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A new generic name for *Anchisomus multistriatus* Richardson 1854 (Tetraodontidae), with notes on its toxicity and pufferfish biting behaviour

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Abstract

A poorly known pufferfish, *Anchisomus multistriatus* Richardson, is redescribed from 25 specimens from northern Australian coastal waters, and placed in a new monotypic genus, *Feroxodon*. It differs from other tetraodontid genera with a similar nasal organ structure (tube with two nostrils) in aspects of frontal and sphenotic osteology. The species has been implicated in unprovoked biting incidents and in a well documented case of fish poisoning fatality.

Introduction

During the tenure of the senior author's fellowship at the Smithsonian Institution, the collections of the National Museum of Natural History in Washington, DC, were examined for their holdings of pufferfishes from the coast of China and adjacent regions. This revealed a relatively large pufferfish (306 mm SL) from Queensland, Australia, that was unknown to either the first (JS) or last listed (JCT) authors.

Not only was the distinctive colour pattern of the specimen unfamiliar, but also its generic affinity was problematic. A letter to numerous colleagues describing the essential features of the fish resulted in positive responses from: J. Barry Hutchins (Western Australian Museum), who had collected and photographed in life during 1978 a specimen from Learmonth, Western Australia (photograph reproduced here); Graham S. Hardy, who identified the fish as *Anchisomus multistriatus* Richardson, 1854 and agreed to collaborate in a redescription of it; and Douglas F. Hoese (Australian Museum), who also identified it as *A. multistriatus.*

In this paper *Anchisomus multistriatus* Richardson is redescribed and placed in a new genus, with detailed comparisons to related genera. In addition, aspects

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of the toxicity of *A. multistriatus* and of biting behaviour in it and in other tetraodontids are presented.

Methods and abbreviations

Measurements were taken by dial caliper and recorded to the nearest 0.1 mm, following the methods of Dekkers (1975), Hardy and Hutchins (1981) and Hardy (1981, 1983), while the osteological usage follows Tyler (1980). Fin ray counts include all visible rays, both branched and unbranched, and in the pectoral fin the small uppermost element that is reduced to a nubbin in adults. Fin ray lengths were determined by measurements from the embedded base. Most of the specimens were radiographed and half of them were cut open along the cheek on the right side to count gill rakers. All counts and measurements are from preserved specimens, and the osteological illustrations are based on photographs of the two specimens cleared and stained.

The following abbreviations are used in the text and tables: SL – standard length; HL – head length; N – number of specimens examined; $\bar{x}$ – average value; D – dorsal fin; A – anal fin; P – pectoral fin; V – vertebrae; PV – precaudal vertebrae; CV – caudal vertebrae; GR – gill rakers; QM – Queensland Museum, Brisbane; AMS – Australian Museum, Sydney; MAGNT – Museum and Art Galleries of the Northern Territory, Darwin; NMNZ – National Museum of New Zealand; USNM – United States National Museum of Natural History, Washington, DC.

Systematics

Five of the seven species first listed in *Anchisomus* by Richardson (1854, based on ms. of J.J. Kaup), i.e. *geometricus* (= *annulatus*), *angusticeps, reticularis* (= *nephelus*), *spengleri,* and *turgidus* (= *maculatus*), clearly are assignable to *Sphoeroides* (Shipp, 1974). A sixth species, *scalaris,* listed by name only, does not appear to have been formally described at any time. It is here considered a *nomen nudum.* Under normal circumstances, the seventh species, *multistriatus,* might have remained in *Anchisomus,* a valid generic name despite its inadequate description by Richardson, owing to its distinctive characteristics which preclude allocation to any other tetraodontid genus (see below). However, Jordan (1919), acting as first reviser, selected *Tetrodon spengleri* Bloch as the logotype of *Anchisomus,* thus making *Anchisomus* a junior subjective synonym of *Sphoeroides.* Consequently, we propose the new generic name *Feroxodon* for *Anchisomus multistriatus* Richardson.

Feroxodon new genus

Type species

Anchisomus multistriatus **Richardson, 1854.**

Diagnosis

Feroxodon is a heavy bodied, monotypic genus of tetraodontid fishes, belonging to the group of genera characterised by a nasal sac with two nostrils. It differs uniquely from the other genera included therein by having the frontals broadly expanding from a point just anterior to the lateral ethmoids, thereby contributing greatly to a posterolaterally directed postorbital wing, in association with a correspondingly reduced sphenotic. The eyes of *Feroxodon* are small, positioned high on the head and are enclosed in a relatively small and bony orbital rim. The anal fin origin is well behind the dorsal fin base. *Feroxodon* further differs from other genera in which, like it, the eye rim is adnate only dorsally, in lacking a ventrolateral skinfold (present in *Torquigener* and *Amblyrhynchotes*); lacking trituration teeth (present in *Tylerius, Sphoeroides, Takifugu* and *Amblyrhynchotes*); possessing medial prootic prongs (absent in *Takifugu, Javichthys, Amblyrhynchotes* and, usually, in *Torquigener*); possessing a lower lateral line posterior to the pectoral fin (absent or remnants only in *Sphoeroides*); and in having the frontals extending anterior to the anterior margins of the lateral ethmoid lobes (not so in *Torquigener, Javichthys* and *Amblyrhynchotes*).

Description

See following description of *F. multistriatus,* the only known species.

Etymology

From the Latin *ferox* = ferocious, and *odon* = teeth, in allusion to the fierce biting habits of the single species, *multistriatus;* to be treated as masculine.

***Feroxodon multistriatus* (Richardson, 1854)**
(Striped Toado)

Figures 1-5; Colour Plate 1

Anchisomus multistriatus Richardson, 1854: 160-161, pl. 30.
Tetrodon multistriatus – Gunther 1870: 285.
Anchisomus multistriatus – Gill 1892: 708; Gunther 1910: 460; Hardy 1983: 8; Gloerfelt-Tarp and Kailola 1984: 293, 363.
Spheroides multistriatus – Ogilby 1915: 128-129; Ogilby1918: 103; McCulloch and Whitley 1925: 178; McCulloch 1929: 429.
Sphaeroides multistriatus – Whitley 1936: 50-51; Whitley 1964: 59.
Sphoeroides multistriatus – Marshall 1964: 495.
Geneion multistriatum – Le Danois 1959: 188-189 (in part); Le Danois 1961: 469 (in part).

Description

The following meristics and measurements are based on 25 specimens, 52.8-320 mm SL, unless otherwise stated. See Table 1 for frequency distributions of meristic features.

Table 1 *Feroxodon multistriatus* meristics

Dorsal fin rays

10	11	12	N	$\bar{x}$
2	22	1	25	11.0

Anal fin rays

9	N	$\bar{x}$
25	25	9.0

Pectoral fin rays

R.+15	R.+16	R.+17	N	$\bar{x}$
9	14	2	25	R.+15.7

Caudal fin rays

11	N	$\bar{x}$
25	25	11.0

Precaudal vertebrae

9	10	N	$\bar{x}$
16	5	21	9.2

Caudal vertebrae

10	11	12	N	$\bar{x}$
2	18	1	21	11.0

Total vertebrae

19	20	21	N	$\bar{x}$
1	15	5	21	20.2

Gill rakers

9	10	11	N	$\bar{x}$
6	5	2	13	9.7

Head length 2.27-2.86 ($\bar{x}$ 2.51) times in SL; snout to origin of dorsal fin 1.42-1.60 ($\bar{x}$ 1.52) times in SL; snout length 1.61-1.97 ($\bar{x}$ 1.76) times in HL; anterior edge of nasal tube to end of snout 2.26-2.79 ($\bar{x}$ 2.46) times in HL; posterior edge of base of nasal tube to anterior edge of eye 5.53-9.43 ($\bar{x}$ 6.56) times in HL; gill slit length 2.93-4.52 ($\bar{x}$ 3.83, 24 specimens) times in HL; caudal peduncle length 4.16-8.12 ($\bar{x}$ 5.76) times in SL; caudal peduncle depth 7.37-10.22 ($\bar{x}$ 9.09) times in SL and 1.18-2.00 ($\bar{x}$ 1.61) in caudal peduncle length; dorsal fin origin to anal fin origin 3.03-3.90 ($\bar{x}$ 3.54, 24 specimens) times in SL; nasal tube base width (diameter) 9.00-16.17 ($\bar{x}$ 12.58, 24 specimens) times in snout length and 17.71-28.75 ($\bar{x}$ 22.29, 24 specimens) in HL; nasal tube height 1.32-3.41 ($\bar{x}$ 2.31, 24 specimens) times in nasal tube base width; nasal tube base width 1.65-3.33 ($\bar{x}$ 2.28, 24 specimens) times in distance between nasal tubes; horizontal diameter of eye 4.98-8.77 ($\bar{x}$ 6.35) times in HL and 1.02-2.73 ($\bar{x}$ 1.43) times in bony interorbital width; bony interorbital width great, 8.87-13.45 ($\bar{x}$ 11.17) times in SL and 3.21-5.35 ($\bar{x}$ 4.47) times in HL; dorsal fin elongate and pointed, longest ray 3.98-5.99 ($\bar{x}$ 4.70) times in SL; anal fin elongate and pointed, origin well behind dorsal fin base, longest ray 4.57-6.08 ($\bar{x}$ 5.23) times in SL; pectoral fin rounded, longest ray 4.80-6.16 ($\bar{x}$ 5.55) times in SL; caudal fin slightly rounded, longest ray 2.93-3.97 ($\bar{x}$ 3.42) times in SL.

Body robust, rounded, tapering to a narrow caudal peduncle; mouth small, terminal; lips thick, covered with numerous short papillae. *Eyes* small, positioned

PLATE 1

Feroxodon multistriatus, lateral view reproduced from an Ektachrome slide by J. Barry Hutchins of a specimen of 240 mm SL, WAM P. 26184-001, caught on handline from the FV *Courageous* anchored off Learmonth, Exmouth Gulf (22°15′S, 114°05′E), Western Australia, 9 May 1978.

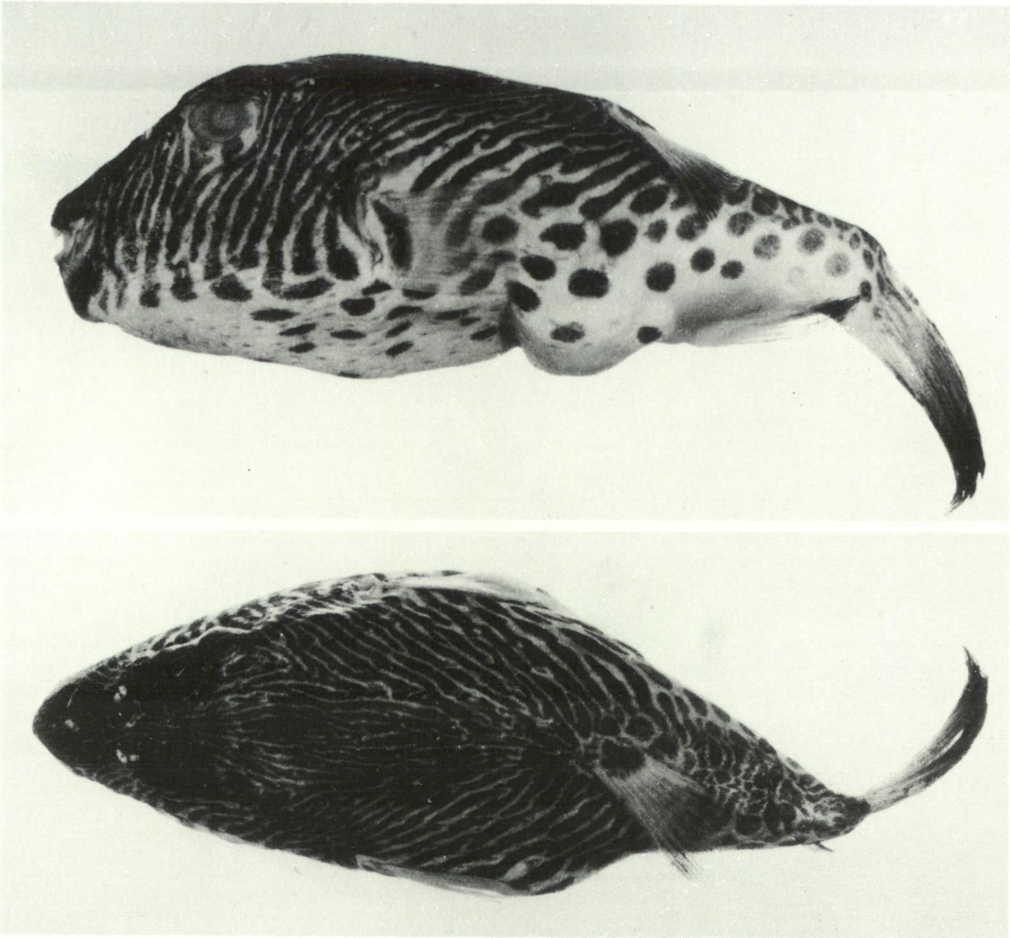

Figure 1 *Feroxodon multistriatus,* dorsal and ventral views of the same specimen, 82.5 mm SL, AMS I.21832-003, Arafura Sea, Northern Territory, 14-16 November 1980.

high on head, lower border well above level of corner of mouth, enclosed in a relatively small orbital rim, dorsally adnate. *Nasal apparatus* a short tube on each side, anterior to eye, two nostrils (medial and lateral), lateral nostril the larger; inner surface of apparatus with several well developed olfactory lamellae. *Lateral lines* distinct; upper line encircling eye with an anterodorsal branch almost meeting in midline anterior to nasal organ; preopercular branch dropping to lateral limit of belly, extending along body to about halfway along caudal peduncle; mid-dorsal branch of lateral line above pectoral fin base not meeting in midline; second lateral line dropping behind mouth corner, extending along

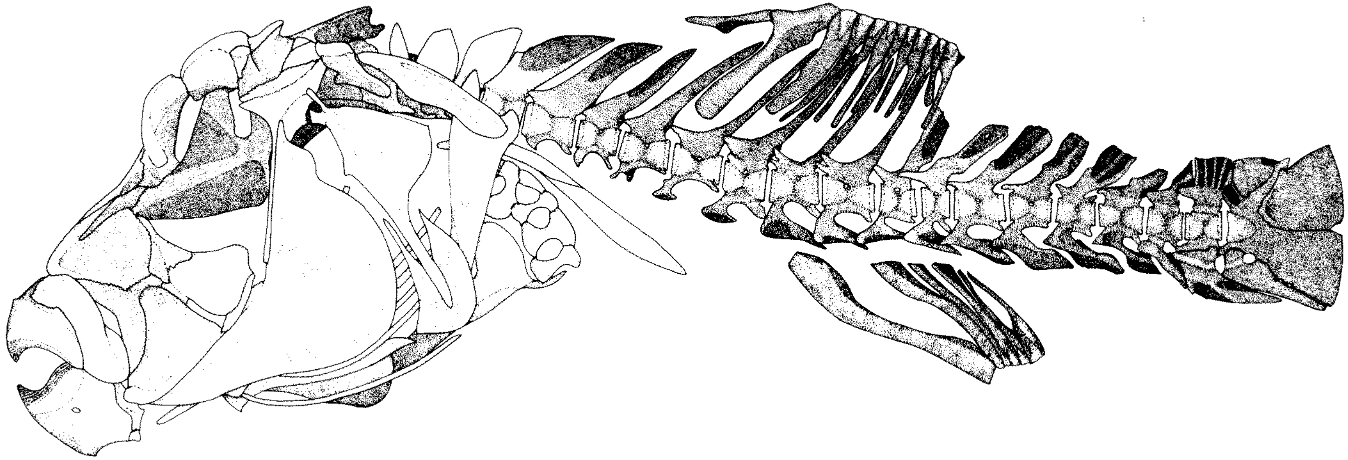

Figure 2 *Feroxodon multistriatus,* lateral view of entire skeleton, 306 mm SL, USNM 176752, Brisbane, Queensland, April-May 1952.

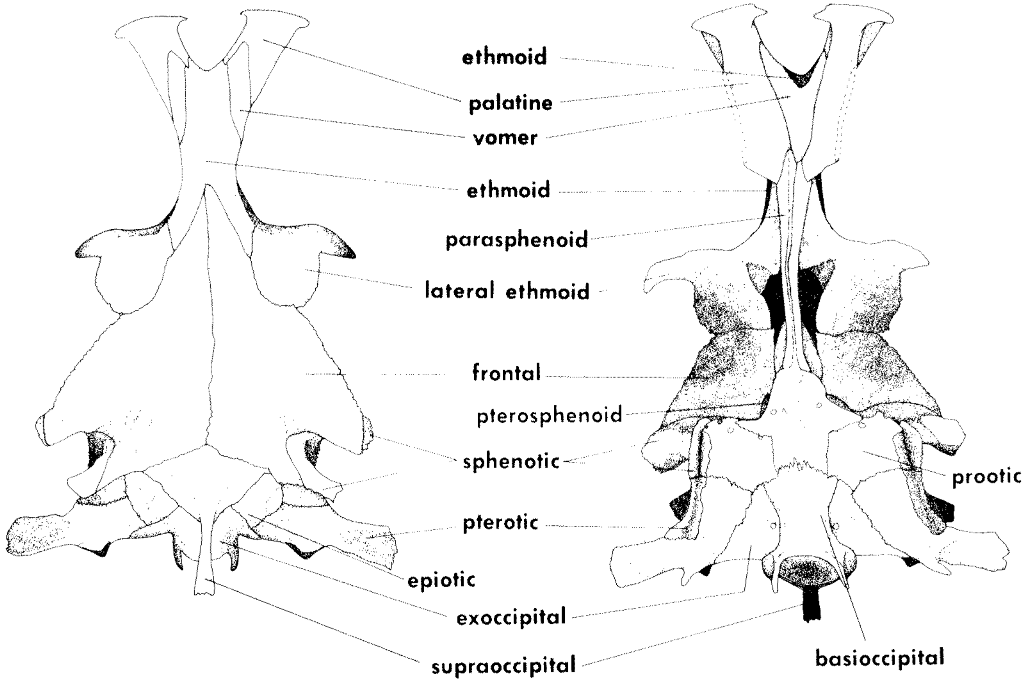

Figure 3 *Feroxodon multistriatus*, dorsal (left) and ventral view of the skull, 306 mm SL, USNM 176752, Brisbane, Queensland, April-May 1952.

lateral region of belly almost to caudal fin base, except for a break ventral to pectoral fin. *Ventrolateral skinfold* absent. *Spines* few, relatively large, on dorsum from nasal tubes to dorsal fin, on belly from chin to anus, and behind pectoral fin; absent from caudal peduncle; 4-11 ($\bar{x}$ 6.4) spines on interorbital region; 11-37 ($\bar{x}$ 15.5) lateral head spines, those of larger specimens fewer and more deeply embedded; 2-8 ($\bar{x}$ 5.2) spines on anterior margin of gill slit.

Colour pattern notes made by GSH on NMNZ P. 9937 after several days in formalin but with much colour still remaining are as follows: body pattern anterior to dorsal fin base comprising alternating dark olive and brown lines, these extending forward diagonally onto sides of body and head and longitudinally between eyes and nostrils; body pattern posterior to dorsal fin base with olive lines anastomosing ventrally and enclosing elongate brown spots; large rounded brown spots on lower half of body sides and caudal peduncle, on a pale background, the spots continuing onto lateral regions of belly but becoming less distinct; belly dirty yellowish; chin with grey smudges on either side; pale around pectoral fin base, but with olive and brown striations; pectoral fin pale; dorsal, anal and caudal fins greyish.

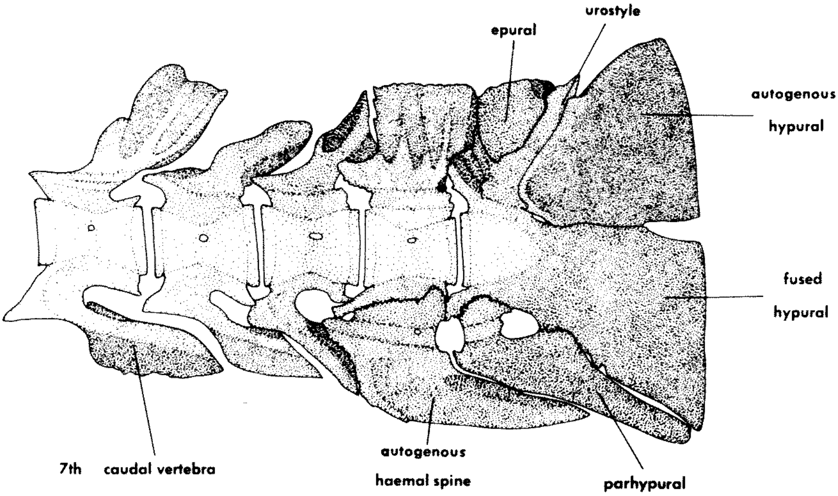

Figure 4 *Feroxodon multistriatus*, lateral view of last five caudal vertebrae, 306 mm SL, USNM 176752, Brisbane, Queensland, April-May 1952.

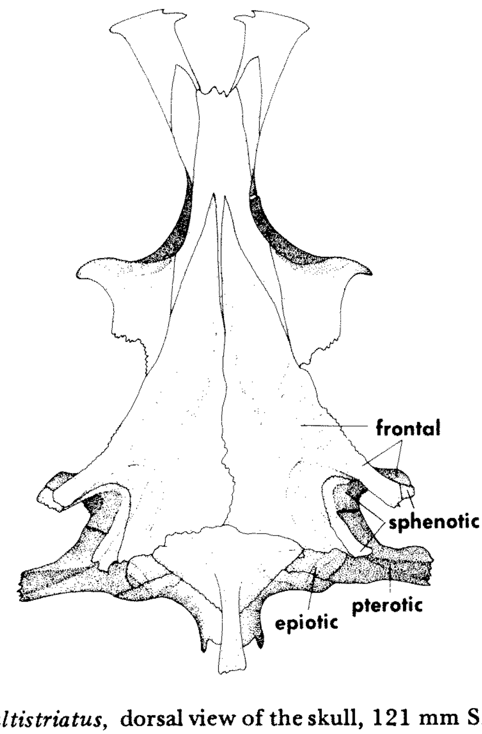

Figure 5 *Feroxodon multistriatus*, dorsal view of the skull, 121 mm SL, QM I.15993, Princess Charlotte Bay, Queensland, 23 February 1979.

Colour in life (based on a 35 mm Ektachrome slide of a fresh specimen of about 240 mm SL from Learmonth, Western Australia). Sides of head with medium brown stripes on pale background, bending obliquely posterodorsally over pectoral fin base and continuing onto dorsal fin base; lateral surface under dorsal fin with large brown ocellated oval spots on pale background, the spots or blotches tending to be anteroventrally elongate and with thin brown lines often helping to outline the ocellations within a reticulate network; belly pale; dorsal, anal and (least so) pectoral fins with a slight yellowish brown cast.

Distribution

Feroxodon multistriatus ranges in shallow inshore waters along the northern half of Australia, from Exmouth Gulf in Western Australia to as far south as Caloundra, just north of Brisbane, in south-east Queensland.

Remarks

All references given above under the names *Anchisomus, Tetrodon* or *Sph[a, o]eroides multistriatus* refer to that species alone, as redescribed here. However, the reference to *Geneion multistriatum* (in Le Danois 1959, 1961), as indicated by the included synonyms *(mela-plathiè, multistriatus, leschenaultii, marmorata, spinosissimus, pleurospilus, whitleyi, marleyi)* and references, represents at least six distinct species (see Jordan and Edwards 1887; Fraser-Brunner 1943; Shipp 1974; Hardy 1982, 1983).

Le Danois' (1959: 188, Figure 151) illustration of the body conceivably could be based on *multistriatus,* since the specimen is shown as having few but large spines and relatively large blotches on the caudal peduncle, and somewhat vertical stripes on the cheek. However, the cheek stripes in Le Danois' illustration are not as narrow nor as sharply defined as those shown by Richardson for *multistriatus* or observed by us. Furthermore, her illustration of the body shows a prominent skin fold on the ventrolateral edge of the caudal peduncle, unlike the *multistriatus* of Richardson and of our specimens. Her illustration of dorsal craniology (Figure 152) does not show the heavy anteroventral flanges of the lateral ethmoids and the prominent posterolateral flanges of the sphenotics observed by us.

The illustrations by Le Danois (1959, Figures 151-152) purportedly are based on the type specimen of *Epipedorhynchus leschenaulti* Duméril, 1855 (Bibron ms.), according to her note on p. 189. No locality for this species was given by Duméril (1855: 278), who simply listed 'Leschenaulti, Bib', without description of any kind. Le Danois (1961: 469) later indicated that MNHN B. 1493 was the specimen originally described as *'Tetraodon melaplathiè'* Leschenault de la Tour manuscript 1818 (on which *Epipedorhynchus leschenaulti* Duméril, Bibron ms., was based), giving 'Ile Maurice' as the type locality.

However, MNHN B. 1493 has not been dissected (examined by GSH through the courtesy of M.L. Bauchot). Therefore, it could not have been the basis for

Le Danois' (1959) Figure 152 skull illustration, nor for her Figure 151 of the complex colour pattern on the body, for the specimen is totally devoid of pigmentation. Indeed, the status of MNHN B. 1493 is entirely questionable. Dr M.L. Bauchot (pers. comm.) has indicated that there is no basis from which we can determine whether or not the specimen is the fish described, in the first instance, by Leschenault in his manuscript or by subsequent workers, for no trace of an original label now remains.

The identity of MNHN B. 1493 remains uncertain. It apparently belongs to the *Torquigener*-like group of genera, but has large, well-formed triturating teeth. The condition of the specimen precludes more precise identification at this stage, but it is not an example of the subject of this paper.

The lack of descriptive characters for *Epipedorhynchus leschenaulti,* not to mention the totally inconclusive status of the purported holotype, lead us to regard *E. leschenaulti* as a *nomen nudum.* The name has no direct relevance to the nomenclatural history of *Anchisomus multistriatus* Richardson.

Osteological notes

Osteological features of *Feroxodon multistriatus* are illustrated in Figures 2-5. The following notes concentrate on features that are either unusual in *F. multistriatus* or of special significance in the eventual establishment of tetraodontid relationships. Branchial and pharyngeal characteristics, which cannot be seen in the illustrations provided, also are described here.

Branchiostegal rays 2 + 4 = 6, with distal end of uppermost ray extending back to edge of gill slit, behind which a small flap of skin protrudes, disrupting otherwise uniform edge of opercular covering. Branchial arches typical of Tetraodontidae, with 3 basibranchials, 3 hypobranchials, 5 ceratobranchials (fifth toothless), 4 epibranchials and 3 pharyngobranchials, 3 gills, no gill slit between gill-less fourth and fifth arches and no gill rakers along posterior edge of fourth arch or on either side of fifth arch. Gill rakers all relatively short and stubby, simple, unbranched, with minute denticulations. First pharyngobranchial with a lunate plate-like portion exposed on roof of mouth, completely covered with fine denticles, these denticulations not easily distinguishable as clusters of individual units in the larger (306 mm SL) cleared and stained specimen, but clearly seen to consist of numerous closely but irregularly arranged separate units in the smaller (121 mm SL) cleared and stained specimen. Second and third pharyngobranchials with exposed surface on roof of mouth slightly shorter but much narrower than that of first pharyngobranchial, and bearing relatively large conical teeth set in individual basal cups (about 20 on second pharyngeal and 10 on third pharyngeal in larger cleared and stained specimen, 12 to 15 on second and 5 to 8 on third in smaller specimen), those of smaller specimen with slightly more sharply pointed distal ends.

Last caudal vertebra with parhypural, lower hypural plate fused to centrum and upper autogenous hypural plate articulated immovably to dorsal edge of lower fused hypural plate and to posterior edge of urostyle; single epural, oriented vertically and obliquely posterodorsally; haemal spine of penultimate vertebra autogenous.

Eleven dorsal fin basal pterygiophores; supraneural element articulated to anterodorsal end of first pterygiophore; six anal fin basal pterygiophores.

The most noteworthy features of the cranium are: well developed lateral ethmoids with heavy downturned anteroventral flanges forming a strong rim around front of eye; great width posteriorly of frontals and their broad contact with lateral ethmoids as they become narrower anteriorly and taper to points overlying ethmoid at level of anterior ends of lateral ethmoids; posterolateral expansion as wings or prongs above skull surface of extreme posterolateral ends of sphenotic (in conjunction with most posterior portions of frontals); sphenotic wing directed toward posterolateral expansions of pterotic; well developed dorsal flange of parasphenoid in interorbital septum making contact dorsally on undersurface of skull with ventromedial edges of frontals; medial prongs from anterior edges of prootics at entrance to myodome relatively well developed; relative large size of the strongly ossified head.

The skeletal structure of the smaller (121 mm SL) of the two cleared and stained specimens is not markedly different from that described above, and illustrated mainly on the basis of the larger (306 mm SL) specimen. The main differences are that the smaller specimen does not yet have the frontals as wide over the orbit or as massively expanded posterolaterally as in the larger specimen, nor are the posterolateral wings of the sphenotic quite as extended laterally.

Comparisons with other genera

In addition to the distinctive features of its colour pattern, which make the species easy to recognise (along with its large maximum size, heavy body, small eye, and restricted northern Australian distribution), *Feroxodon multistriatus* is unique in its particular combination of 18 external and internal features considered especially significant as generic level diagnostic and phylogenetic indicators for tetraodontids. These features are summarised in Table 2, comparing the conditions in *Feroxodon* with those of 13 other Indo-Pacific genera with a nasal apparatus consisting of a tube with two nostrils. The more salient of these 18 characters in the other appropriate genera as compared to *Feroxodon* are discussed below.

One of the most significant features of *Feroxodon* is the anterior tapering of the frontals in comparison to their very considerable lateral development in the postorbital region. In addition, the anal fin origin is well behind the dorsal fin base, whereas in all of the remaining genera, with the exception of *Tylerius* in which it is just behind, the anal fin originates under the dorsal fin base. The eyes of *Feroxodon* are small, highly positioned on the head, and are enclosed

Table 2 Summary of major anatomical features of *Feroxodon* and related genera

	Feroxodon	*Polyspina*	*Reicheltia*	*Marilyna*	*Colomesus*	*Torquigener*	*Tylerius*	*Contusus*	*Lagocephalus*	*Sphoeroides*	*Takifugu*	*Amblyrhynchotes*	*Javichthys*	*Tetractenos*
Eye condition	dorsally adnate	completely adnate	completely adnate	completely adnate	completely adnate	dorsally adnate	dorsally adnate	completely adnate	dorsally adnate	dorsally adnate	dorsally adnate	dorsally adnate	dorsally adnate	completely adnate
Ventrolateral skinfold	absent	absent	present	present	absent	present	absent	absent	present	usually absent	present or absent	present	absent	present
Lower lateral line posterior to pectoral fin	present	absent	absent	present	present	present	present	absent	present	absent, or remnants only	present	present	present	present
Anal fin origin	well behind dorsal	under dorsal	under dorsal	under dorsal	under dorsal	under dorsal	just behind dorsal	under dorsal	under dorsal	under dorsal	under dorsal	under dorsal	under dorsal	under dorsal
Epural orientation	oblique	oblique	oblique	oblique	oblique	oblique	oblique	oblique	horizontal	oblique	oblique	oblique	oblique	oblique
Interhyal	present	absent	absent	absent	absent	absent	absent	absent	present	usually absent	absent	absent	absent	absent
Triturating teeth	absent	small or absent	absent	small or absent	present	small or absent	present	absent	present	present	present	present	absent	absent
Last basal pterygiophore posterior prongs	absent	absent	absent	absent	absent	absent	absent	absent	moderate to well developed	absent	absent	absent	absent	absent
Medial pro-otic prongs	well developed	absent	absent	absent	present	absent to moderately developed	present	absent	moderate to well developed	absent to well developed	absent	absent	absent	absent
Frontal width over orbit	broad	moderately narrow	broad	broad	broad	narrow	broad	broad	broad	narrow to broad	broad	broad	narrow	broad
Lateral ethmoid contact with palatine	no	yes	no	yes	yes	yes or no	no	yes	no	no	yes or no	yes	no	yes
Lateral post-orbital expansion of frontal	extensive	small	moderate	nil	nil	small	nil	small	moderate to extensive	nil	small	small	nil	small
Dorsal hypohyal	present	present	present	present	present	present	present	present	usually absent	usually present	absent	absent	present	present
Parasphenoid dorsal lobe in orbit	present	present	present	present	present or absent	present	present	present	usually present	usually absent	present	present	present	present
Supraoccipital/sphenotic contact	no	no	no	yes	yes	no	no	yes	no	no	no	no	no	no
Ethmoid	long	short	short	moderately long	long	long	short	short	long	long	short to moderate	long	long	short
Frontal position relative to anterior margin of pre-frontal lobe	in front	behind	in front	behind	behind	behind	in front	in front	in front or behind	in front or behind	in front	behind	behind	level
Posterior margin of nostrils relative to eyes	well forward	just forward	level	level	level	well forward	well forward	well forward	well forward	well forward	well forward	just forward	well forward	just forward

in a relatively small bony orbital rim, comparatively far smaller than in the other genera. While examination of the anatomical features included in Table 2 indicates a diverse array of characters defining the various genera, it also shows that those genera with the eye rim completely adnate share, as a group, rather fewer characters with *Feroxodon* than do the remaining genera.

The incompletely adnate eye condition appears to be a specialisation within the Tetraodontinae (a completely adnate eye rim characterises both the Canthigasterinae and also the nearest outgroup, the Diodontidae). It follows, therefore, that *Feroxodon,* which has the eye dorsally adnate only, should first be compared with those genera similarly characterised, and from within which group its closest relation is likely to be found; i.e. *Lagocephalus, Torquigener, Javichthys, Sphoeroides, Takifugu, Tylerius* and *Amblyrhynchotes.*

Lagocephalus — Although *Lagocephalus* is the genus most closely similar to *Feroxodon* in the degree of frontal contribution to the postorbital wing, *Lagocephalus* differs from *Feroxodon* in several cranial features. The six species of *Lagocephalus* illustrated by Tyler (1980: Figures 197, 263-264) have the posterolateral wings of the frontals more slender and elongate (in comparison to the straighter, upraised posterior edge of the frontal in *Feroxodon*), and a marked depression in the dorsal surface of the frontal as it approaches the postorbital association with the sphenotic. The shape and orientation of the lateral ethmoids in *Feroxodon,* featuring a heavy and strongly downturned anterolateral wing, differ in *Lagocephalus,* in which the lateral ethmoids may be relatively broad (as in *lagocephalus, lunaris* and *spadiceus*) or tapering anterolaterally (as in *sceleratus*), but are not especially heavy or thick and downturned anterolaterally. *Feroxodon* lacks a median dorsal exposure of the vomer, while in *Lagocephalus* the vomer is usually prominently exposed on the dorsal surface of the anterior end of the skull between the palatines and in front of the ethmoid. Additional features present in *Lagocephalus,* but absent in *Feroxodon,* include well developed posterior prongs from the last basal pterygiophores of the dorsal and anal fins, triturating teeth, and a ventral skinfold. Dorsal hypohyals, which usually are absent in *Lagocephalus,* are present in *Feroxodon.* Overall, *Lagocephalus* has a more elongate and streamlined body, in keeping with a pelagic or semi-pelagic existence, than the chunkier, more deep-bodied *Feroxodon* found in inshore coastal regions.

Torquigener and *Javichthys* — Both of these genera have the frontals narrow over the orbit, in direct contrast to *Feroxodon.* Also, in *Torquigener* and *Javichthys* the frontals fail to extend anterior to the anterior margins of the lateral ethmoid lobes and have either no postorbital expansion of the frontals toward the sphenotic or only a moderate expansion, whereas in *Feroxodon* the frontals extend well anterior to the anterior margins of the lateral ethmoid lobes and have a well developed posterolateral flange from the frontals directed toward the lateral ends of the pterotics. Medial prootic prongs, well developed in *Feroxodon,* are absent from *Javichthys* and in most species of *Torquigener*. *Torquigener* further differs from *Feroxodon* in possessing a ventrolateral skinfold.

Sphoeroides – Differs from *Feroxodon* in having a minimal postorbital lateral development of the frontals, the presence of triturating teeth, and the absence (usually) of an interorbital dorsal lobe of the parasphenoid contacting the frontal. The lower lateral line, which if present at all in some species of *Sphoeroides* is represented only by remnants, in *Feroxodon* is distinctly present, although faint.

Takifugu and *Tylerius* – Both of these genera have short, or at best only moderate, dorsal exposure of the ethmoid, compared with the larger ethmoid more fully exposed dorsally in *Feroxodon*. In addition, the frontals of *Takifugu* and *Tylerius* have only a minimal postorbital development laterally, and both genera have triturating teeth, which are absent in *Feroxodon*. Medial prootic prongs, present in *Feroxodon* and *Tylerius*, are absent from *Takifugu*.

Amblyrhynchotes – The structure of the dorsal surface of the skull in *Amblyrhynchotes* bears little resemblance to that of *Feroxodon*. The frontals in *Amblyrhynchotes*, which taper progressively to a point just behind the anterior margins of the lobes of the lateral ethmoids, have limited postorbital lateral expansion, and are somewhat reduced posteriorly. The lateral ethmoids in *Amblyrhynchotes* are spade-like and flattened, unlike the strongly downturned elements in *Feroxodon*. The ethmoid is extensive in *Amblyrhynchotes*, but whereas the lateral ethmoids and palatines fail to contact in *Feroxodon*, they do so extensively in *Amblyrhynchotes*. In addition, triturating teeth are present and medial prootic prongs are absent in *Amblyrhynchotes*, conditions opposite to those in *Feroxodon*. The general countenance of the two genera is also rather different, particularly regarding the anterodorsal orientation of the jaws in *Amblyrhynchotes*, which also has a ventrolateral skinfold, whereas in *Feroxodon* the jaws are in the normal terminal position and there is no skinfold.

All of the genera with the eye completely adnate (*Tetractenos, Contusus, Polyspina, Reicheltia, Marilyna* and *Colomesus*) have a dorsal cranial configuration significantly different from *Feroxodon*. Of these six genera only *Colomesus* has medial prootic prongs and a longish ethmoid, but the complete or almost complete domination of the supraorbital rim by the lateral ethmoid and sphenotic bones in *Colomesus*, a condition most closely paralleled by *Marilyna*, is strikingly different in *Feroxodon*. The possession in these six genera of other characters in common with *Feroxodon* varies discordantly amongst all of them (see Table 2), leading to the conclusion that none of this group of six genera are particularly closely related to *Feroxodon*.

Of a much different group of tetraodontid genera, characterised by a divided nasal organ comprising one or two lobes, the single-lobed *Omegophora*, revised by Hardy and Hutchins (1981), bears some resemblance to *Feroxodon* in the configuration of the head and snout profile (particularly regarding the long ethmoid region and small, highly positioned eye). However, major differences occur in some body proportions, fin shape, lateral line, shape of the frontal rim over the orbit, and spination. It appears that any superficial similarities between *Omegophora* and *Feroxodon* are most likely to have arisen from convergence within groups phyletically distinct on the basis of the fundamental nature of the nasal apparatus.

Remaining tetraodontid genera in groups with highly unusual plate-like or open plicated disk nasal apparatuses, including the highly specialised *Pelagocephalus, Chonerhinos* and *Xenopterus,* bear no significant resemblances to *Feroxodon,* over the basic tetraodontid characteristics, and are accordingly omitted from this discussion.

Material examined

Total of 25 specimens (52.8-320 mm SL). QM I.1462, Townsville, Queensland; QM I.12330, off Prudhoe I., Queensland; QM I.10277, Exmouth Gulf, Western Australia; QM I.15993 (3 specimens), Princess Charlotte Bay, Cape York, Queensland; QM I.15907, 1-9 km E of Capt. Billy Creek, Cape York, Queensland; QM I.16759, Torres Straits, Queensland, 10°02′S, 142° 28′E; QM I.16758, Torres Straits, Queensland; QM I.20496 (2 specimens), off Cairns, Queensland; QM I.4049, off Caloundra, Queensland; AMS I.21832-003, I.21839-009, I.21830-009, all from the Arafura Sea, Northern Territory; AMS I.20958-015, Princess Charlotte Bay, Cape York, Queensland; AMS I.20771-031 (3 specimens), 1-12 km E of Capt Billy Creek, Cape York, Queensland; MAGNT S.10031-087 (2 specimens), N of Smith Point, Cobourg Peninsula, Northern Territory; MAGNT S.10266-001, Shoal Bay, Northern Territory; MAGNT S.10938-018, Groote Eylardt, Northern Territory; USNM 176752, Brisbane, Queensland; NMNZ P.9937, Gove, Melville Bay, Northern Territory.

Stomach contents and gonads

Among the identifiable contents in the stomachs of the specimens examined were: remains of an elongate fish with many fin rays per vertebral segment and no scales, perhaps an eel (an opinion shared by Victor G. Springer, pers. comm.) in one specimen of QM I.15993, while another specimen from the same lot had the remains of a large crab-like crustacean and the same eel-like fish in addition to ctenoid scales; remains of a crustacean and a fish with a forked caudal fin in QM I.20496; crustacean remains and ctenoid scales in AMS I.20771-031; large crustacean fragments in NTMS 10938-018.

We have found both ripe males and females among the specimens examined, without any sexual dimorphism apparent to us in colour pattern or morphometrics.

Toxicity

Because of its rare details of the symptoms preceding death, and the pathological conditions included, we present in its entirety the pers. comm. of Dr J.M.N. Hilton, Forensic Pathologist, Queen Elizabeth II Medical Centre, Nedlands, Western Australia, concerning a recent fatality resulting from consumption of *Feroxodon multistriatus.*

'Briefly, the deceased was a 71 year old Philippino (sic) visiting Australia, living in a caravan in a small town in the far north west of the State (Onslow). Sometime in the afternoon of the 10th December 1984 he caught a fish which he left under a rock for a couple of hours before retrieving it, cleaning and cooking parts thereof. It is believed he ate the fish at about 2400 hours. Within half an hour it is said he became weak, nauseated, gagging. He was taken to the local hospital where he was seen by a nursing sister, diagnosed as having an anaphylactic reaction to fish, she having been informed that the fish in question was a stingray. She noted his weakness and gagging. No doctor lives in the district and there was telephone contact with the nearest practitioner. Treatment commenced, but he suffered a cardiac arrest and died at 0315 hours. The total time lapse between ingestion and death did not much exceed three hours.

His body was flown to Perth for post mortem examination, accompanied by part of the skin of the fish and some liver and roe said to be from the fish. The skin was identified by Barry Hutchins.

Post mortem examination of the deceased showed marked congestion and gross oedema of the lungs; the coronary arteries showed moderate atherosclerosis of the short segments and moderate narrowing of each major branch without occlusion. There was a vene puncture wound present in the left antecubital fossa with an 8 cm area of bruising around it and further puncture wounds present in the right antecubital fossa. These were iatrogenic. There were no other abnormal findings on macroscopic examination. Micro examination of the tissues from the various organ systems showed intense pulmonary oedema and moderate congestion.'

Biting habits of *Feroxodon multistriatus* and other tetraodontoid species

Two unprovoked attacks upon humans in 1979 near Proserpine, Queensland, are almost certainly attributable to *F. multistriatus* (Jeffrey W. Johnson, pers. comm.). In one of these attacks, a girl lost three toes, attesting to the considerable biting power of large tetraodontids. Similar mutilation suffered by a youngster, reported in 'The West Australian' newspaper (17 April 1977), is believed attributable to the silver toadfish, *Lagocephalus sceleratus* (J. Barry Hutchins, pers. comm.).

Such opportunistic 'feeding' behaviour in tetraodontids is indicative of a sometimes highly aggressive predatory nature, which can be likened to a feeding frenzy. Personal experience of such a frenzy, by the small blowfish *Torquigener pleurogramma,* was reported to us by J. Barry Hutchins, and local belief in potentially fatal mass attacks by the large and mainly freshwater dwelling *Xenopterus naritus* was mentioned by Day (1875). The report of triggerfishes fatally attacking soldiers during World War II (Straughan 1958) is unsubstantiated, unlike the author's observations on *Balistes vetula* attacking sharks, and the biting power of *B. carolinensis* (= *capriscus*). Wood (1953) described an attack upon a mating loggerhead turtle by several *B. carolinensis*, directed toward the erected penis and most aggressive following periods of profuse bleeding.

Further reports of the opportunistic biting of humans, including the mutilation of male genital organs, by pufferfishes are given by Salanoue-Ipin (1910), Gimlet (1923), and Tirant (1929). Indeed, genital mutilation led to the unsubstantiated suggestion by Buddle (1930), repeated by Caras (1946), that local consumption of pufferfishes in Singapore, despite the dangers of tetrodotoxin poisoning, continued in the belief of special aphrodisial properties.

In addition to reports on opportunistic biting, are those on biting ability and power: e.g. Allan *in* Darwin (1845) and Adams (1848), both citing *Diodon*, and Boulenger (1907), on *Tetraodon fahaka* (= *lineatus*). More recently, Hutchins (1980) and Hutchins and Thompson (1983) have commented on nuisance biting of fishermen and bathers.

Of a different nature, biting between conspecific pufferfishes, particularly around the flanks, belly and anus of the female, generally is attributed to breeding behaviour. First reported by Uno (1955) for *Fugu niphobles*, and since elaborated upon by other Japanese workers (see Honma *et al.* 1980), such behaviour apparently is widespread among marine and freshwater pufferfish species. Thus, Feigs (1955), Merckens (1958), Breder and Rosen (1966), and Chlupaty (1962) reported induction of spawning by biting in the African freshwater species *Tetraodon schoutedeni*, while Klausewitz (1957a, b), Hass (1959), Richter (1982), and Leipzig (1982) reported similarly for the south-east Asian freshwater species *Carinotetraodon somphongsi* (= *lorteti*). On the other hand, Roberts (1982) attributed bite marks on *Chonerhinus nefastus* to conspecific fin snipping as a food item and to agnostic behaviour rather than to breeding ritual.

Among marine pufferfishes, adult females of *Sphoeroides* (especially *S. maculatus*) often have belly scars (Shipp 1966), these being particularly numerous on individuals apparently in prime spawning condition. Similar marks on the deepwater species *S. pachygaster*, at first believed attributable to cephalopod suckers (Shipp 1974) are now thought to have resulted as well from spawning-related, conspecific biting (Robert L. Shipp, pers. comm.). Examination of museum holdings have disclosed bite scars, predominantly around the flanks and anus, which we believe also related to spawning behaviour, but present on both males and females in *S. testudineus, S. annulatus, Takifugu oblongus, Xenopterus naritus* (JS and JCT, pers. obs.) and several species of *Torquigener, Contusus* and *Tetractenos* (GSH, pers. obs.).

We conjecture that snout nudging on the flanks of female balistoids, ostracioids and diodontids during breeding behaviour (Clark 1950; Sakamoto and Suzuki 1978; Moyer 1979; Lobel and Johannes 1980; Kawabe 1984) may in fact be considered a behavioural precursor of flank biting in tetraodontids.

In this paper, reference is made to *Takifugu* in place of *Fugu*, upon the recommendation of K. Matsuura, pers. comm.

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