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Nomenclature and distribution of the species of the porcupinefish family Diodontidae (Pisces, Teleostei)

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Abstract

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The tetraodontiform fish family Diodontidae is widely distributed in tropical and temperate marine waters. The family has more than 70 nominal species, over 60% of which were described in the 100 years following Linnaeus. As a consequence, many descriptions are less than detailed, and many types are no longer extant, if they existed at all. The high incidence of synonymy, the many 'old' descriptions and the wide geographical distributions of the species has led to a great deal of confusion. The present study, based on examination of diodontid holdings in 29 major collections, and including the extant types of all but two of the nominal species, attempts to clarify the nomenclature and distribution of the species of the family. Although some species boundaries are not entirely clear, only 18 or 19 of the nominal species are herein regarded as valid (one as a subspecies). Tentative assignments of species to genera maintain current usage. Final assignments to genera must await a cladistic analysis of relationships within the family. Four species are circumtropical, four species (plus a subspecies) are confined to the Atlantic and appear to form a species group, four species are widely distributed in the tropical Indo-Pacific, two species are confined to tropical Australasia, and three are endemic to temperate Australia. One species described from New Zealand either occurs also in Australia, or is a synonym of an Australian species. Synonymies, a key to the recognized species and a table of the identities of nominal species are provided.

Keywords

Tetraodontiformes, burrfish, *Allomycterus*, *Chilomycterus*, *Cyclichthys*, *Dicotylichthys*, *Diodon*, *Lophodiodon*, *Tragulichthys*

Introduction

The porcupinefish family Diodontidae contains about 19 species in seven or eight genera of warm to temperate seas. There are about 75 nominal species in the family, and several of the species have very wide distributions. The species are conspicuous, readily captured, of unusual morphology, and have been the focus of interest by naturalists from ancient times. Several species have pelagic stages that reach large sizes and differ in appearance from the demersal adults. All this has led to a great deal of confusion as to the number of species, their distributions and the correct names for them. The purpose of this paper is to clarify a number of nomenclatural issues and the distributions of the species. Due to their wide distributions, the species are obvious targets for molecular genetic studies, and it is reasonable to expect that some taxa that are currently, on the basis of morphology alone, considered to represent a single, widespread species will be subdivided once genetic studies are undertaken. Conversely, some Atlantic taxa have less than clear separations and may eventually be considered conspecific. Therefore, it is important to lay some groundwork for these expected future studies.

This paper lists the senior synonym of each morphologically-defined species, followed by the junior synonyms. Brief justifications for synonymies are provided, as are descriptions of the distribution of the species based on material examined or on identifiable literature records. In addition to the key provided here, regional keys to the species, and illustrations of them, can be found in Leis (1986, ref. 5686 – western Indian Ocean); Leis (2001, ref. 26318 – western central Pacific Ocean: this key also covers all species in the eastern Indian Ocean); Allen and Robertson (1994, ref. 22193 – eastern Pacific Ocean); Leis (2003, ref. 27121 – western central Atlantic Ocean); Leis (in press, eastern central Atlantic Ocean). The key in Leis (2001, ref. 26318) includes all Indo-Pacific species and genera recognized herein, except the two temperate Australasian species *Diodon nicthemerus* Cuvier and *Allomycterus pilatus* Whitley (for these, see Kuiter, 1993, ref. 23929, or Gomon et al., 1994, ref. 22532).

Materials and methods

Abbreviations of fins are as follows: D, dorsal; A, anal; P, pectoral; C, caudal. The spines mentioned are the dermal spines (i.e., modified scales): fins of diodontids lack spines. These

dermal spines have subdermal bases (or roots) that have either two approximately opposing bases upon which the exposed spine pivots when it elevates, or three (occasionally four) broadly more or less equidistantly spaced bases that render the exposed spine immobile. The exposed portion of the spine varies in length and shape, but erectile spines are generally round in cross-section, whereas fixed spines can vary from round to compressed in cross-section. See Leis (1978, ref. 5529; 1986, ref. 5686; or 2001, ref. 26318) for more information on spine morphology. Behind the massive beak-like jaws of diodontids is a grinding, or trituration, plate formed by the fused premaxillae and dentaries. This plate is often armed with transverse plates of teeth, called trituration teeth.

Specific information on types is included only if it supplements or corrects information in Eschmeyer (2005; 17 Oct 2005 version). To keep the literature cited list to a manageable length, it includes only references not included in Eschmeyer's (2005) on-line database (http://www.calacademy.org/research/ichthyology/catalog/fishcatmain.asp). The Eschmeyer reference number is included with the text citation. Information on *Diodon* is included in Leis (1978, ref. 5529) and in Leis and Bauchot (1984, ref. 12539). For *Diodon*, only information on species described since 1978 and information updating species distributions is included here.

I examined specimens of diodontids from the following institutions (codes after Leviton et al., 1985, ref. 9683): AMS, ANSP (loans based on holdings list), BMNH, BPBM, CAS, CSIRO, FAKU, FMNH (loans based on holdings list), FRSKU, LACM, MCZ, MNHN, NMNZ, NMV, NSMT, NTM, QM, RMNH, ROM, RUSI, SAMA, SIO, SMF, UA, USNM, WAM, ZMA, ZMB, ZMUC. Distributions are based primarily on museum specimens examined, but are supplemented with reliable literature accounts.

Results

Family Diodontidae

Diagnosis. Small to medium-sized fishes to 1 m in length, commonly 20–50 cm. Body wide and capable of great inflation, covered with massive spines that may be quite long; spines with large bases, or roots, under the skin; long spines usually erectile and two-rooted, short spines usually fixed in erect position by their three-rooted bases. Head broad and blunt; gill opening a relatively small, vertical slit immediately before pectoral-fin base; nasal organ usually in small tubes located in front of large eyes; mouth large, wide and terminal; teeth fused to form a strong, beak-like crushing structure without a median suture dividing the upper and lower jaws into left and right halves. Dorsal and anal fins without spines, set far back on body, and, like caudal fin, generally rounded; most fin rays branched; bases of fins often thick and fleshy; no pelvic fins. Lateral line inconspicuous. No normal scales.

Genera. There is no generally agreed-upon allocation of species to the nominal genera, nor is there any cladistic analysis of the family or any subset of it. Most authors recognize *Diodon* (five species, revised by Leis, 1978, ref. 5529) for species in which nearly all the dermal spines are erectile. Four monotypic Indo-Pacific genera, three of which are confined to Australasia, contain species that have a mixture of fixed and erectile spines – *Allomycterus, Dicotylichthys, Lophodiodon* and *Tragulichthys* – are usually recognized (see Gomon, 1994, ref. 22532 ; Leis, 2001, ref. 26318) and are in this paper. *Chilomycterus* sensu lato (about ten species with nearly all dermal spines fixed and immovable) has been more problematical. Tyler (1980, ref. 4477) recognized three groupings of *Chilomycterus*: 1) 'Atlantic *Chilomycterus'* (five species confined to the Atlantic, and called by him *antennatus, antillarum, mauretanicus, schoepfii* and *spinosus*); 2) what I call herein 'Circumtropical *Chilomycterus'* (a circumtropical group considered by Tyler to consist of four species called by him *affinis, atinga, reticulatus* and *tigrinus*); and 3) 'Indo-Pacific *Chilomycterus'* (considered by Tyler to consist only of *orbicularis*). I agree with Tyler (1980, ref. 4477) that nominal species in each of these three groups are morphologically more similar to each other than they are to species in the other groups. The type species of *Chilomycterus* is *Diodon reticulatus* Linnaeus (1758, ref. 2787); thus, if these groupings prove to be valid at the generic level, the circumtropical group becomes *Chilomycterus,* and I use it in that sense herein. *Cyclichthys* typically is used for several Indo-Pacific species (including two not mentioned by Tyler [1980, ref. 4477]), and the type of *Cyclichthys* is the Indo-Pacific *orbicularis;* thus, the Indo-Pacific grouping can be considered *Cyclichthys* for the purposes of this paper. The Atlantic group of species, regarded by Tyler to be the most phylogenetically basal, is nearly always included in *Chilomycterus.* If these Atlantic species were removed from *Chilomycterus*, the generic name available for them is *Lyosphaera*, based on the unique pelagic stage found in at least some members of this group. Unfortunately, the identity of the type species is not clear (on the basis of distribution, *schoepfii* seems most likely). *Lyosphaera* has not been used as a generic name for these five Atlantic species, and until a full cladistic analysis is performed on the group, its use is not recommended. For the purposes of this paper, I use Tyler's term, "Atlantic *Chilomycterus*", to identify this grouping.

Chilomycterus (ex Bibron) Brisout de Barneville, 1846 (sensu stricto)

Chilomycterus (ex Bibron) Brisout de Barneville, 1846 (type species, *Diodon reticulatus* Linnaeus)

Cyanichthys Kaup, 1855 (type species is *D. coeruleus* [non-*D. caeruleus* Quoy and Gaimard] Kaup = *D. reticulatus* Linnaeus, 1758)

Diagnosis. All spines fixed, with long subdermal bases but short or absent external spines (relatively smaller in larger individuals); some spines on top of head with 4 bases; 10 C rays; 21–23 vertebrae; heavy jaw teeth, but trituration teeth few; no tentacles; nostril in adult an open, cup-shaped organ with reticulations; 1 or more spines wholly on dorsal surface of caudal peduncle; fins spotted; no large blotches on dorsal surface of head or trunk. Some additional osteological characters are given by Tyler (1980, ref. 4477).

The type species of *Chilomycterus* is *Diodon reticulatus* Linnaeus (1758, ref. 2787). *Cyanichthys coeruleus* Kaup (1855, ref. 2571) was based on an unregistered BMNH specimen of 43 mm SL (see also Günther, 1870, ref. 1995). Although Kaup

Table 1. Nominal diodontid species and their current identity. *Allomycterus jaculiferus* McCulloch is included because of confusion about its identity. Bibliographic details can be found in Eschmeyer (2005).

Nominal species	Current identity
affinis Günther 1870	*Chilomycterus reticulatus* (Linnaeus 1758)
antennatus Cuvier 1816	*Chilomycterus antennatus* (Cuvier 1816)
antillarum Jordan & Rutter 1897	*Chilomycterus antillarum* Jordan & Rutter 1897
areolatus Gronow in Gray 1854	*Chilomycterus schoepfii* (Walbaum 1792)
armillatus Whitley 1933	*Diodon hystrix* Linnaeus 1758
atinga Bloch 1785	*Diodon hystrix* Linnaeus 1758
atringa Linnaeus 1758	not identifiable
bertolettii Lema Lucena Saenger & Oliveria 1979	*Diodon eydouxii* Brisout de Barneville 1846
bleekeri Günther 1910	*Diodon liturosus* Shaw (ex Lacepède) 1804
blochii Castelnau 1872	*Diodon nicthemerus* Cuvier 1818?
bocagei Steindachner 1866	*Diodon holocanthus* Linnaeus 1758
brachiatus Bloch and Schneider 1801	*Diodon hystrix* Linnaeus 1758
briareos Metzelaar 1919	*Chilomycterus antennatus* (Cuvier 1816)
caeruleus Quoy & Gaimard 1824	*Cyclichthys orbicularis* (Bloch,1785)
californiensis Eigenmann 1891	*Chilomycterus reticulatus* (Linnaeus 1758)
calori Bianconi 1854	*Lophodiodon calori* (Bianconi 1854)
cornutus Kaup 1855	*Chilomycterus spinosus spinosus* (Linnaeus 1758)?
digitalis Breder 1927	*Chilomycterus antennatus* (Cuvier 1816)
diversispinis Bleeker (ex Verreaux) 1865	*Dicotylichthys punctulatus* Kaup 1855
echinatus Linnaeus 1758	*Chilomycterus reticulatus* (Linnaeus 1758)
eydouxii Brisout de Barneville 1846	*Diodon eydouxii* Brisout de Barneville 1846
fuliginosus deKay 1842	*Chilomycterus schoepfii* (Walbaum 1792)
galapagosensis Klausewitz 1958	*Chilomycterus reticulatus* (Linnaeus 1758)
geometricus Bloch & Schneider 1801	*Chilomycterus antillarum* Jordan & Rutter 1897
grandoculis Ogilby 1910	*Tragulichthys jaculiferus* (Cuvier 1818)
hardenbergi de Beaufort 1939	*Cyclichthys hardenbergi* (de Beaufort 1939)
holocanthus Linnaeus 1758	*Diodon holocanthus* Linnaeus 1758
hystrix Linnaeus 1758	*Diodon hystrix* Linnaeus 1758
jaculiferus (non-Cuvier) McCulloch 1921	*Allomycterus pilatus* Whitley 1931
jaculiferus Cuvier 1818	*Tragulichthys jaculiferus* (Cuvier 1818)
lineatus Bloch & Schneider 1801	*Chilomycterus schoepfii* (Walbaum 1792)
lissogenys Günther 1910	*Chilomycterus reticulatus* (Linnaeus 1758)
liturosus Shaw (ex Lacepède) 1804	*Diodon liturosus* Shaw (ex Lacepède) 1804
maculato-striatus Mitchill 1815	*Chilomycterus schoepfii* (Walbaum 1792)
maculatus Duméril 1855	*Diodon liturosus* Shaw (ex Lacepède) 1804
maculatus Hermann 1804	not identifiable
maculifer Kaup 1855	*Diodon holocanthus* Linnaeus 1758?
mauretanicus Le Danois 1954	*Chilomycterus spinosus mauretanicus* (Le Danois 1954)
melanopsis Kaup 1855	*Diodon eydouxii* Brisout de Barneville 1846
meulenii Walbaum 1792	*Chilomycterus schoepfii* (Walbaum 1792)
multimaculatus Cuvier 1818	*Diodon holocanthus* Linnaeus 1758
myersi Ogilby 1910	*Dicotylichthys punctulatus* Kaup 1855
nicthemerus Cuvier 1818	*Diodon nicthemerus* Cuvier 1818
nigrolineatus Ayres 1842	*Chilomycterus schoepfii* (Walbaum 1792)
nigropunctatus Smith 1957	*Lophodiodon calori* (Bianconi 1854)
novemmaculatus Cuvier 1818	*Diodon holocanthus* Linnaeus 1758
nudifrons Jenkins 1904	*Diodon hystrix* Linnaeus 1758
orbe Lacepède 1798	*Chilomycterus spinosus spinosus* (Linnaeus 1758)
orbicularis Bloch 1785	*Cyclichthys orbicularis* (Bloch,1785)
orbitosus Poey 1875	*Chilomycterus antillarum* Jordan & Rutter 1897?
paraholocanthus Kotthaus 1979	*Diodon holocanthus* Linnaeus 1758
parcomaculatus von Bonde 1923	*Cyclichthys orbicularis* (Bloch,1785)
pentodon Atkinson in Bryant 1888	*Chilomycterus schoepfii* (Walbaum 1792)
pilatus Whitley 1931	*Allomycterus pilatus* Whitley 1931
pilosus Mitchill 1815	*Diodon holocanthus* Linnaeus 1758
plumierii Lacèpede 1798	*Diodon hystrix* Linnaeus 1758?
punctatus Cuvier 1818	*Diodon hystrix* Linnaeus 1758
punctulatus Kaup 1855	*Dicotylichthys punctulatus* Kaup 1855
quadradicatus Waite 1900	*Chilomycterus reticulatus* (Linnaeus 1758)
quadrimaculatus Cuvier 1818	*Diodon holocanthus* Linnaeus 1758
reticulatus Linnaeus 1758	*Chilomycterus reticulatus* (Linnaeus 1758)
rivulatus Cuvier 1818	*Chilomycterus schoepfii* (Walbaum 1792)
schoepfii Walbaum 1792	*Chilomycterus schoepfii* (Walbaum 1792)
sexmaculatus Cuvier 1818	*Diodon holocanthus* Linnaeus 1758
spilostylus Leis & Randall 1982	*Cyclichthys spilostylus* (Leis and Randall 1982)
spinosissimus Cuvier 1818	*Diodon hystrix* Linnaeus 1758
spinosus Linnaeus 1758	*Chilomycterus spinosus spinosus* (Linnaeus 1758)
tigrinus Cuvier 1818	*Chilomycterus reticulatus* (Linnaeus 1758)
torosus Larrañaga 1923	*Chilomycterus spinosus spinosus* (Linnaeus 1758)?
totara Curtiss 1938	*Diodon hystrix* Linnaeus 1758
triedricum Cuvier 1818	*Diodon hystrix* Linnaeus 1758
verrucosus deKay (ex Mitchill) 1842	*Chilomycterus schoepfii* (Walbaum 1792)
whiteleyi Phillipps 1932	*Allomycterus pilatus* Whitley 1931?

identified this specimen as *D. coeruleus* Quoy and Gaimard (an alternate spelling of *caeruleus*), it is clearly a juvenile, pelagic specimen of *Chilomycterus reticulatus* (Linnaeus). Kaup (1855, ref. 2571) asserted the specimen was from New Guinea, but according to Günther (1870, ref. 1995) the locality of the specimen "was never known at the British Museum". A single species (see below).

Chilomycterus reticulatus (Linnaeus, 1758)

Diodon reticulatus Linnaeus, 1758: 334 (India)
Diodon echinatus? Linnaeus, 1758: 335 (India)
Diodon tigrinus Cuvier, 1818: 127, pl. 6 (Moluccas)*
Chilomycterus affinis Günther, 1870: 314 (unknown locality)*
Chilomycterus californiensis Eigenmann, 1891: 1133 (San Pedro, California)*
Euchilomycterus quadradicatus Waite, 1900: 208 (Lord Howe I.)*
Chilomycterus lissogenys Günther, 1910: 476, pl. 179 (Hawaii)
Chilomycterus galapagosensis Klausewitz, 1958: 82, fig. 7 (Galapagos Is.)*
*extant type

Based on examination of 55 museum specimens, including extant types, from throughout its range (circumglobal in warm waters), I can find no morphological differences among the different nominal species or among geographic locations. There is variation in colour pattern similar to that found in the circumtropical *Diodon holocanthus* (see Leis, 1978, ref. 5529) but, like that species, it is not obviously geographically based. Spotting on the body is variable, although usually present to some degree, but smaller spots are present on at least some, and usually all, of the fins. The pelagic juvenile phase has a distinctly different colour phase from the benthic adult. The species remains pelagic to about 200 mm SL, thus providing ample opportunity for dispersal and maintenance of genetic continuity. Therefore, I regard Tyler's group of 'circumglobal *Chilomycterus*' to consist of a single species. The rationale for calling this species *Chilomycterus reticulatus* (Linnaeus) follows.

Diodon atringa Linnaeus (1758, ref. 2787) is frequently regarded as a synonym (often the senior synonym) of this species. This name is often misspelled *atinga* by authors. This is clearly incorrect: Linnaeus used the spelling *atringa* in both his tenth and twelfth editions. Nelson et al. (2004, ref. 27807) recently explained why *atringa* is correct; and Eschmeyer (2005) used *atringa*. To avoid confusion with *D. atinga* Bloch (1785, ref. 4866), a synonym of *D. hystrix*, I herein use the spelling *atringa* for the Linnaean species, regardless of the spelling used by any subsequent author. Unfortunately, *D. atringa* Linnaeus is not identifiable. There is no type, and Linnaeus' description could apply to any of several species of *Chilomycterus* or *Cyclichthys (*including *C. reticulatus, C. antennatus* or *C. spinosus*), and the same is true of Artedi (1738), the only source cited by Linnaeus, and the pre-Linnaean authors cited by Artedi. Artedi, 1738 mentioned that the fins of his "Ostracion bidens sphaericus…", upon which Linnaeus based his *D. atringa,* were spotted, but large individuals of *C. antennatus* (Cuvier, 1816, ref. 993) also have spotted fins (see below), so this is not diagnostic, as is often assumed. Linnaeus (1766, ref. 2786) cited a plate in Seba (1759, ref. 18716) that represents either *C. reticulatus* or *C. antennatus*. Brisout de Barneville (1846, ref. 296) was the first author to express a clear opinion, and considered *D. atringa* Linnaeus to be synonymous with *D. orbe* Lacepède (1798, ref. 2708). The latter was based on a specimen from Brazil – no longer extant – that is clearly identifiable as the Atlantic *Diodon spinosus* Linnaeus (see below). Le Danois (1959, ref. 12003) considered *atringa* Linnaeus to be approximately equivalent to Tyler's "Atlantic *Chilomycterus*" group (which includes *D. spinosus* Linnaeus) with several subspecies roughly equivalent to Tyler's species.

In contrast, *D. reticulatus* Linnaeus (1758, ref 2787) is readily identifiable. Linnaeus based his description on Artedi's "*Ostracion subrotudus*…". Atredi (1738) cited a Willughby (1686) plate of "Orbis muricatus and reticulatus" that is clearly identifiable as *reticulatus* by its colour, general morphology, spine distribution and spine shape. The name *reticulatus* has been in regular use as a senior synonym (in addition to the nine 1870–1926 references listed by Fowler, 1936, ref. 6546 and the >30 post-1985 references listed by Eschmeyer, [2005]: Lowe, 1844, ref. 2833; Brisout de Barenville, 1846, ref. 296; Günther, 1870, ref. 1995; Poey, 1876, ref. 3510; Goode, 1876, ref. 1832, 1877, ref. 13360; Jordan and Gilbert, 1883, ref. 2476; Eigenmann, 1885; Poll, 1959, ref. 12014; Tyler, 1980, ref. 4477; Leis, 1981, 1984; Leis and Bauchot, 1984, ref. 12539). Some authors, apparently following Jordan and Evermann (1898, ref. 2444, have considered *reticulatus* to be a junior synonym of *atringa*, but none have attempted to justify this view. It is clear from Jordan and Evermann's description and key that they incorporated more than one species in their concept of *C. atringa*, including at least *C. reticulatus* and *C. antennatus*. Jordan and Evermann (1898) described *C. atinga* as having dark dorsal blotches and a 'supraocular cirrus', both features that are lacking in *C. reticulatus* (Linnaeus) and in Tyler's 'circumtropical *Chilomycterus*', but present in species of the 'Atlantic *Chilomycterus*' group.

There is a great deal of confusion in the literature as to just what constitutes *C. reticulatus* and *C. atringa*. For much of the 19th century, most authors accepted Bloch's (1785, ref. 21381) concept of *D. atinga* (=*D. hystrix* Linnaeus, 1758, ref. 2787), and although Brisout de Barneville (1846, ref. 296) pointed out that this was in error, the use of *D. atinga* sensu Bloch persisted for some years. Séret and Opic (1981) stated without reasons that *reticulatus* was a synonym of *C. atringa* (Linnaeus), but their illustration of C. *atringa* shows what appears to be *C. antennatus* (Cuvier) (Séret and Opic kindly provided unpublished dorsal and lateral views of the specimen that strengthen this opinion). Similarly, Tortonese (1973, ref. 7192), without comment, listed *reticulatus* as a junior synonym of *atringa*, but, later, Tortonese (in Whitehead et al., 1986, ref. 13677) illustrated as *C. atringa* a specimen of the eastern Atlantic *C. spinosus mauretanicus* (Le Danois), but with spotted fins, a feature I have not observed in the latter species. Smith-Vaniz et al., 1999 (ref. 25013) listed *C. atringa* (Linnaeus) as occurring in Bermuda, but had seen no specimens, stating that their listing was based on Goode's (1876, ref. 1832; 1877, ref. 13360) and Günther's (1870, ref. 1995) records of *C. reticulatus*. Unfortunately, this leads to ambiguity because, Smith-Vaniz et al. (1999, ref. 25013) could be interpreted as considering *reticulatus* a synonym of *atinga*, or as considering that the other authors misidentified their

specimens. Some other workers (e.g., Fowler, 1936, ref. 6546; Lozano Rey, 1952) have included *reticulatus* of authors in their synonymies of *atringa*, but not *reticulatus* Linnaeus (1758, ref 2787), implying that they questioned others' concept of *reticulatus* rather than that they considered *reticulatus* Linnaeus to be a junior synonym of *atringa*.

In more recent years, a view has developed among some American workers that Atlantic individuals of this taxon are *C. atringa*, whereas the Indo-Pacific individuals are either *C. affinis* (Robins et al., 1991, ref. 14237) or *C. reticulatus* (Nelson et al., 2004, ref. 27807), but, again, no justification for this or means of distinguishing the two nominal species has ever been presented. Tyler (1980, ref. 4477) tentatively recognized four species in this complex that have, based on his material examined and text, different distributions: *C. atringa* (western Atlantic); *C. reticulatus* (eastern Atlantic and Indo-Pacific); *C. tigrinus* (western Indian Ocean); and *C. affinis* (Eastern Pacific). However, Tyler (1980, ref. 4477) said that *C. tigrinus* may be the young of *C. reticulatus* (I agree). So confusion about the identity and distribution of these species continues.

In summary, *D. atringa* Linnaeus is unidentifiable, and the post-Linnaean use of the name by various authors has been inconsistent as to what species was being included: at least four species and two multi-species groups have been identified as *D. atringa* by various authors at various times. In spite of the use of *C. atringa* (usually spelled *atinga*) by several authors, the name should be regarded as a nomen dubium, and not used. *Diodon reticulatus* Linnaeus is clearly identifiable, and the use of the name has been remarkably consistent: it should be used for this species.

Diodon echinatus Linnaeus (1758, ref 2787) is seemingly equivalent to his *Chilomycterus reticulatus* (see Leis and Randall, 1982). Linnaeus' (1758, ref 2787) description and the Marcgrave plate to which Artedi (1738) referred could apply to any *Chilomycterus* or *Cyclichthys* species. Linnaeus (1766, ref. 2786) referred to a Seba (1759, ref. 18716) figure that is clearly *Diodon hystrix*. Gronow (1854, ref. 6828), in his account of "*Holocanthus echinatus*", cited a Seba (1759, ref. 18716) figure that is either *Chilomycterus reticulatus* or *C. antennatus*, and a Willughby (1686) figure that clearly represents *C. reticulatus*.

The holotype of *Diodon tigrinus* Cuvier (1818, ref. 18059) is a specimen in the pelagic colour phase of *C. reticulatus*. The species was recognized as a synonym of *C. reticulatus* as long ago as Brisout de Barneville (1846, ref. 296).

Chilomycterus affinis Günther (1870, ref.1995) was based on a specimen of unknown locality that is dried and thickly varnished. The holotype has minimal spotting on the body, and the spines, particularly on the head, are distorted by the taxidermy and insertion of large, blue glass eyes. However, there is nothing outside of the range of *C. reticulatus* variability in this specimen. In the absence of any locality information, it is unclear why most authors regarded this as a Pacific species.

Chilomycterus californiensis was described by Eigenmann (1891, ref. 18744) on the basis of a specimen that he initially did not obtain from the fisherman who captured it "on account of the unreasonable price asked for it". However, the fish was subsequently "procured by the National Museum", and Eigenmann (1892) redescribed and figured it. Therefore, USNM 43860 is in fact the holotype, in spite of Eigenmann's statement in the original 1891 description that "I did not obtain it". The holotype is in the pelagic colour phase of *C. reticulatus*.

Euchilomycterus quadradicatus Waite (1900, ref. 4558) from Lord Howe I. was based on a dried specimen – apparently a beach wash-up – subsequently preserved in ethanol and in poor condition. Although not figured by Waite, Whitley (1952) illustrated the holotype (with some artistic license) clearly showing the caudal-peduncle spine and four-rooted spines on the head that in combination are diagnostic of *Chilomycterus reticulatus*.

Chilomycterus lissogenys Günther (1910, ref. 14460) was based on an illustration by Garrett of a Hawaiian fish. Although Garrett omitted some of the spines on the side of the head, he clearly showed the spine on the caudal peduncle that is characteristic of *C. reticulatus*. The illustration showed relatively few spots on the body, but heavily spotted fins, a condition well within the range of colour variation in this species.

The description and photo of *Chilomycterus galapagosensis* Klausewitz (1958, ref. 12080) are clearly that of *C. reticulatus*. The description of the nostrils alone is diagnostic. Klausewitz distinguished his new species from *C. atringa*, which he described as having a supraorbital cirrus and large dorsal blotches (presumably based on the description of Jordan and Evermann [1898, ref. 2244], which was based on more than one species), by its lack of these two characteristics. He distinguished it from *C. californiensis* by colour, but the latter is in pelagic-phase colour, whereas *C. galapagosensis* has typical, spotted demersal colour.

Distribution. Circumglobal in warm temperate to tropical waters:

W Atlantic – 39°N to 24°S

E Atlantic – Madeira (and possibly to Portugal) and Cape Blanco to Angola

W Indian Ocean – South Africa to Tanzania and Reunion, Seychelles and Mauritius

E Indian Ocean – Broome, Western Australia to Bali and Timor

W and central Pacific – Japan to Lord Howe I. and northern New Zealand, to Tuamotos to Hawaii (and in the east Pacific barrier)

E Pacific – San Pedro, California to Chile, Galapagos and Revillagigedos

Occurrences of this species are patchy, and many are based on pelagic juveniles: in particular, adults are unknown from broad areas of the Indo-Pacific. Pelagic juveniles are frequently found poleward of the distribution of adults in areas of strong, poleward currents.

If future work indicates that *C. reticulatus* contains more than one geographically distinct species, several names are available for Indo-Pacific populations, but no name is clearly based on Atlantic material. Most of the extant types are either dried or fixed in alcohol, so it may be possible to obtain genetic data from them that could be helpful. Unfortunately, there are no Linnaean types that might assist in this regard, and Linnaeus' usage of 'habitat in India' cannot be taken at face value in most cases.

Cyclichthys Kaup, 1855

Cyclichthys Kaup, 1855 (type species *Diodon orbicularis* Bloch)

Diagnosis. All but 1 or 2 spines fixed; all spines with 3 bases, except in *C. spilostylus* which has some spines on top of head with 4 bases; 9 C rays; 19–20 vertebrae; no tentacles in adults; nostril in adult a short tube with 2 openings; no spines wholly on dorsal surface of caudal peduncle; no fins spotted; no large blotches on dorsal surface. Some additional osteological characters are given by Tyler (1980, ref. 4477) for *C. orbicularis*.

The type species of this genus is *C. orbicularis* (Bloch, 1785, ref. 21381). Kaup (1855, ref. 2571) included two species in his *Cyclichthys – orbicularis* Bloch, and *cornutus* Kaup – but designated neither as type species for the genus. Subsequently, Bleeker (1865, ref. 416) was apparently the first to designate a type species for *Cyclichthys* and chose *orbicularis* Bloch (Eschmeyer, 2005). Fraser-Brunner (1943, ref. 1495) used *Cyclichthys* as a subgenus of *Chilomycterus*. He did not consider *C. hardenbergi*, but included *C. orbicularis*, the "Atlantic *Chilomycterus*" species, and *C. echinatus* non-Linnaeus (= *C. spilostylus*) in his concept of the subgenus *Cyclichthys*. Tyler (1980, ref. 4477) pointed out that *C. orbicularis* had osteological differences from the other diodontids he studied, and placed the species in a group on its own. However, he was not able to examine specimens of *C. spilostylus* or *C. hardenbergi*. Based on external morphology, it appears that *C. orbicularis* differs from other species that have been included in *Cyclichthys* by Fraser-Brunner (1943, ref. 1495), and there is merit in Tyler's placement. If this were done, then a new genus would probably have to be described for *hardenbergi* and *spilostylus*, as they do not appear to be monophyletic with the "Atlantic *Chilomycterus*" species. Pending a cladistic analysis of relationships in the family, I recognize three species in *Cyclichthys*, which has been standard practice in recent years.

Cyclichthys orbicularis (Bloch, 1785)

Diodon orbicularis Bloch, 1785: 73, pl. 127 (Jamaica?, Cape of Good Hope & Moluccas)*?

Diodon caeruleus Quoy and Gaimard, 1824: 201, pl. 65 (fig. 5) (North of New Guinea, 142°E, at the Equator)*

Chilomycterus parcomaculatus von Bonde, 1923: 38, pl. 9 (fig. 2) (Natal, South Africa)

* extant type

Based on examination of 88 lots from throughout the range, including the extant types. There has been no real question as to the identity of this wide-spread and common species.

Although Bloch's (1785, ref. 21381) types might all be lost, his plate showing the arrangement of spines, especially those near the mouth, is diagnostic of this species. There is one specimen of unknown origin in ZMB that may be a syntype of this species (Paepke, 1999, ref. 24282), but definitive evidence is lacking. The alleged type locality of Jamaica appears to be in error.

The holotype of *Diodon caeruleus* Quoy and Gaimard (1824, ref. 3574) was described and figured, and the specimen is extant (see Leis and Bauchot, 1984, ref. 12539), leaving no doubt that it is conspecific with *C. orbicularis* (Bloch).

Chilomycterus parcomaculatus von Bonde (1923, ref. 521) was based on a specimen that was 'inadvertently destroyed' (S.X. Kannemeyer, personal communication, 1/2/80), but the description and figure are diagnostic.

Distribution. Indo-west Pacific

W Indian Ocean – Capetown, South Africa to Red Sea, Oman and Persian Gulf, Maldives, Reunion.

E Indian Ocean – Shark Bay, Western Australia to Burma

W Pacific – southern Japan and Sea of Japan to Sydney, Australia and east to Philippines and New Caledonia.

Cyclichthys hardenbergi (de Beaufort, 1939)

Chilomycterus hardenbergi de Beaufort, 1939: 33–34 (New Guinea)*

*extant type

Based on examination of 21 museum specimens from throughout the limited range, including the holotype. There are no real questions as to the identity of this species: de Beaufort's (1939, ref. 17230) description is diagnostic, and the type is extant. This species has one of the more limited ranges within the family.

Distribution. Indo-Pacific

North-western Australia to the west coast of Cape York, and the south coast of New Guinea. Kailola (1975) also recorded it from the Trobirand Islands.

Cyclichthys spilostylus (Leis and Randall, 1982)

Chilomycterus spilostylus Leis and Randall, 1982: 363, figs 1, 2 (Red Sea)*

*extant types

Based on examination of 23 museum specimens, including the types. This species was mis-identified as *Cyclichthys echinatus* (Linnaeus, 1758, ref. 2787) by some authors (see Leis and Randall, 1982, ref. 8453), but *echinatus* is most likely a synonym of *Chilomycterus reticulatus* (Linnaeus). Other than this, there are no real questions as to the identity of this wide-ranging species. The pelagic stage of this species has a tentacle emerging from each spine. These tentacles are lost at settlement.

Distribution. Indo-Pacific

W Indian Ocean – Capetown, South Africa to Gulf of Elat, Red Sea, Muscat to western India and Mauritius (also a Mediterranean record from Israel by Golani (1993), presumably via Suez Canal)

E Indian Ocean – Northwest Cape, Western Australia to Bali

W Pacific – Southern Japan to Hong Kong, Philippines, New Caledonia, and northern Great Barrier Reef.

E Pacific – Galapagos (single record, including photograph, by Humann [1997], repeated by Grove and Lavenberg [1997], ref. 24023).

"Atlantic *Chilomycterus*"

Lyosphaera Evermann and Kendall, 1898: 131 (type species *Lyospharea globosa* Evermann and Kendall, possibly = *Diodon schoepfii* Walbaum, 1792)

Atinga Le Danois, 1954: 2356. (type species *Diodon atringa* Linnaeus – see Eschmeyer, 2005, and below).

Diagnosis. All spines fixed; all spines with 3 bases; 9 C rays; 19–20 vertebrae; tentacles present on lower jaw and usually over eye; nostril in adult a short tube with 2 openings; no spines wholly on dorsal surface of caudal peduncle; no fins spotted (except in large *C. antennatus*); large blotches present on dorsal surface. Some additional osteological characters are given by Tyler (1980, ref. 4477). At least 2 of the species of this group share the "*Lyosphaera*" larval stage (*antennatus* and the type species of *Lyosphaera*), and others may do the same.

Although the genus *Lyosphaera* Evermann and Kendall (1898, ref. 1281) is available as a generic name for this group, I recommend against its use until a cladistic analysis of the "Atlantic *Chilomycterus*" species and their relationship to other diodontids is undertaken. *Lyosphaera* has never been used in this way, and the identity of the type species is unclear (although most likely to be *schoepfii* based on distribution). The species upon which *Atinga* Le Danois (1954, ref. 6451) is based is unclear. The type species, *D. atringa* Linnaeus (1758, ref. 2787), is not identifiable (see above under *C. reticulatus*). It is clear that Le Danois' (1954, ref. 6451; 1959, ref. 12003; 1962, 21440) concept of *atinga* included a species of the "Atlantic *Chilomycterus*" group, although which species is unclear as her illustrations of *Atinga atinga atinga* in the 1954 paper are of *C. antillarum* (identified as male) and *C. spinosus mauretanicus* (identified as female). In view of this confusion about the identity of the type species, use of *Atinga* Le Danois (1954: ref. 6451) is not recommended. It has been little used since its description.

The "Atlantic *Chilomycterus*" is a group of similar species previously recognized in various ways by Günther (1870, ref. 1995), Le Danois (1959, ref. 12003) and Tyler (1980, ref. 4477). See above regarding the generic status of these species. *Chilomycterus antennatus* is the only member of this group that I can separate on morphological grounds; principally, the development of the fleshy tentacles over the eye. It also has a colour pattern that differs more from the other species of the "Atlantic *Chilomycterus*" group than they do from each other. The other four taxa differ only in colour, and have largely non-overlapping distributions. In all but the case of the very similar forms, *C. spinosus* (Linnaeus, 1758, ref. 2787) and *C. mauretanicus* (Le Danois, 1954, ref. 6451), the distributions do at least seem to come into contact. In contrast, the latter two taxa occur only on opposite sides of the Atlantic and they have only very minor differences in colouration. Hence, I treat these two as subspecies: *Chilomycterus spinosis spinosus* and *Chilomycterus spinosus mauretanicus*. In some cases, colour patterns do exhibit intermediacy. *Chilomycterus schoepfii* adults have a distinctive lined pigment pattern, but the youngest *C. schoepfii* have a colour pattern not unlike that of *C. spinosus* (dark background with lighter, diffuse spotting), and at intermediate sizes, the dark background may have shrunk to a mesh-like pattern with expanded lighter centres similar to that of *C. antillarum*. Similarly, in northern South America, a colour pattern with elements of both *C. spinosus* and *C. antillarum* is present. Examination of the genetics of these "Atlantic *Chilomycterus*" species would be very interesting.

Chilomycterus spinosus spinosus (Linnaeus, 1758)

Diodon spinosus Linnaeus, 1758: 335 (India)
Diodon orbe Lacepède, 1798: 124, pl. 3 (Rio de Janeiro)
Cyclichthys cornutus Kaup, 1855: 231? (unknown locality)*
Tetrodon torosus Larrañaga, 1923: 390? (Uruguay)
*extant type

Based on examination of 24 lots (50–200 mm) from throughout the range, and the extant type of *C. cornutus* Kaup (BMNH 1849.1.15.36).

Linnaeus (1758, ref. 2787) based his description of *Diodon spinosus* on Artedi (1738), who cited an illustration by Willughby (1686). This information is sufficient to determine that the species is one of the "Atlantic *Chilomycterus*" species, but without any lines or small spots on the body. This eliminates *schoepfii*, *antennatus*, *antillarum* and *mauretanicus*, leaving *spinosus* as the unlined, unspotted species of this group.

Lacepède (1798, ref. 2708) provided a figure of *D. orbe* that clearly shows the arrangement of spines and the diagnostic dorsal blotches and lack of small spots or lines on the body. This and the type locality leave no doubt that *Diodon orbe* is conspecific with *C. spinosus* (Linnaeus).

The type of *Cyclichthys cornutus* Kaup (1855, ref. 2571) is a small, stuffed specimen of unknown origin with a thick coat of varnish, but the spine arrangement and presence of a supraocular tentacle show that it is clearly a species of the "Atlantic *Chilomycterus*" group. The visible colour pattern best fits *C. spinosus* (Linnaeus).

Tetrodon torosus Larrañaga (1923: 390 ref. 22561: not seen by me) has been regarded as a synonym of *Chilomycterus spinosus* (Linnaeus) since 1925 (Devincenzi, 1925, ref. 20322, see Eschmeyer, 2005) and I am unaware of any subsequent use of the name. If the synonymy of Devincenzi is correct, Uruguay would represent the southernmost record of *C. spinosus spinosus*.

As noted above, eastern Atlantic specimens of *C. spinosus* have oblique, irregular lines laterally on the trunk and head that are lacking in western Atlantic specimens. Therefore, I have recognized the western Atlantic population as the nominate subspecies and the eastern Atlantic population as *C. spinosus mauretanicus* (Le Danois) (see below).

Distribution. Western Atlantic

From northern coast of South America (Surinam and British Guiana) to Rio de Janeiro, Brazil.

Chilomycterus spinosus mauretanicus (Le Danois, 1954)

Atinga atinga mauretanicus Le Danois, 1954: 2354 (Mauritania, Gulf of Guinea)*
*extant types

Based on examination of 21 lots from throughout the range, including the syntypes. This nominal species is considered a subspecies of *C. spinosus* (Linnaeus) because only minor colour differences separate it from its western Atlantic counterpart. Le Danois (1954, ref. 6451) briefly described this nominal species, apparently inadvertently, in a paper on sexual dimorphism in diodontids, then redescribed it in 1959 (ref. 12003) and provided more information – some of it conflicting – in 1962 (ref. 21440). See Leis and Bauchot (1984, ref. 12539) for information on the status of the types.

Distribution. Eastern Atlantic.

From central Angola to Canary Is. and perhaps Portugal.

Chilomycterus schoepfii (Walbaum, 1792)

Diodon schoepfii Walbaum, 1792: 601 (New York)
Diodon meulenii Walbaum, 1792: 602 (unknown locality)
Diodon geometricus var. *lineatus* Bloch and Schneider, 1801: 513 (New York)
Diodon maculato-striatus Mitchill, 1815: 470 (New York)
Diodon rivulatus Cuvier, 1818: 129, pl. 6 (unknown locality [New York, USA according to Eschmeyer, 2005])*
Diodon nigrolineatus Ayres, 1842: 68 (Brookhaven, Long Island, New York)
Diodon fuliginosus deKay, 1842: 324, pl. 55 (fig. 181) (New York)
Diodon verrucosus deKay (ex Mitchill), 1842: 325, pl. 55 (fig. 1)? (New York)
Holocanthus areolatus Gronow in Gray, 1854: 27? (Cape of Good Hope, South Africa?)
Chilomycterus pentodon Atkinson in Bryant, 1888: 18 (Beaufort, North Carolina, USA)
* extant type.

Based on examination of 62 lots from throughout the range. Unfortunately, I could locate types of only one of the ten nominal species represented here.

Walbaum's (1792, ref. 4572) description of *D. schoepfii* mentions the diagnostic lined colour pattern of this species, as do the descriptions of *Diodon meulenii* Walbaum (1792, ref. 4572), *Diodon geometricus* var *lineatus* Bloch and Schneider (1801, ref. 471), *Diodon maculato-striatus* Mitchill (1815, ref. 13292), *Diodon rivulatus* Cuvier (1818, ref. 18059), *Diodon nigrolineatus* Ayres (1842, ref. 15926), *Diodon fuliginosus* deKay (1842, ref. 1098), *Holocanthus areolatus* Gronow in Gray (1854, ref. 6828) and *Chilomycterus pentodon* Atkinson in Bryant (1888, ref. 13034), thus confirming their identification. The type locality of South Africa for *H. areolatus* provided by Gronow introduces some doubt, but this may well be an error, as there is no diodontid species with a lined colour pattern in that area. *Diodon verrucosus* deKay (ex Mitchill) (1842, ref. 1098) has a pigment pattern similar to that of *C. antillarum*, but, apparently, *C. schoepfii* passes through an early life-history phase with this colour pattern, and the type locality of New York would seem to eliminate the tropical *C. antillarum*, so I tentatively consider *verrucosus* to be a synonym of *C. schoepfii*.

Distribution. Western North Atlantic

From Halifax, Nova Scotia (waif) to Belize (apparently with a gap between southern Texas and Belize) on the mainland and Cuba, Bermuda and Bahamas.

Chilomycterus antennatus (Cuvier, 1816)

Diodon antennatus Cuvier, 1816: 185, pl. 9 (unknown locality)*?
Chilomycterus briareos Metzelaar, 1919: 173, fig. 55 (Lesser Antilles, St Eustatius)*
Lyosphaera digitalis Breder, 1927: 81, fig. 34 (locality unknown Western North Atlantic or W Indies)*
*extant type.

Based on examination of 37 lots, including extant types (see Leis and Bauchot, 1984, ref. 12539, for a discussion of the status of the types of *D. antennatus* Cuvier [1816, ref. 993]). In spite of assertions to the contrary, *C. antennatus* can have spotted fins. Fin spotting in *C. antennatus* begins basally on all fins at about 50 mm SL. The caudal fin becomes mostly or entirely spotted by 100–150 mm SL. Spotting on other fins seems variable, but basal one-third to one-half of the P, D and A fins can be spotted in specimens as small as 127 mm SL, whereas other specimens as large as 200 mm may have spots only on the extreme base on these fins. Because many ichthyologists have assumed that any *Chilomycterus* with spotted fins is *C. reticulatus* (or one of its synonyms), this has led to many misidentifications of C. *antennatus*, and is probably the basis for Jordan and Evermann's (1998, ref. 2244) inclusion of what are apparently characteristics of *C. antennatus* in their description of *C. atringa*.

Aside from colour differences, *C. antennatus* has larger fleshy tentacles, particularly over the eye, than do the other "Atlantic *Chilomycterus*" species. It clearly has a *Lyosphaera* stage larva (Heck and Weinstein, 1978).

Cuvier's (1816, ref. 993) description and figure were diagnostic of the species, and what is probably the type is extant in MNHN (see Leis and Bauchot, 1984, ref. 12539), leaving no doubt about the identity of this distinctive species.

The description and figure of *Chilomycterus briareos* Metzelaar (1919 ref. 2982) clearly refers to C *antennatus*, and the type is extant. The fish has spots on the fins, particularly on the caudal fin, which is common in larger individuals of *C. antennatus*.

In contrast, *Lyosphaera digitalis* Breder (1927, ref. 635), is the young '*Lyosphaera* stage' of this species, virtually lacking spines. Heck and Weinstein (1978) have documented the transition of this distinctive '*Lyosphaera* stage' to the juvenile of *C. antennatus*.

Distribution. Western Atlantic (possibly eastern Atlantic).

W Atlantic – Key West Florida to Panama, Colombia and Tobago, Bermuda, and throughout Caribbean and Antilles.

E Atlantic – no specimens, but see below.

There are persistent reports of *C. antennatus* from the eastern Atlantic, but I have seen no specimens from this area. Where published descriptions or illustrations of "*Chilomycterus antennatus*" from the eastern Atlantic are diagnostic, they are usually of *C. spinosus mauretanicus*, or in some cases *C. reticulatus*. However, there is one published illustration of a fish from Senegal that does appear to be *C. antennatus*, although it is identified in the publication as *C. atringa* (Linnaeus) (Séret and Opic, 1981). Unfortunately, the specimen was not retained (B. Séret, personal communication). When I requested a specimen for study, Séret, who was not in Senegal at the time, kindly arranged for a colleague to send me one: it was *C. spinosus mauretanicus*. Therefore, it is possible that *C. antennatus* does occur rarely in the eastern Atlantic, most likely as a waif from the west. Specimens are needed to confirm this.

Chilomycterus antillarum Jordan and Rutter, 1897

Diodon geometricus Bloch and Schneider, 1801: 513, pl. 96 (coast of Brazil)
Chilomycterus antillarum Jordan and Rutter, 1897: 131 (Kingston, Jamaica)*

* extant type

Based on examination of 41 specimens including extant types. Although D. *geometricus* Bloch and Schneider (1801, ref. 471) is an older name than *C. antillarum* Jordan and Rutter (1897, ref. 10644), and the Bloch and Schneider figure clearly applies to the same species, the name has been little used since its description other than as a junior synonym of either *spinosus* or *schoepfii*. Other than Paepke's (1999, ref. 24282) catalogue of Bloch types (unfortunately, the type of *geometricus* is lost), the most recent correct use of *geometricus* was Günther (1870, ref.1995), and this for only one of his 'varieties' (i.e., beta). In contrast, *C. antillarum* has been widely, almost universally, used for this species (see Eschmeyer, 2005, for 13 publications between 1983 and 2003; in addition, Bailey et al., 1960, ref. 27285; 1970, ref. 27286; Böhlke and Chaplin, 1968, ref. 23150; Randall, 1968; 1996; Tyler, 1977; 1980, ref.4477; Robins et al., 1980, ref. 7111; 1991, ref. 14237; Lieske and Myers, 1994; Cervigón, 1996, ref. 24489; Smith, 1997; Lyczkowski-Schultz, et al., 2005). Because the senior synonym (*geometricus*) has not been used as a valid name after 1899, and because the junior name has been used in at least 25 works published by at least ten authors over the last 50 years, this meets the criteria of Articles 23.9.1 and 2 of ICZN (1999, ref. 26875), and prevailing usage (of *antillarum*) must be maintained. In 2003, I suggested that current usage of *C. antillarum* be maintained in the interests of stability (Leis, 2003, ref. 27121), and here provide evidence that ICZN criteria require this to be met.

Chilomycterus orbitosus Poey (1875: 69, ref. 18564) is clearly a species of the "Atlantic *Chilomycterus*" group, but there is no known extant type. Poey's brief description on Cuban specimens seems to be based on a composite of *C. antillarum* and *C. schoepfii* from Cuba, but perhaps best fits the former. The name *orbitosus* has not been used since its description, as far as I can ascertain. So, even if it could be established that *orbitosus* Poey, 1875 and *antillarum* Jordan and Rutter, 1897 are conspecific, I would recommend against the use of the older *orbitosus* in the interests of stability.

Distribution. W Atlantic.

Florida, Bahamas and Cuba to Venezuela, Barbados and Brazil

Some Brazilian specimens are intermediate in colour between the crisp, dark hexagonal pattern typical of *C. antillarum* and the dark background with vague lighter spots typical of *C. spinosus spinosus*. The significance of this is unknown, and further investigation is required.

Tragulichthys Whitley, 1931

Tragulichthys Whitley, 1931 (type species *D. jaculiferus* Cuvier)

Diagnosis. All spines fixed, except those in pectoral axil which are by far the longest on the body; all spines except those in the P axil with 3 bases; spines long to medium; 9 C rays; 19 vertebrae; no tentacles in adults; nostril in adult a short tube with 2 openings, but may become bifurcate in larger individuals; no spines wholly on dorsal surface of caudal peduncle, but large spines extend over the peduncle nearly to the caudal-fin base; no fins spotted; no large blotches on dorsal surface. Some additional osteological characters are given by Tyler (1980, ref. 4477) as *Diodon jaculiferus*.

The type species of this monotypic genus is *D. jaculiferus* Cuvier (1818, ref. 18059). Most of the spines are fixed in the normal 'burrfish' manner, but those in the pectoral axil, which are by far the longest on the body, are erectile. Some have regarded *Tragulichthys* Whitley (1931, ref. 4673) as a synonym or subgenus of *Diodon* (Fraser-Brunner, 1943, ref. 1495; Tyler, 1980, ref. 4477). But, until a full analysis of the phylogeny of the family is forthcoming, it seems best to maintain current usage and to recognize *Tragulichthys* at the generic level because the only species has a number of morphological differences from the five species normally included in *Diodon*.

Tragulichthys jaculiferus (Cuvier, 1818)

Diodon jaculiferus Cuvier, 1818: 130, pl. 7 ('Indian Ocean via Peron')*

Chilomycterus grandoculis Ogilby, 1910: 19 (Moreton Bay, Queensland)*

*extant type

Based on examination of 50 lots, including extant types, from throughout the range. Aside from confusion regarding the designation of a type species for *Allomycterus* (see below), there have been few nomenclatural issues regarding this tropical Australian species. References to this species from New Zealand are of *Allomycterus pilatus* (see below): *T. jaculiferus* does not occur in New Zealand.

Cuvier's (1818, ref. 18059) description, figure, and the extant type leave no doubt about the identity of this distinctive species. The description of *Chilomycterus grandoculis* Ogilby (1910, ref. 3288) details the diagnostic spination, and the extant type makes it clear that it is conspecific with *T. jaculiferus*.

Distribution. Northern Australia.

From Derby, Western Australia to Darwin (including Rowley Shoals) to Torres Strait and south to Moreton Bay, Qld.

Dicotylichthys Kaup, 1855

Dicotlylichthys Kaup, 1855 (type species *Dicotylichthys punctulatus* Kaup)

Atopomycterus Bleeker (ex Verreaux), 1865 [type species *Atopomycterus diversispinus* Bleeker (ex Verreaux)]

Diagnosis. Spines on head and belly erectile, those on back and sides fixed; fixed spines with 3 bases, erectile spines with 2 bases; spines long to medium; 9 C rays; 21 vertebrae; no tentacles; nostril in adult bifid; no spines wholly on dorsal surface of caudal peduncle, but large spines extend over the peduncle nearly to the caudal-fin base; no fins spotted; no large blotches on dorsal surface, but lateral bars present. Some additional osteological characters are given by Tyler (1980, ref. 4477).

The type species of *Dicotylichthys* is *D. punctulatus* Kaup (1855, ref. 2571). The sole species in this genus has erectile spines on the head and belly, but fixed ones on the back and sides. In contrast to the arrangement adopted here, some authors follow Fraser-Brunner (1943, ref. 1495) and include all diodontids that develop bifid nasal organs in *Dicotylichthys*.

This would place in the same genus such disparate species as *pilatus* with all fixed spines, *punctulatus* with a mixture of erectile and fixed spines, and *nicthemerus* with all erectile spines. However, *Dicotylichthys* is very similar to the monotypic *Lophodiodon* (see below). Bleeker's (1865, ref. 416) description of *Atopomycterus* (based on an unpublished manuscript by Verreaux held in MNHN) is brief, but fortunately the types of *A. diversispinus* Bleeker are extant (see below), thus clearly showing that *Atopomycterus* is a synonym of *Dicotylichthys*.

Dicotylichthys punctulatus Kaup, 1855

Dicotylichthys punctulatus Kaup, 1855: 230 (Cape of Good Hope, South Africa and Mauritius, but these localities are apparently incorrect, see below)*

Atopomycterus diversispinis Bleeker (ex Verreaux), 1865: 49 (Australia)*

Dicotylichthys myersi Ogilby, 1910: 18 (Moreton Bay, Queensland, Australia)*

* extant type

Based on over 50 lots from throughout the range, including all extant types. Kaup's (1855, ref. 2571) description is not detailed, but the extant specimens upon which he based his description are all of this distinctive species.

Although Bleeker's 1865 description of *Atopomycterus diversispinis* is brief, and not detailed, the syntypes are extant and readily identified as *D. punctulatus* Kaup (1855, ref. 2571; see Leis and Bauchot, 1984, ref. 12539).

Dicotylichthys myersi Ogilby (1910 ref. 3288) was said by Ogilby to differ from *D. punctulatus* by the relative size of the abdominal spines, but the syntypes are well within the range of relative spine size of *D. punctulatus*.

Distribution. South-eastern Australia.

From Moreton Bay, Qld to Bass Strait.

Kaup (1855, ref. 2571) reported that his type specimens came from the Cape of Good Hope and Mauritius. Subsequently, Günther (1870, ref. 1995) reported that the only specimen in BMNH identified as being from Mauritius was of questionable locality, and that the sole specimen from the Cape of Good Hope (which he identified as the 'type' of *D. punctulatus*) was "presented by Sir A. Smith". Smith was a medical doctor resident in Cape Town who procured many specimens from passing ships, and then provided them to the British Museum, where they were generally assumed to have originated in Cape Town (Bass et al., 1975, ref. 7409). Thus, there is good reason to question the locality data of Smith specimens (Bass et al., 1975, ref. 7409) if other evidence is inconsistent with them. Other than this BMNH specimen, I have been unable to find any institution (including RUSI) that has specimens of *D. punctulatus* from anywhere but Australia, where it is abundant within its range. Thus, I conclude that Sir A. Smith procured his specimen from a passing ship, not from the Cape of Good Hope, and that this species is endemic to south-eastern Australia.

Allomycterus McCulloch, 1921

Allomycterus McCulloch, 1921 (type species *Allomycterus jaculiferus* [non-Cuvier] McCulloch = *Allomycterus pilatus* Whitley)

Diagnosis. All spines fixed except 1 or 2 in P axil; spines with 3 bases except erectile ones; spines long or short; 9 C rays; no tentacles in adults; nostril in adult bifid; no spines wholly on dorsal surface of caudal peduncle, but large spines that extend over the peduncle nearly to the caudal-fin base; no fins spotted; no large blotches on dorsal surface, but lateral bars may be present.

The type species of this genus is *A. jaculiferus* (non-Cuvier) McCulloch. McCulloch (1921, ref. 2945), apparently following Günther's (1870, ref. 1995) concept of *jaculiferus*, provided an excellent illustration of the species he was proposing as the type of his new genus. However, it was not *D. jaculiferus* of Cuvier (1818, ref. 18059). Whitley (1931, ref. 4673) realized this, and also realized that McCulloch's fish was undescribed. Whitley therefore described as new *Allomycterus pilatus*, and designated as his holotype the specimen illustrated and described by McCulloch (1921). Not surprisingly, this has caused some confusion.

Allomycterus pilatus Whitley, 1931

Allomycterus jaculiferus (non-Cuvier) McCulloch, 1921: 141, pl. 23 (fig. 2) (New South Wales, Australia)

Allomycterus pilatus Whitley, 1931: 125 (NSW, Australia)*

Allomycterus whitleyi Phillipps, 1932: 13, fig. 5 (New Zealand)*

*extant type

Based on 38 lots from throughout the range, including the extant types. Confusion over the specific name of this species is dealt with under the genus. There seem to be two forms of this species, one with long, blade-like spines (*A. whitleyi* form), and another with short, compressed spines. Both forms occur off the Australian mainland, but I have seen only the long-spine form from New Zealand, and the specimens with the longest spines seem to be from New Zealand. These differences are not obviously connected with sexual dimorphism. Therefore, there may be two species of *Allomycterus*, and a genetic study would be useful in clarifying the situation. In addition, Kuiter (1993, ref. 23929) illustrates two colour morphs among south-eastern Australian specimens of *A. pilatus*, referring to deep-water and shallow-water forms. The basis for the colour differences is unclear and should be investigated. References to *Allomycterus jaculiferus* from New Zealand are based on *A. pilatus* (see discussion under *Allomycterus*).

Whitley's (1931, ref. 4673) description and McCulloch's (1921, ref. 2945) illustration are clear, and could apply to no other species. In addition, the holotype is extant.

Phillipps' (1932, ref. 16393) *A. whitleyi* constitutes the long-spined form from New Zealand, and although both holotype and paratype are stuffed and distorted, they appear to differ from *A. pilatus* only in the length and shape of the spines. Phillipps' description contains two spellings of the specific name: two as *whitleyi* and one as *whiteleyi*. Given the correct spelling of Gilbert Whitley's name (to whom the patronym refers), "*whiteley*" is clearly a typographical error even though it appears before the two uses of *whitleyi* within Phillips' article.

Distribution. Southern Australia and New Zealand.

Rottnest I., WA, to Botany Bay, NSW, including Tas.; Tasman Sea seamounts and ridges; and New Zealand.

Lophodiodon Fraser-Brunner, 1943

Lophodiodon Fraser-Brunner (type species *Diodon calori* Bianconi*)*

Diagnosis. Spines on head and belly erectile, those on back and sides fixed; fixed spines with 3 bases, erectile spines with 2 bases; spines short to medium; anteriorly-pointing spines on snout; 9 C rays; a small supraorbital tentacle in adults; nostril in adult a short tube with 2 openings; no spines wholly on dorsal surface of caudal peduncle, but large spines extend over the peduncle nearly to the caudal-fin base; no fins spotted; no large blotches on dorsal surface, but bars present laterally.

The type species of this genus is *D. calori* Bianconi (1854, ref. 17949). The sole species in this genus has most spines on head and belly erectile, and those on back and sides fixed. This genus is similar in many ways to *Dicotylichthys*, differing primarily in that the nasal organ in *Dicotylichthys* is bifid, whereas in *Lophodiodon*, it is a hollow tube with two distinct nostrils. There is reason to expect that two genera may eventually be considered to be synonymous.

Lophodiodon calori (Bianconi, 1854)

Diodon calori Bianconi, 1854: 69 (Mozambique)
Lophodiodon nigropunctatus Smith, 1957: 222, fig. 4 (Port Alfred, South Africa)*
*extant type

Based on 13 specimens from most of the range, including the extant types. This species is widely distributed, but uncommon in collections.

Although the name *Diodon calori* dates from Bianconi, 1854 (ref. 17949), the illustration of *Diodon calori* in Bianconi (1855, ref. 295) is diagnostic for this species, with its large number of short spines, four lateral bars and no dorsal blotches.

Lophodiodon nigropunctatus Smith (1957, ref. 12171) was based on juveniles (30–60 mm SL), and the apparent difference in colour pattern with *L. calori* can be attributed to this. The spination of Smith's specimens is diagnostic.

Distribution. Indo-Pacific.

The 13 specimens I have examined are all from east Africa and Seychelles, but the species is reliably reported from Oman, Bali, Timor, the Australian Northwest Shelf, the South China Sea and New Caledonia, and somewhat less reliably as the similar *D. punctulatus* from New Guinea by Tortonese (1964, ref. 9080) and Munro (1967, ref. 6844).

Diodon Linnaeus, 1758

This genus was revised by Leis (1978, ref. 5529) with additional information on nomenclature and types in Leis and Bauchot (1984, ref. 12539), and information contained there is not repeated. Only information on *Diodon* species described since 1978 and on noteworthy new distributional information is included here. Note that figs 9 and 17 of Leis (1978) were switched (see 1979 errata facing p. 956, US Fishery Bulletin 76[4]): fig. 9 labelled *Diodon hystrix* is actually *D. holocanthus* and fig. 17 labelled *Diodon holocanthus* is actually *D. hystrix*.

Diodon eydouxii Brisout de Barneville, 1846

Diodon bertolettii de Lema, de Lucena, Saenger and de Oliveira, 1979: 35–38, figs 18–19 (Brazil)*
**extant type*

Diodon bertolettii can readily be identified as a synonym of *D. eydouxii* Brisout de Barneville based on its semi-lunate fins, blue colour, fin-ray counts, and from the photographs provided by de Lema et al. (1979, ref. 8836).

Leis (1978, ref. 5529) examined specimens of *D. eydouxii* Brisout de Barneville (1846, ref. 296) from 19 scattered localities in all warm oceans. I have now seen an additional 31 lots. These plus four acceptable literature records extend the known distribution of this species.

Distribution. Pelagic, Atlantic, Indian and Pacific Oceans.
W Indian – Cape of Good Hope to Zanzibar
E Indian – only record is Andaman Sea
W Pacific – Indonesia to Okinawa
Central Pacific – from near Samoa to Hawaii
E Pacific – equator to 20°N plus a California record (Lea, 1998: from Los Angeles Harbour, but misidentified as *C. reticulatus* [Linnaeus]).
W Atlantic – 28°S to 37°N
E Atlantic – 30°W is eastern-most specimen examined, but there are apparently valid literature records from the Azores (Azevedo, 2004) and from Spain (Crespo et al., 1987).

Diodon holocanthus Linnaeus, 1758

Diodon paraholocanthus**,** Kotthaus, 1979: 39, fig. 492 (Bab-el-Mandeb, southern Red Sea)*
**extant type*

Kotthaus (1979, ref. 8818) confused *Diodon liturosus* Shaw with *Diodon holocanthus* Linnaeus, as is obvious from his description and photograph (his fig. 491) of what he called *D. holocanthus*. Then, having encountered the true *D. holocanthus* in the north-western Indian Ocean, he described it as a new species, *D. paraholocanthus*. The description and photo (his fig. 492) of the holotype are entirely consistent with *D. holocanthus* Linnaeus.

Leis (1978) examined 141 specimens of *D. holocanthus* Linnaeus (1758, ref. 2787) from all warm oceans. I have now seen more than 100 additional lots that extend the known distribution of the species (see below). It is noteworthy that there are still no records of *D. holocanthus* from the Pacific Plate other than those reported by Leis (1978): Hawaii, Easter and Pitcarin Is. Reference in Robertson et al. (2004) and Mundy (2005, ref. 28379) to *D. holocanthus* occurring in the Line Is. is incorrect (B.C. Mundy, personal communication).

Distribution. Circumtropical in Atlantic, Indian and Pacific Oceans (except only peripherally on Pacific Plate).

W Indian – from Cape of Good Hope, South Africa to Oman and Red Sea, Sri Lanka, Mascarenes, and Seychelles.
E Indian – Andaman Sea to Australia
W Pacific – west of Pacific Plate: Japan to New Caledonia and Elizabeth and Middleton Reefs, Tasman Sea.

In Australia, south to Ulladulla, NSW (36°S) off east coast, and to Freemantle, WA (32°S) off west coast.

Central Pacific – Hawaii, Easter and Pitcarin Is. only.

E Pacific – southern California to Colombia

W Atlantic – Hudson Canyon (off New Jersey) to Argentina.

E Atlantic – Liberia and Nigeria to northern Angola .

Diodon hystrix Linnaeus, 1758

Leis (1978) examined 43 specimens of *Diodon hystrix* Linnaeus (1758, ref. 2787) from all warm oceans. I have now seen an additional 80 lots that extend the documented distribution of the species (see below).

Distribution. Circumtropical in Atlantic, Indian and Pacific Oceans

W Indian Ocean – throughout the area from South Africa (Tsitsikamma Coastal National Park) to the Red Sea, Sri Lanka, and all major island groups.

Australia – south to Elizabeth and Middleton Reefs, Lord Howe I., and northern NSW (29°S) off the east coast, and Rowley Shoals on west coast.

W Pacific – New Caledonia and Kermadecs to Rotuma, Pitcarin I., Hawaii and southern Japan.

E Pacific – Mexico to Chile

W Atlantic – 36°N to ca 20°S

Central Atlantic – Ascension and St Helena

E Atlantic – only 1 confirmed record at Fernando Po

Diodon liturosus Shaw, 1804

Leis, 1978 examined 30 specimens of *Diodon liturosus* Shaw (1804, ref. 4015) primarily from the western Pacific. I have now seen an additional 45 lots that extend the documented distribution of the species (see below).

Distribution. Indo-west Pacific

W Indian Ocean – South Africa (Algoa Bay) to Oman and southern Red Sea, Mascarenes, Seychelles, Laccadives and Maldives.

E Indian Ocean – Phuket, Thailand to Ningaloo Reef, WA

W Pacific – from Maizuru, Japan to northern NSW, Australia to New Caledonia to Society and Marshall Is.

Diodon nicthemerus Cuvier, 1818

Leis (1978) examined nine specimens of *Diodon nicthemerus* Cuvier (1818, ref. 18059), all from southern Australia. Museums in Australia contain large numbers of this species, and its distribution is confirmed as being confined to the waters of southern Australia. I have seen specimens from an area ranging from Houtman Abrolhos Is., WA (28°S), to Nadgee, NSW (37°S), although Kuiter (1993) reports *D. nicthemerus* as far north as Seal Rocks (32°S). This is the most restricted distribution of any species of *Diodon*.

Key to genera and species of the family Diodontidae

NB: in juveniles relative spine length and body colour generally differ from those of adults

1. All body spines erectile and 2-rooted (except a few around gill opening or dorsal-fin base) ..... *Diodon* 10
— All or most body spines of back and sides fixed in an erect position and 3-rooted 2

Non-*Diodon*

2. Indian and Pacific in distribution 3
— Atlantic in distribution .....
(NB: 1 Indo-Pacific species, *Cyclichthys spilostylus,* has penetrated the eastern Mediterranean Sea through the Suez Canal 14

Indo-Pacific non-*Diodon*

3. Spines on top of head and on belly erectile 4
— Spines on top of head and on belly fixed in an erect position 5
4. 2 to 4 spines in the 1st row on the snout point toward the mouth when not erect; no small, black spots scattered more or less uniformly over head and trunk .....
..... *Lophodiodon calori* (Indo-west Pacific)
— All erectile spines point toward tail when depressed; small, black spots scattered more or less uniformly over head and trunk .....
..... *Dicotylichthys punctulatus* (south-east Australia)
5. A small spine or 2 wholly on the dorsal surface of the caudal peduncle; normally 10 caudal rays; nasal organ of adults an open ridged cup; adults with fins spotted .....
..... *Chilomycterus reticulatus* (circumtropical)
— No spines wholly on the caudal peduncle; normally 9 caudal rays; nasal organ of adults a short tube with either 2 openings or split at the end (not an open cup); no spots on fins of adults 6
6. A set of 4 long fixed spines with their bases near the dorsal and anal-fin bases – their pointed ends extend over the caudal peduncle; a few spines in P axil erectile 7
— No especially long spines around dorsal and anal fin bases; spines in P axil fixed 8
7. Very long spines (longer than rays of pectoral fin) in pectoral-fin axil; 3–4 black spots (< eye) on sides of head and trunk, none on back .....
..... *Tragulichthys jaculiferus* (tropical Australia)
— Spines of pectoral-fin axil not particularly elongate; some eye-size dark spots on back generally associated with spine bases ..... *Allomycterus pilatus* (temperate Australia, Tasman Sea and New Zealand)
8. Few black spots on body, those present at base of spines dorsally and dorso-laterally; D, A and C fins with dusky distal margin; only 2 spines over eye; 2 spines between nostrils, 1 immediately adjacent to each nostril .....
..... *Cyclichthys hardenbergi* (tropical Australia, southern New Guinea)
— Black spots in clusters dorsally and laterally, or associated with spine bases laterally and ventrally; D, A and C fins either clean or with faint, parallel bands; 3 spines over eye; only 1 spine between nostrils, located medially 9

9. Spines few, 4 dorsally between pectoral-fin bases, 8 or 9 anterior to dorsal-fin base; a short, moveable spine near corner of mouth; all spines on top of head with 3 bases; black spots in clusters dorsally and dorsolaterally ..... *Cyclichthys orbicularis* (Indo-west Pacific)
— Spines more numerous, 5 or 6 dorsally between pectoral-fin bases, 11 or 12 anterior to dorsal-fin base; no moveable spines; some spines on top of head with 4 bases; black spots at base of spines laterally and ventrally ..... *Cyclichthys spilostylus* (Indo-Pacific)

Diodon

10. None of spines wholly on caudal peduncle; body with several large, dark dorsal or lateral blotches; no small, dark spots on fins 11
— One or more small spines wholly on the dorsal surface of caudal peduncle; body without large dorsal blotches; all fins (anal sometimes excepted) heavily spotted 13
11. Temperate Australian waters only; no small, fixed, tri-base spine immediately above gill opening; no small, flat spines on the anterior border of the depression surrounding the gill opening; 11 or fewer spines from lower jaw to anus; adult colour pattern dominated by 4, large, lateral bars, dorsum uniformly dark ..... *Diodon nicthemerus* (southern Australia).
— Tropical waters, with strays into warm temperate water; 1 or 2 small, fixed tri-base spines above gill opening; 3 or 4 small, flat spines forming the anterior border of depression surrounding the gill opening; 12 or more spines from lower jaw and anus; adult colour pattern dominated by several large, dorsal blotches 12
12. Frontal spines obviously much shorter than spines immediately behind pectoral fin; small downward-pointing spine below anterior margin of eye; 17–22 spines from lower jaw to anus; large dorsal blotches with distinct pale border; blotch below eye not continuing over top of head ..... *Diodon liturosus* (Indo-Pacific)
— Frontal spines slightly shorter to much longer than spines immediately behind the pectoral-fin base; small downward-pointing spine below anterior margin of eye absent (Indo-Pacific) or present (most Atlantic specimens); 12–15 spines from lower jaw to anus; dorsal blotches without distinct pale border; blotch below eye continues over interorbital in Indo-Pacific specimens ..... *Diodon holocanthus* (circumtropical)
13. Pectoral-fin rays 19–22; anal-fin rays 16–18; dorsal and anal fins somewhat pointed to semilunate in adults; relatively streamlined, head width of adults 3.3–4.0 in standard length; 10–14 spines from lower jaw to anus; a wholly pelagic species coloured dark-blue dorsally ..... *Diodon eydouxii* (circumtropical)
— Pectoral-fin rays 22–25 (rarely 21); anal-fin rays 14–16; dorsal and anal fins rounded in adults; relatively robust, head width of adults 2.4–3.3 in standard length; 14–19 spines from lower jaw to anus; juveniles (up to 20 cm) pelagic and coloured blue dorsally, adults demersal and coloured tan to brown ..... *Diodon hystrix* (circumtropical)

Atlantic non-*Diodon*

14. 1 or 2 small spines wholly on the dorsal surface of the caudal peduncle; normally 10 caudal-fin rays; nasal organ of adults, an open, ridged cup; adults with fins spotted; on top of head some spines with 4 roots ..... *Chilomycterus reticulatus* (circumtropical)
— No spines wholly on the caudal peduncle; normally 9 caudal-fin rays; nasal organ of adults, a short hollow tube with 2 openings; fins of adults usually without spots; all spines with 3 roots ..... "Atlantic *Chilomycterus*" 15
15. A large (ca. = eye diameter) tentacle above eye; colour pattern dominated by large dorsal blotches and with small spots scattered on back and sides, on fins only basally, except on most or all of caudal fin from 10–15 cm standard length, and on other fins from 20 cm ..... *Chilomycterus antennatus* (central-west Atlantic)
— Tentacles above eyes absent or small; no small spots on fins or on back and sides; dorsal and lateral dark blotches present 16
16. Network of hexagonal to circular black lines on back and sides in adults ..... *Chilomycterus antillarum* (central-west Atlantic)
— Black lines on back and sides absent in adults, or if present, wavy or approximately parallel – not intersecting to form rings or polygons 17
17. Extensive series of dark-brown to black parallel lines densely covering back and sides in adults ..... *Chilomycterus schoepfii* (western North Atlantic)
— No black lines on back; dorsal background dark with diffuse lighter spots ..... *Chilomycterus spinosus* 18
18. No black lines on sides of head or trunk; South American in distribution ..... *Chilomycterus spinosus spinosus* (east coast South America)
— Irregular, approximately parallel black lines on sides of head and trunk; eastern Atlantic in distribution ..... *Chilomycterus spinosus mauretanicus* (west coast Africa)

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