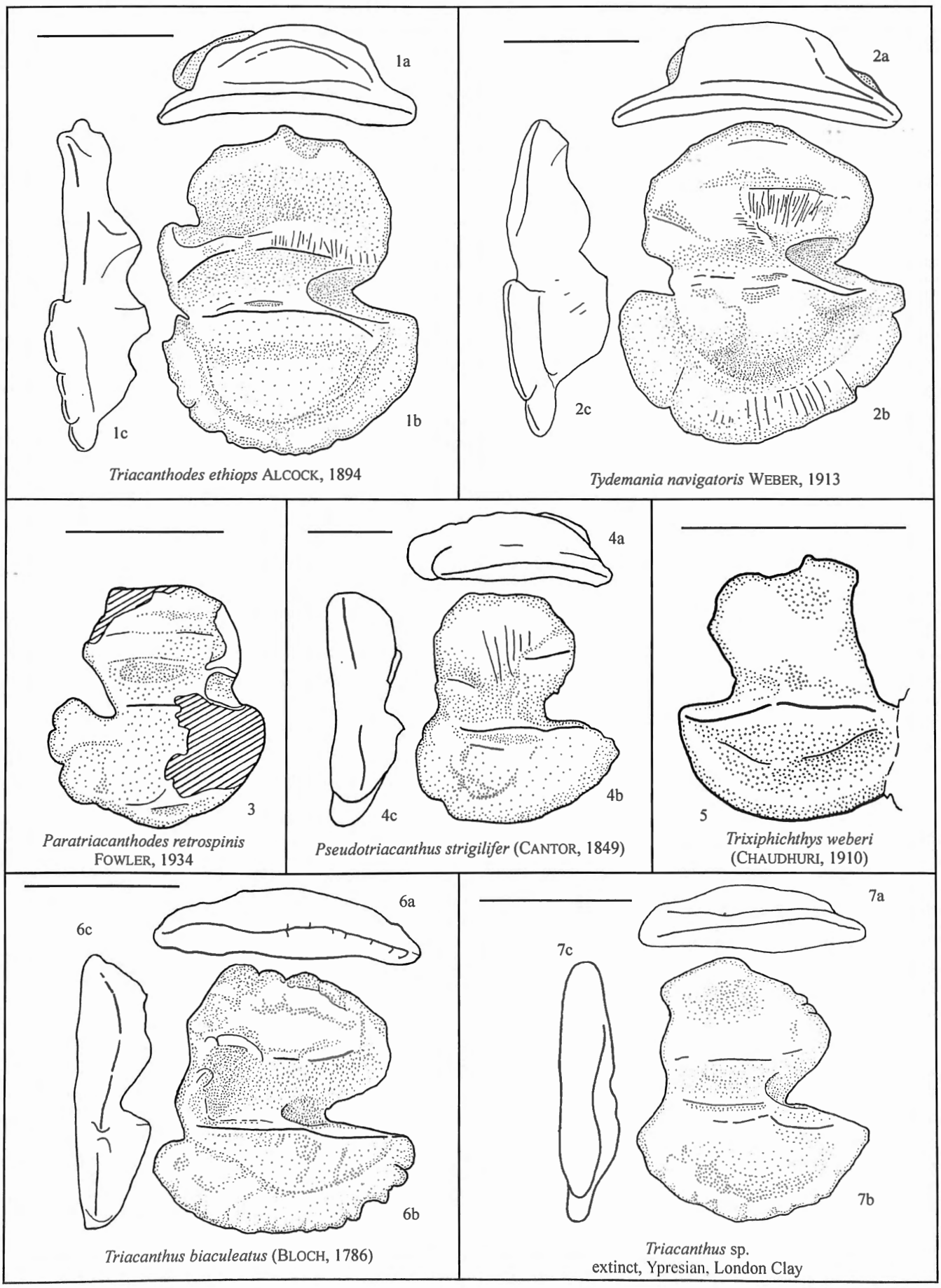


Plate 6. Otoliths of Triacanthodidae and Tricanthidae

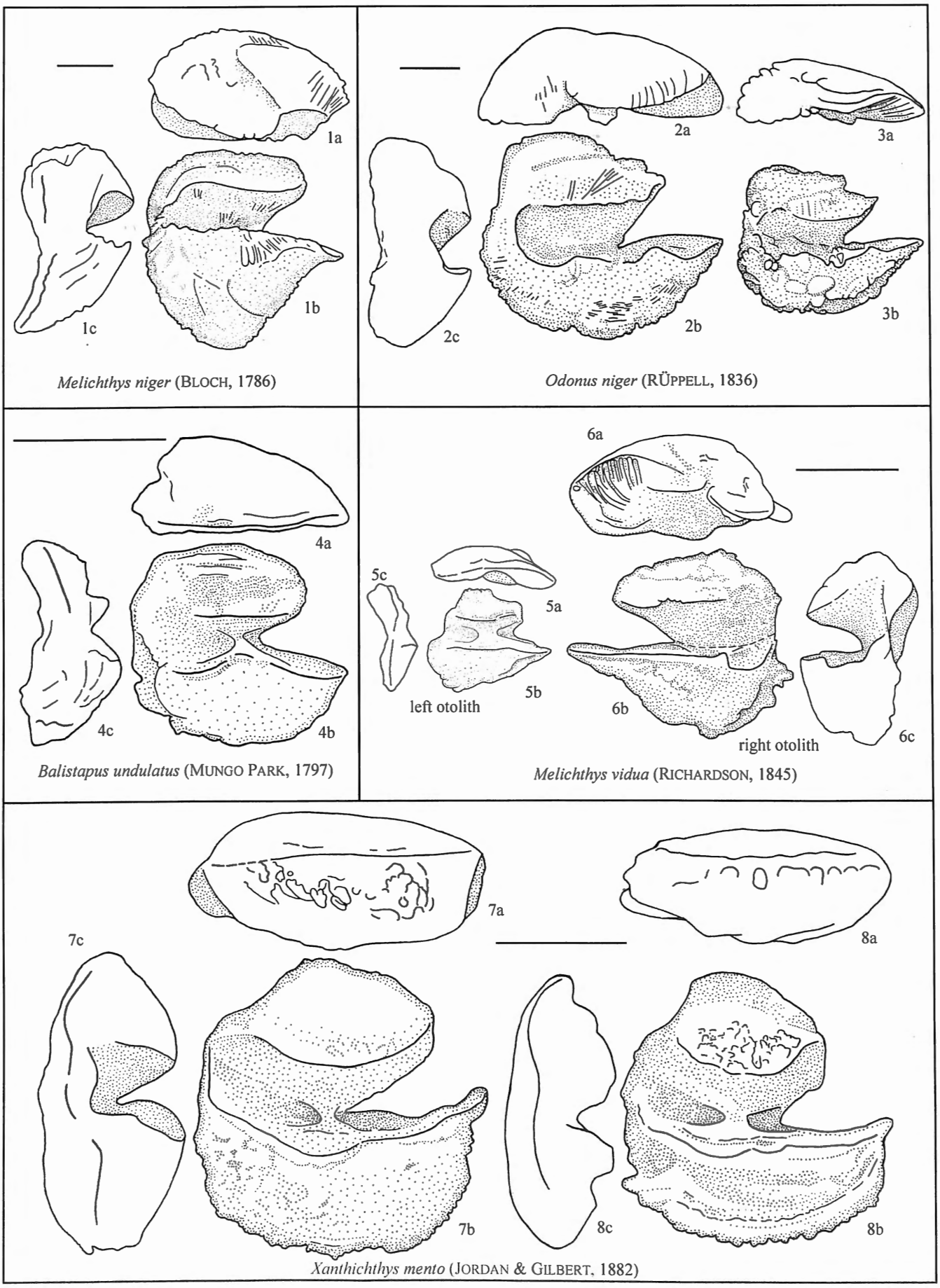


Plate 7. Otoliths of Balistidae (partim): *Balistapus, Melichthys, Odonus* and *Xanthichthys*

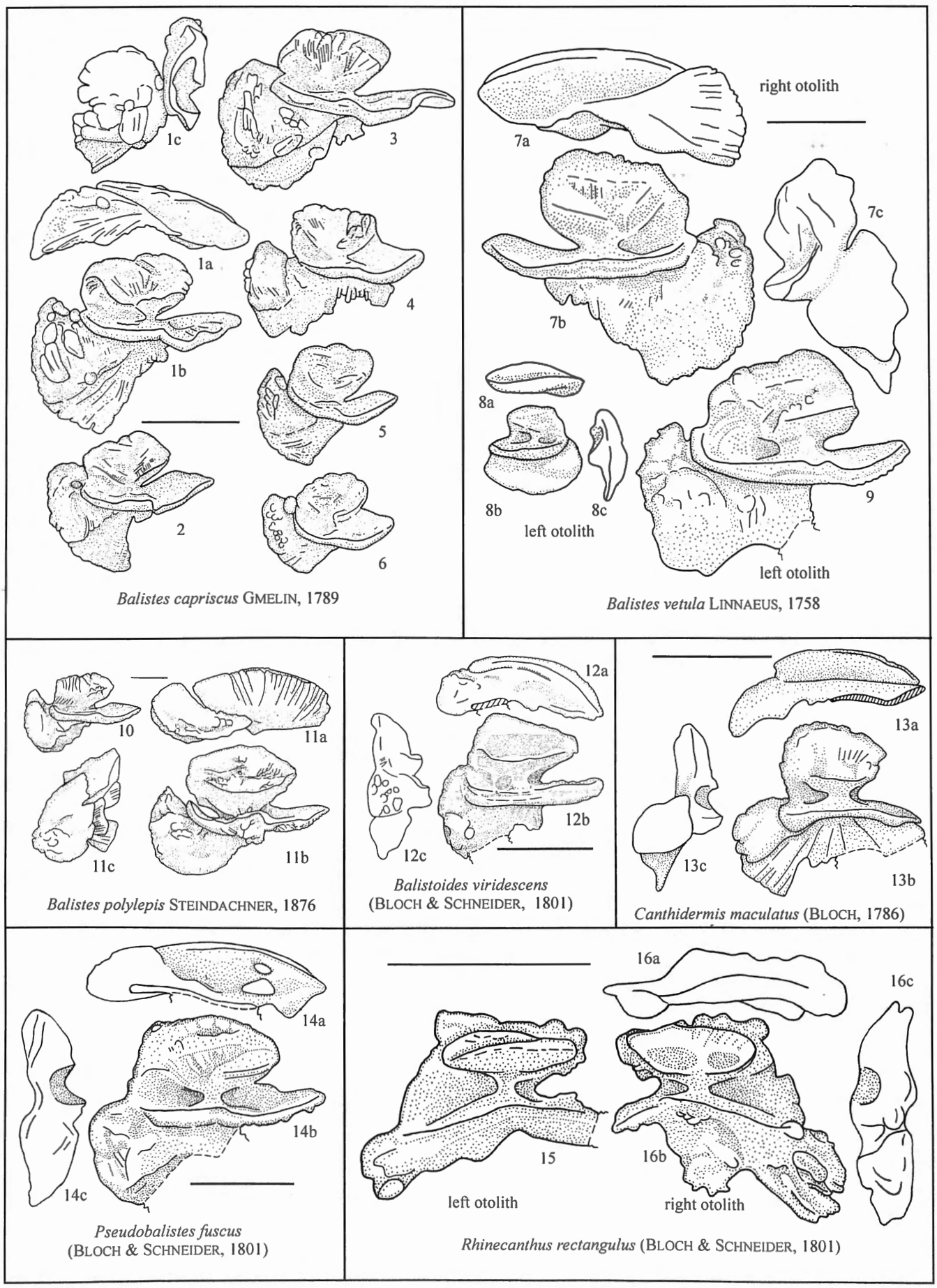


Plate 8. Otoliths of Balistidae (partim): *Balistes, Canthidermis, Pseudobalistes* and *Rhinecanthus*

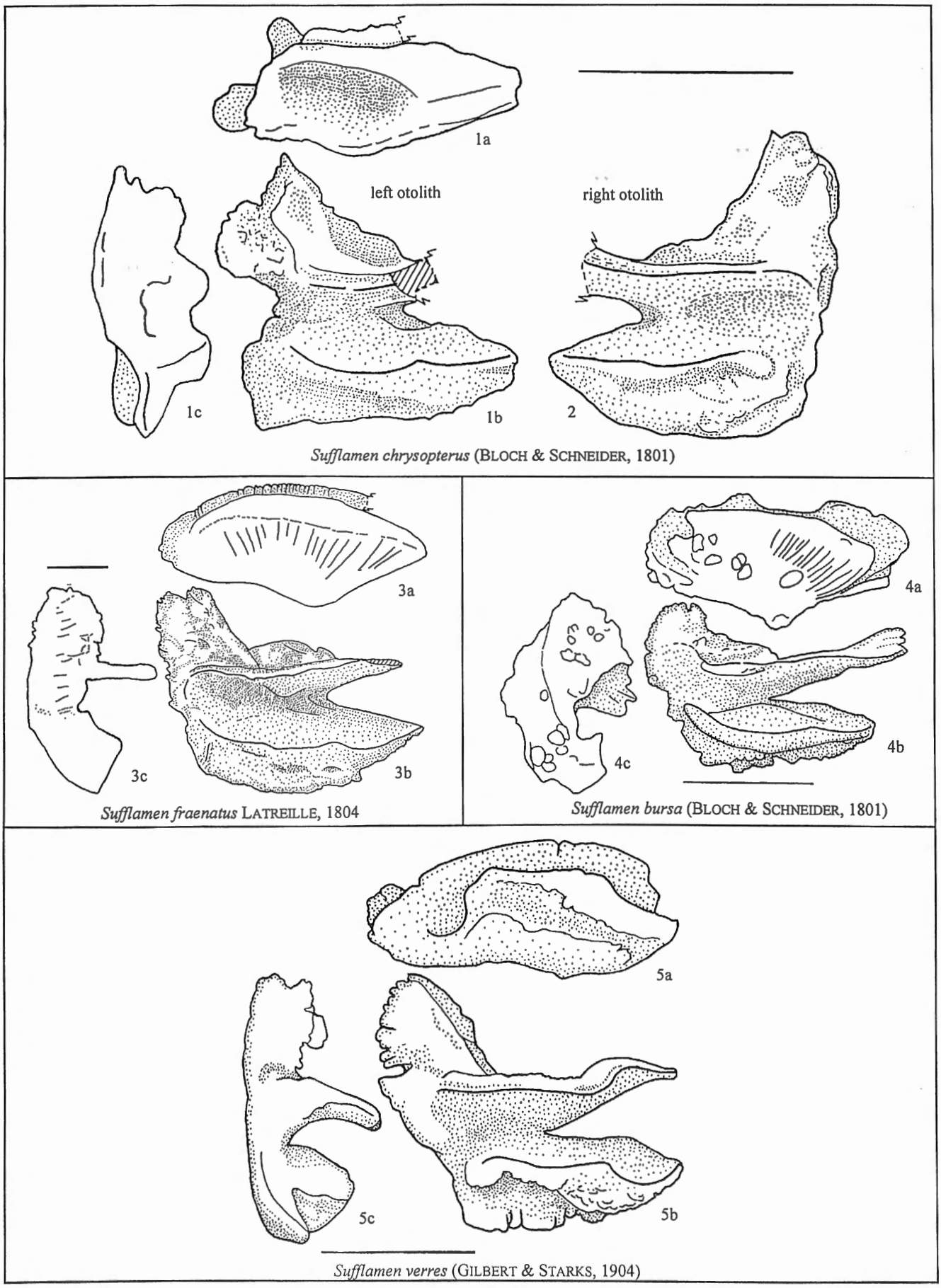


Plate 9. Otoliths of Balistidae (partim): *Sufflamen*

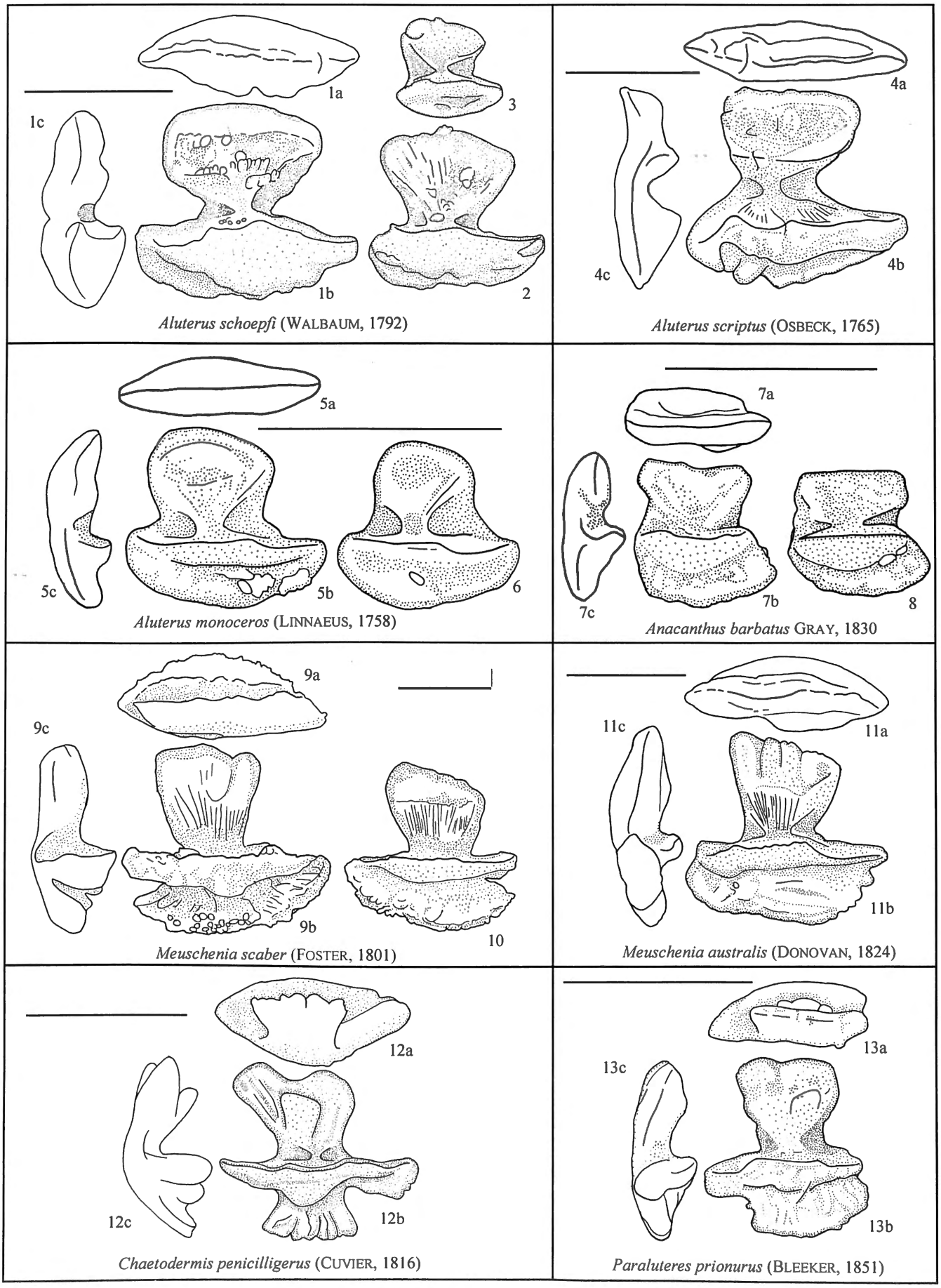


Plate 10. Otoliths of Monacanthidae (partim): *Aluterus, Anacanthus, Chaetodermis, Meuschenia, Paraluteres*

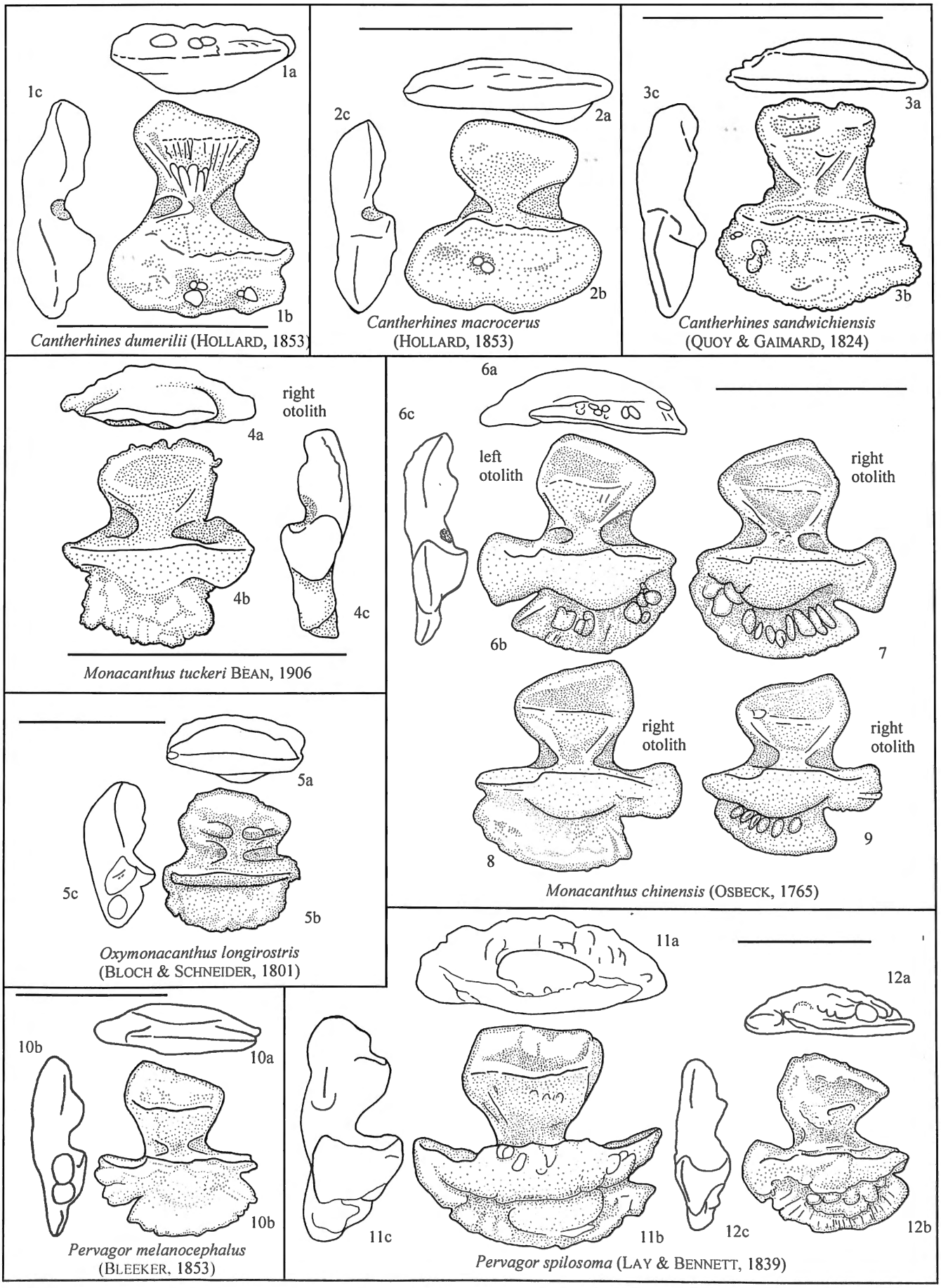


Plate 11. Otoliths of Monacanthidae (partim): *Cantherhines, Monacanthus, Pervagor* and *Stephanolepis*

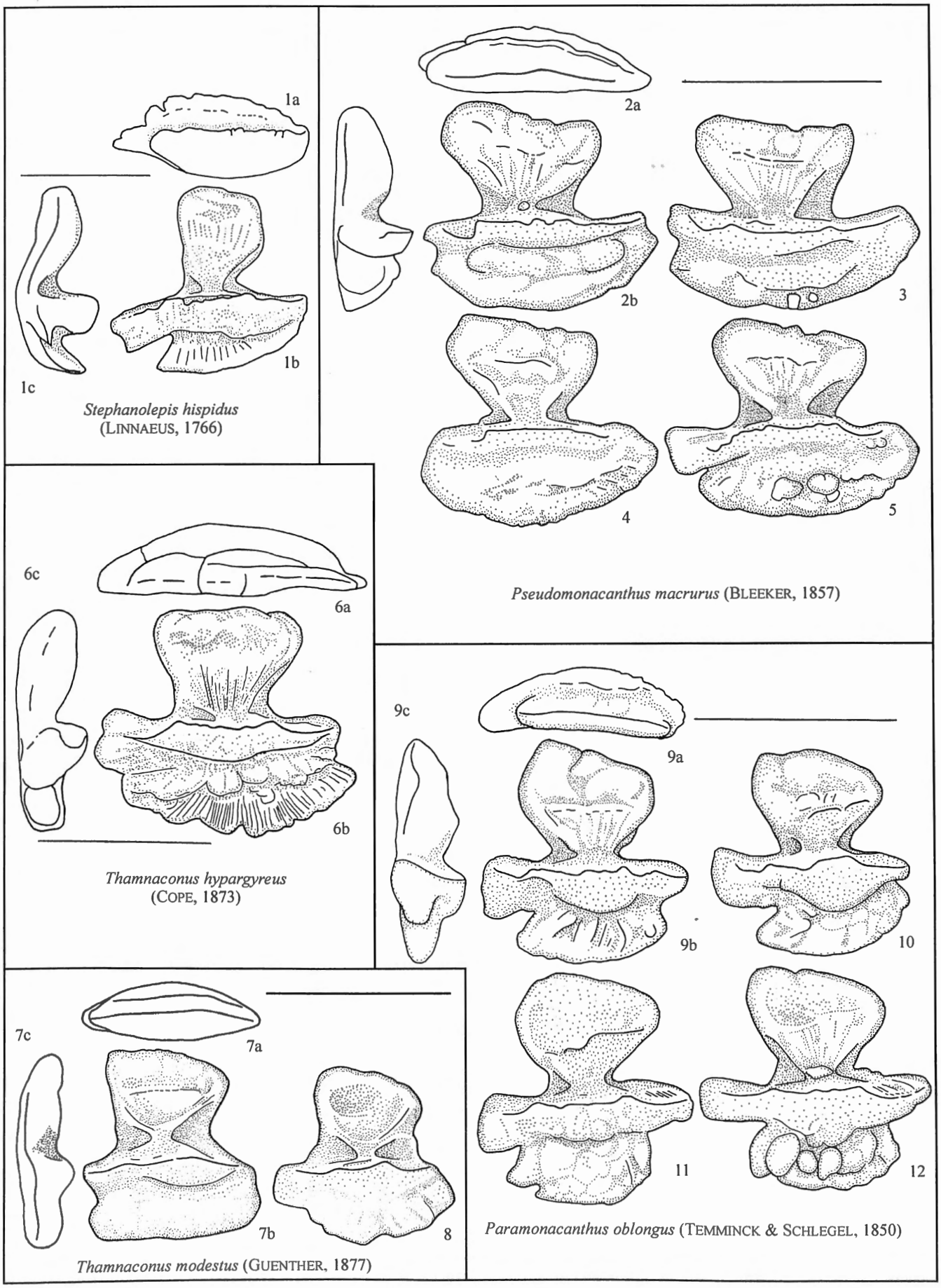


Plate 12. Otoliths of Monacanthidae (partim): *Paramonacanthus, Pseudomonacanthus, Stephanolepis* and *Thamnaconus*

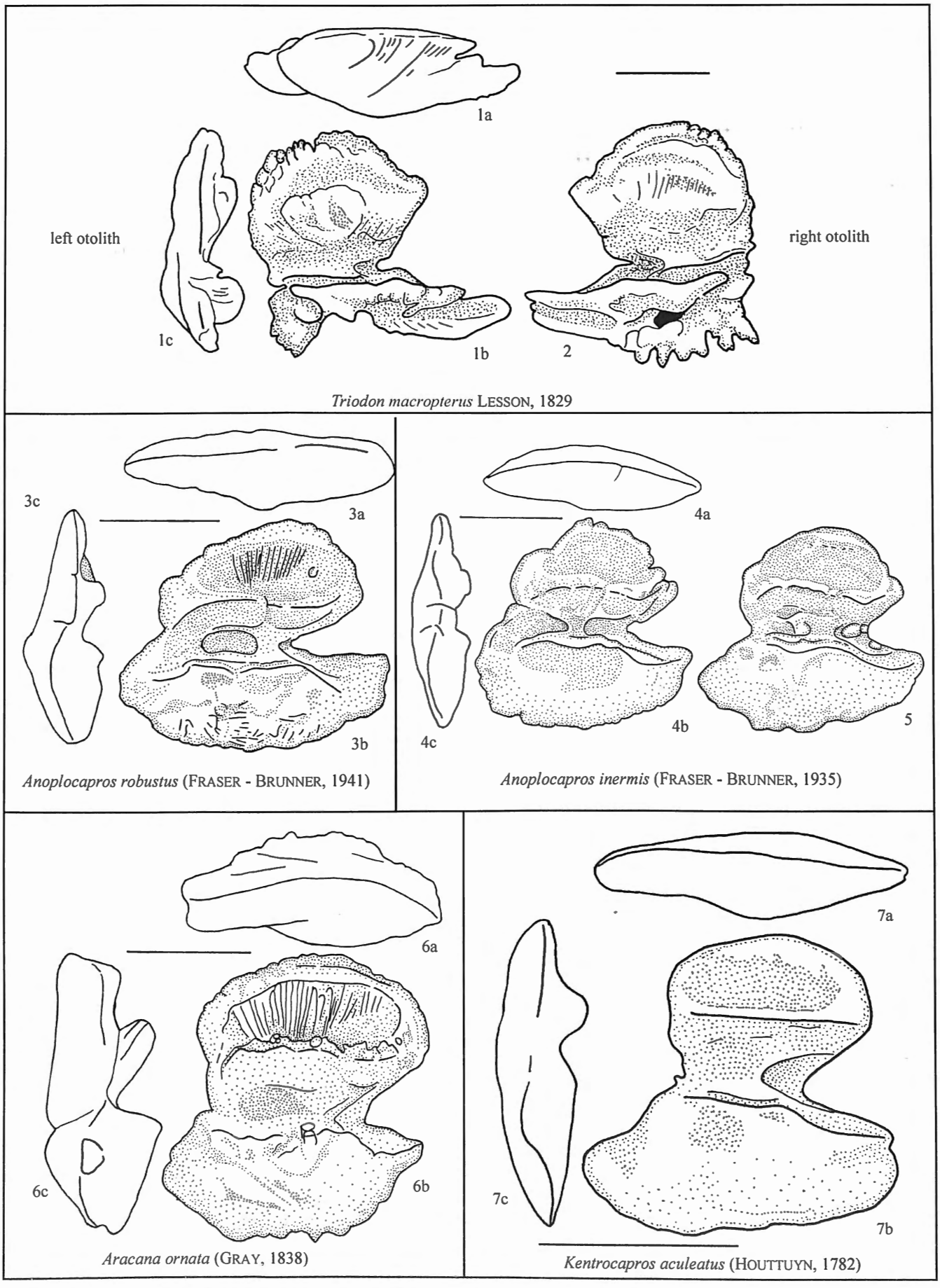


Plate 13. Otoliths of Triodontidae and Aracanidae

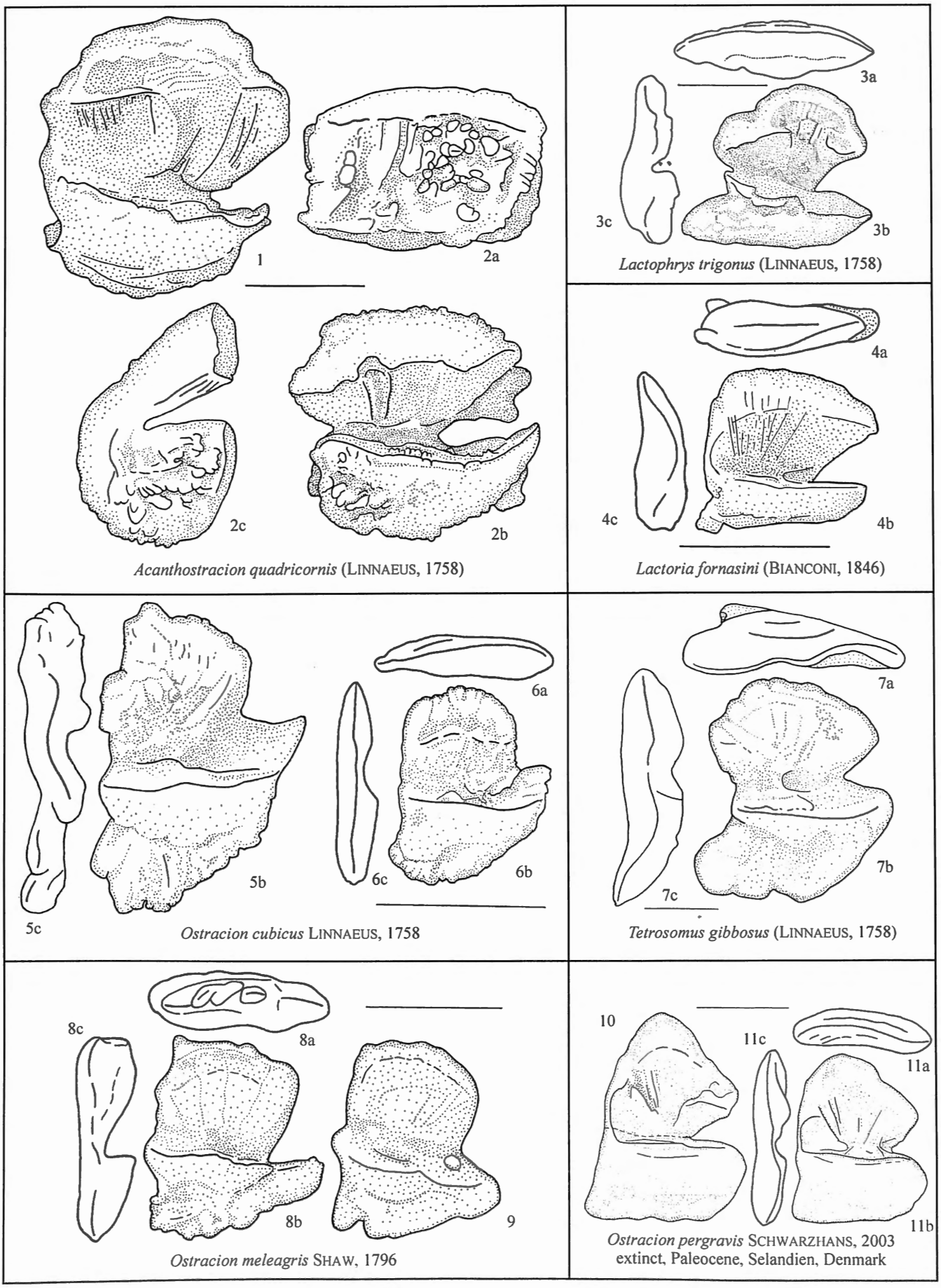


Plate 14. Otoliths of Ostraciidae

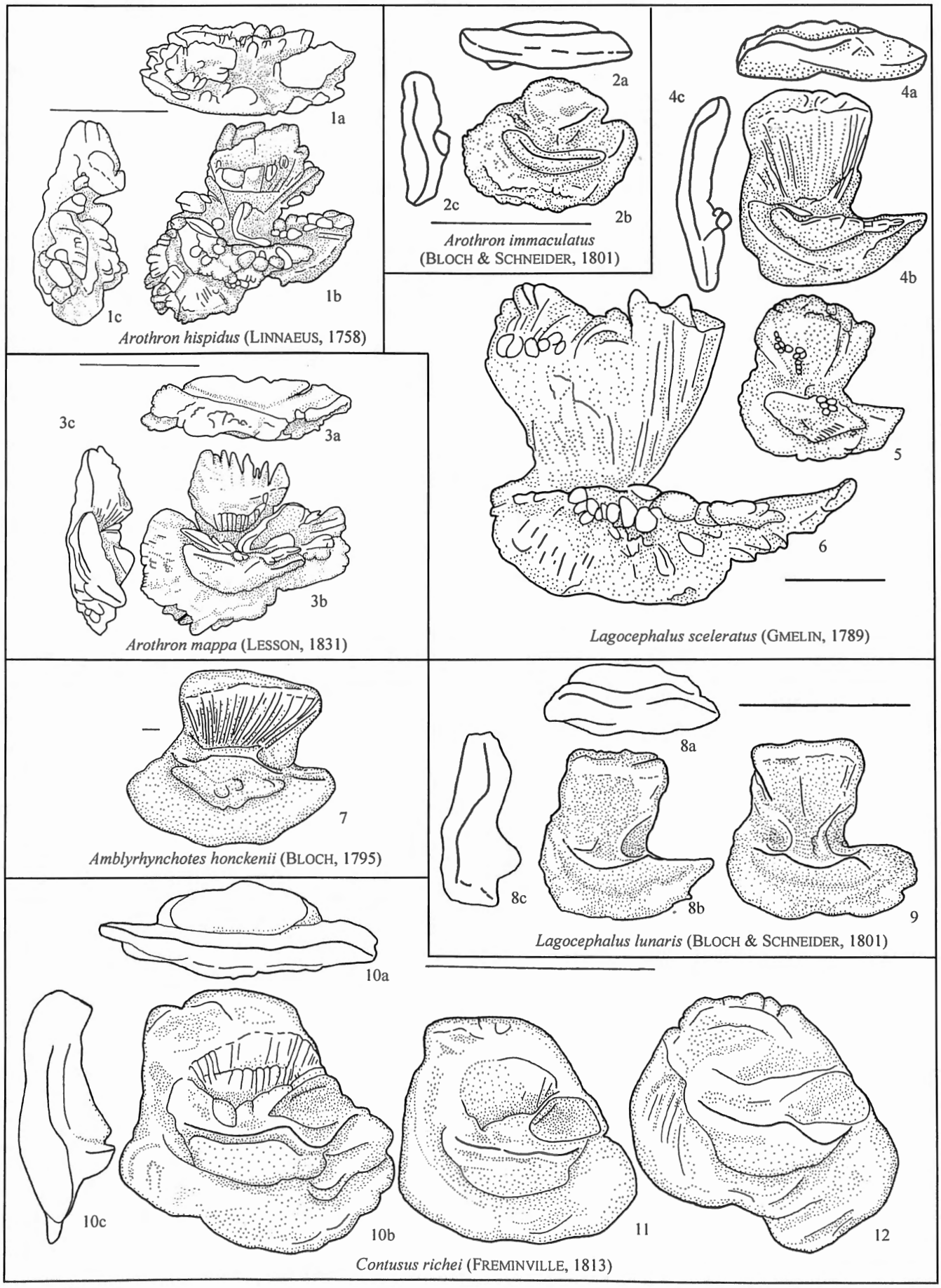


Plate 15. Otoliths of Tetraodontidae: *Amblyrhynchotes, Arothron, Contusus, Lagocephalus*

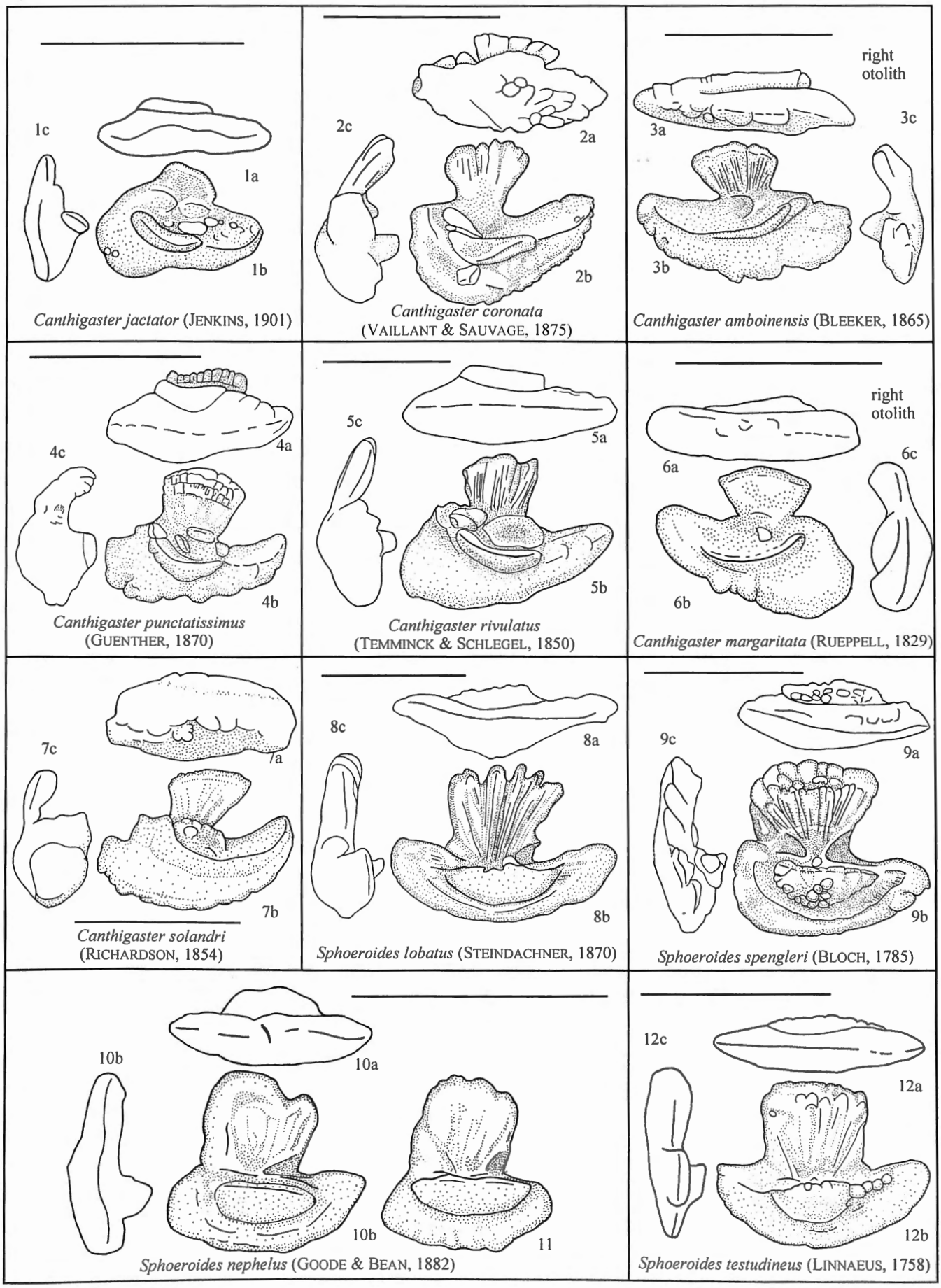


Plate 16. Otoliths of Tetradontidae: *Canthigaster* and *Sphoeroides*

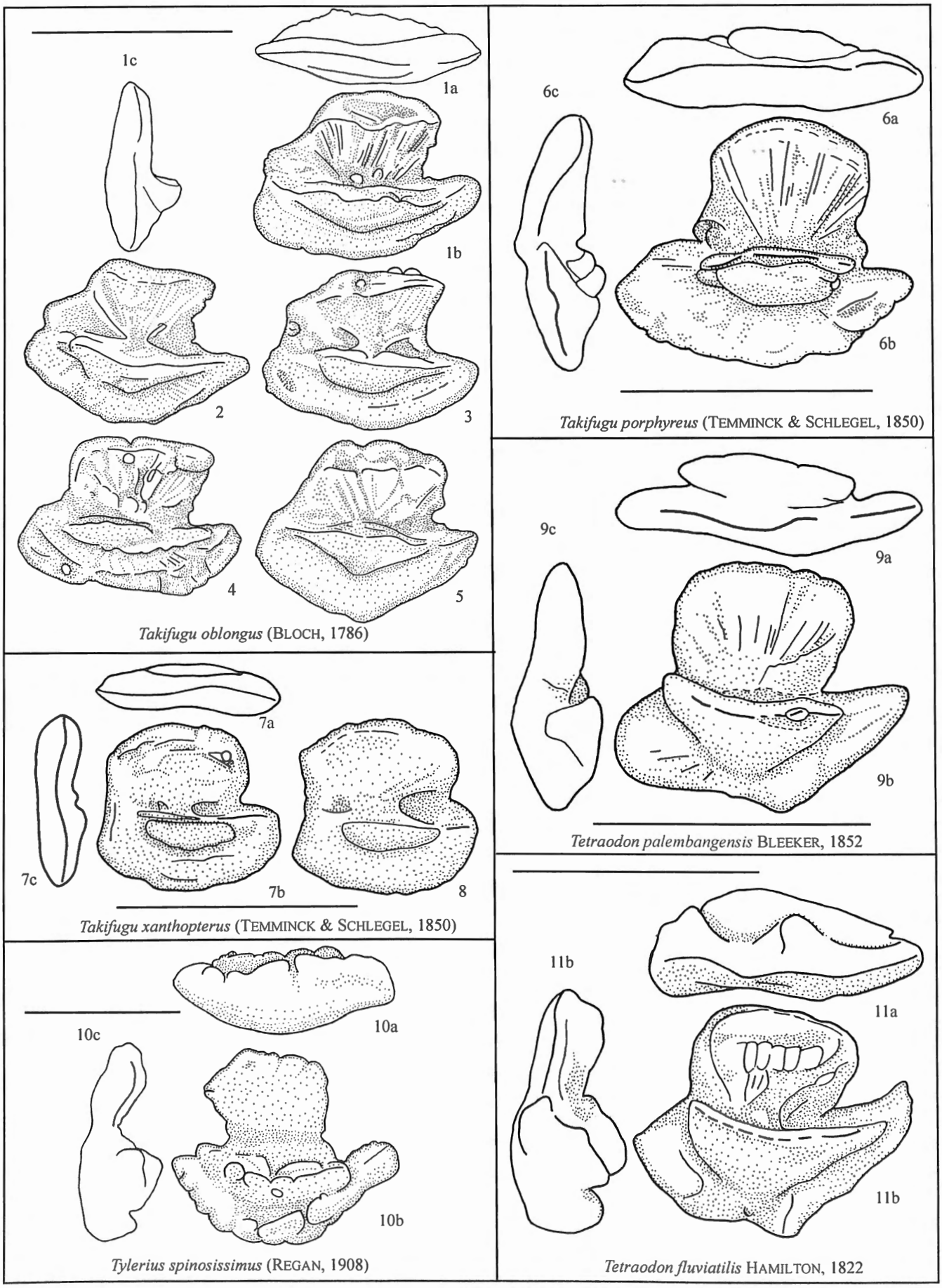


Plate 17. Otoliths of Tetraodontidae: *Takifugu, Tetraodon* and *Tylerius*

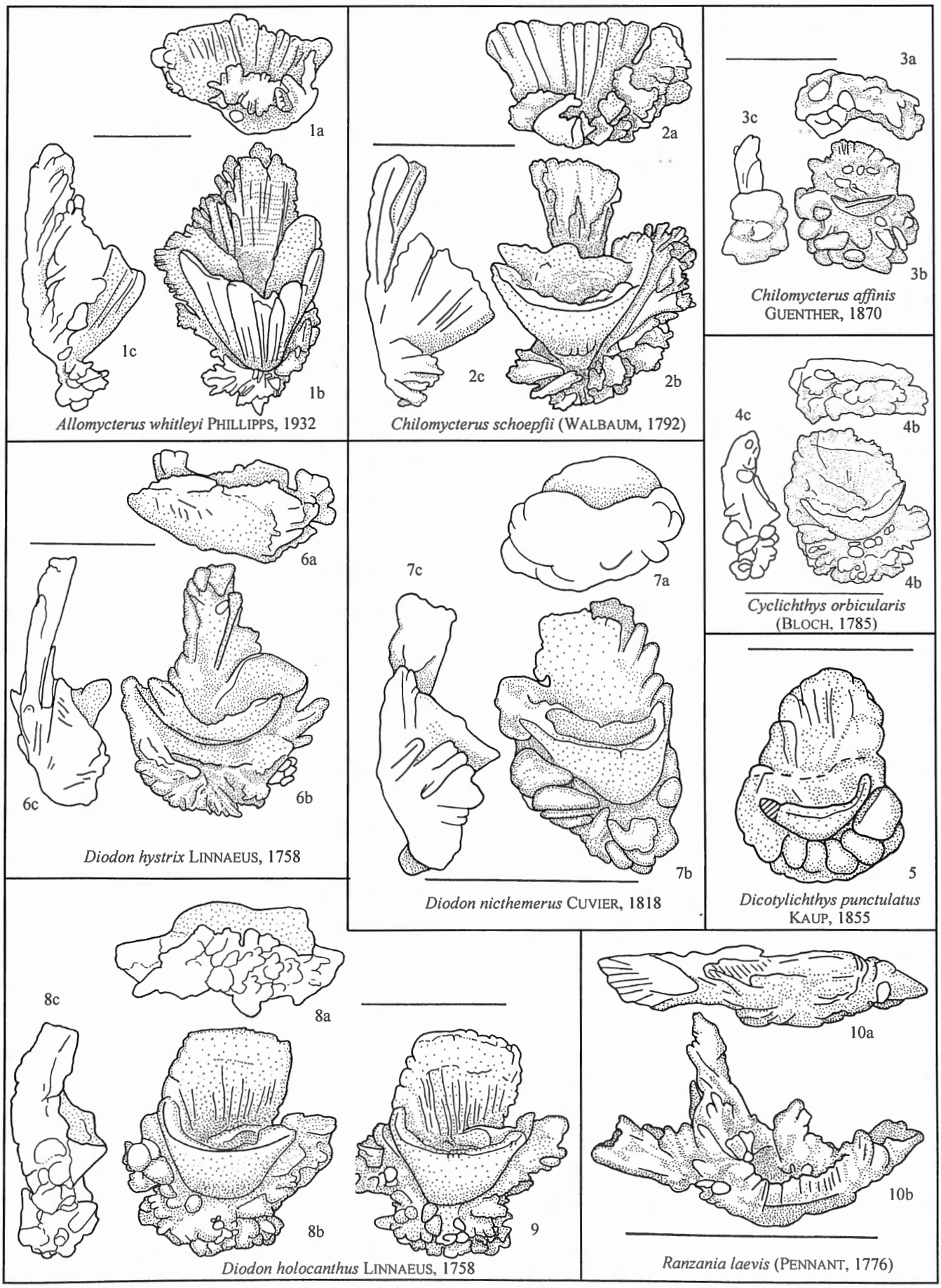


Plate 18. Otoliths of Diodontidae

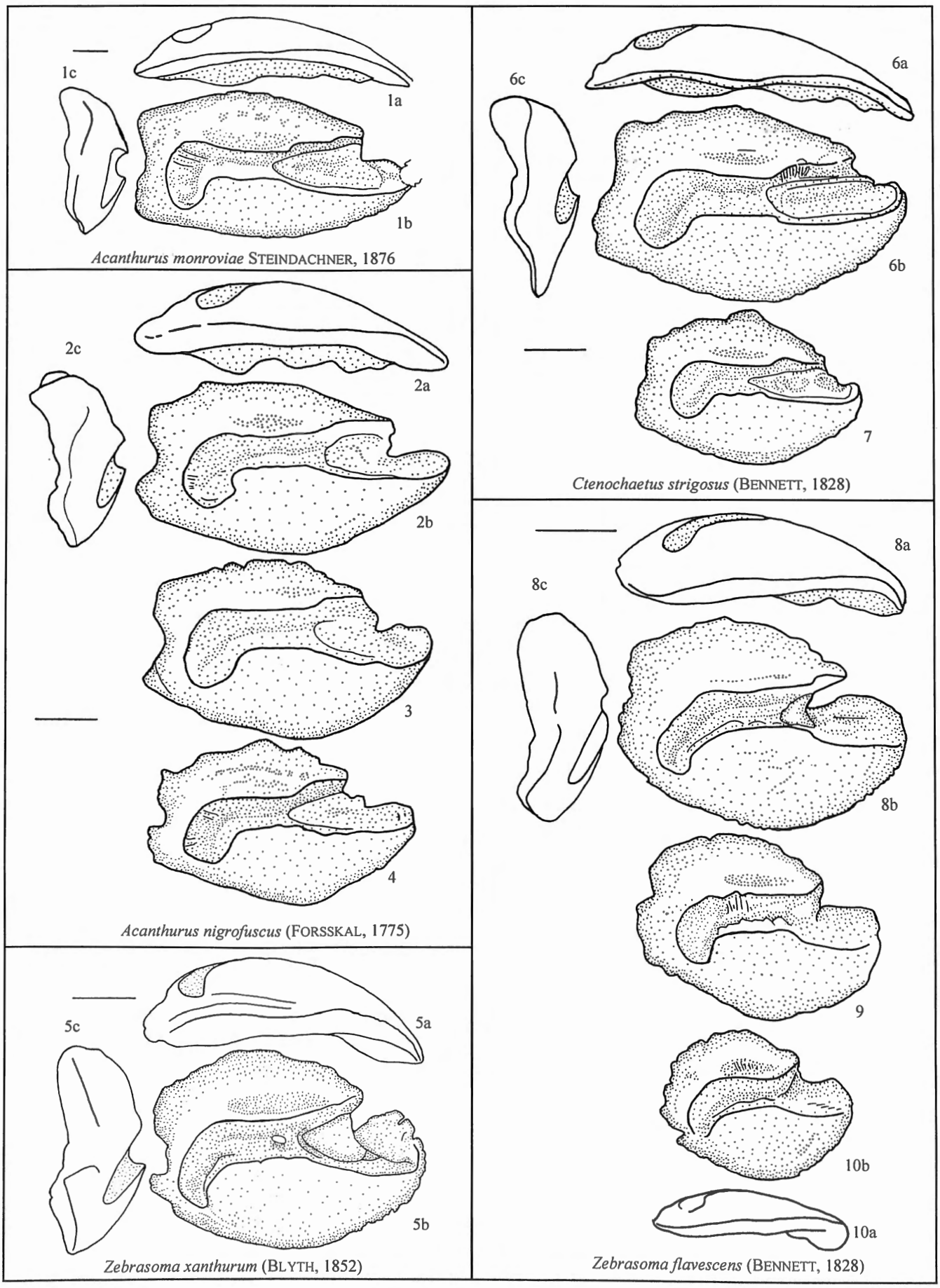


Plate 19. Otoliths of Acanthuridae (partime): *Acanthurus, Ctenochaetus* and *Zebrasoma*

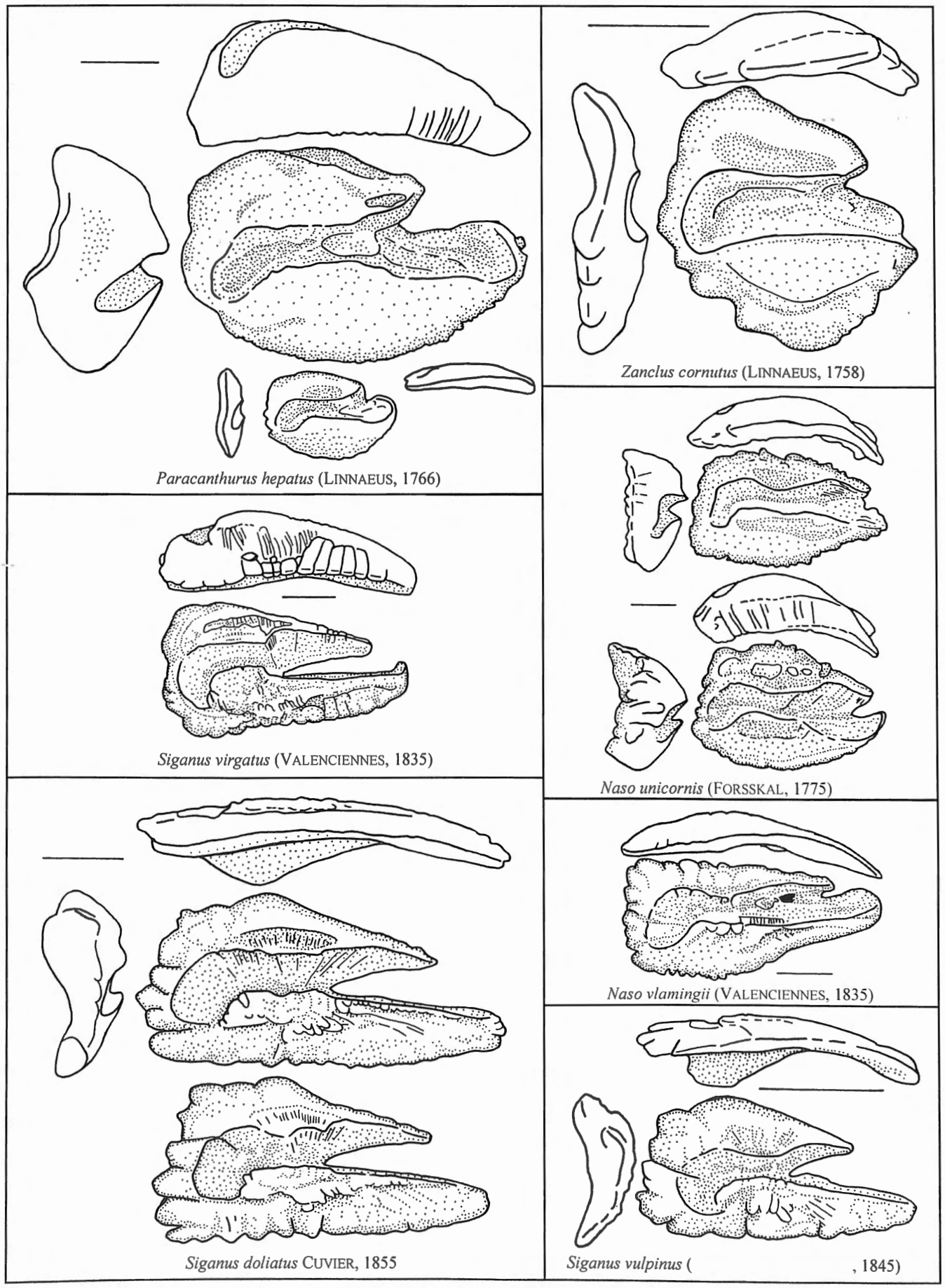


Plate 20. Otoliths of Acanthuridae (partim): *Paracanthurus* and *Naso*; Siganidae; Zanclidae