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# Ontogeny of the jaw apparatus and suspensorium of the Tetraodontiformes

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## Abstract

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The jaw apparatus and suspensorium of adult Tetraodontiformes are well adapted to a durophagous feeding habit. Anatomical indicators are the short, stout jaws and a suspensorium in which the quadrate lies in the same vertical plane as the autopalatine. In contrast, the palatoquadrate of larval Tetraodontiformes generally resembles that of larval percomorphs – a more posteriorly positioned quadrate and a slender and long Meckelian cartilage. Among Tetraodontiformes, the Triacanthodidae retain a protrusible upper jaw and a versatile suspensorium. The jaws of the Balistoidei have greater mobility achieved by a reduced autopalatine that has lost its bony contact with the suspensorium. In contrast to the Balistoidei, the beak-like jaws of the Tetraodontoidae lack individual teeth in the biting part of the jaws. The autopalatine is enlarged, which results in immobilization of the ethmopalatine articulation. The Ostraciidae are exceptional in having the distal part of the autopalatine reduced, while the proximal part remains attached to the suspensorium.

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## Introduction

The Tetraodontiformes have attracted considerable attention in diverse fields of biological research such as genetics (Brainerd and Murray 2000; Amemiya *et al.* 2001; Aparicio *et al.* 2002; Amores *et al.* 2004), functional morphology (Brainerd 1994; Turingan and Wainwright 1993; Turingan *et al.* 1995; Wainwright *et al.* 1995; Wainwright and Turingan 1996, 1997; Brainerd and Patek 1998; Bartol *et al.* 2003), comparative anatomy (Tyler 1968; Winterbottom 1974; Fujita 1992; Santini and Tyler 2003; Nakae and Sasaki 2004; Britz and Johnson 2005a,b; Johnson and Britz 2005), and systematics (Winterbottom 1974; Tyler 1980; Leis 1984; Rosen 1984; Holcroft 2004, 2005; Yamanoue *et al.* 2007, 2008). Accordingly, they are one of the most extensively studied teleost groups.

Tetraodontiformes are characterized by the absence of parietals, nasals, extrascapulars, infraorbitals, anal-fin spines, ribs, fewer than 21 vertebrae, and 12 or fewer caudal fin rays, among other features (Tyler 1980; Tyler and Holcroft 2007; Wiley and Johnson 2010). These reductions are accompanied

by a high degree of specialization of all sorts of structures in particular in the more derived taxa, e.g. the inflatable stomach of the Tetraodontidae and Diodontidae (Breder and Clark 1947; Brainerd 1988, 1994), the locking mechanism of both the pelvic and dorsal fin spines of the Triacanthodidae, Triacanthidae, or only the latter in the Balistidae and Monacanthidae (Tyler 1968, 1980), the expandable skin flap of the Balistidae, Monacanthidae, and *Triodon macropterus* (Breder and Clark 1947), and the subdivision of the adductor mandibulae muscle into six to eight portions (Winterbottom 1974).

The jaw apparatus of teleost fishes has attracted much interest, because of the surmise that it is intrinsically tied to the evolution and tremendous diversification of this vertebrate taxon (Schaeffer and Rosen 1961; Lauder 1980, 1982, 1985; Westneat 2003, 2004; Wilga 2008). Suction feeding, through generating negative pressure, represents the plesiomorphic mode for teleost fishes (Schaeffer and Rosen 1961; Lauder 1980, 1982, 1985; Westneat 2003, 2004; Wilga 2008) and is facilitated by a rapid expansion of the buccal cavity (Lauder 1980, 1985; Lauder and Liem 1980, 1981). During their evolution, the jaw apparatus has become elaborated and

optimized (Schaeffer and Rosen 1961; Wainwright and Bellwood 2002; Westneat 2003). The premaxillae and maxillae, which form the upper jaw, have become free from the braincase to allow a rostral protrusion. The freeing of the upper jaws from the braincase also allows a greater lateral expansion of the buccal cavity facilitated by the suspensorium, a functional unit formed by endoskeletal and exoskeletal elements of the viscerocranium. Two joints enable the lateral movement of the suspensorium, one anteriorly between the palatine and the ethmoid region and one posteriorly between the hyomandibular and the otic capsule.

The jaws of the Tetraodontiformes have drastically departed from the aforementioned grundplan because of a durophagous feeding habit (Tyler 1968; Targett 1978; Lauzanne 1988; Turingan and Wainwright 1993; Turingan 1994; Duncan and Szelistowski 1998). Their jaws are specialized and well adapted for this mode of feeding, specifically through the preceding reduction in upper jaw protrusibility and mobility of the suspensorium. Many studies have investigated the evolution, diversity, and/or functional relevance of the motor pattern of the musculature for durophagy in these fishes (Turingan and Wainwright 1993; Wainwright and Turingan 1993, 1997; Turingan 1994; Turingan *et al.* 1995; Ralston and Wainwright 1997; Friel and Wainwright 1998, 1999; Wainwright and Friel 2000). However, in these studies, the anatomical differences of the jaws and suspensorium have often been simplified and treated as similar among the different families of the suborder.

The goal of this study is to evaluate the published information about anatomy of the jaws and suspensorium of the Tetraodontiformes and to add new information by investigating the ontogeny of members of most of the families. We also show that two completely different anatomical specializations have evolved within the Tetraodontiformes, each derived from the grundplan represented by the Triacanthodidae. In light of the new data, we discuss problems with some previous morphological and phylogenetic analyses.

## Material and Methods

Specimens were cleared and double stained (c&s) for bone and cartilage following Taylor and Van Dyke (1985). Photographs of the cleared and double-stained specimens were taken either with a ProgRes C 12 plus digital camera attached to a Zeiss Tessovar microscope or with a Zeiss digital camera attached to a Zeiss Discovery V20 dissecting scope. The suspensoria and jaws were dissected under a Zeiss DRC dissecting scope where possible. In *Diodon hystrix* and *Ranzania laevis*, the jaws were excluded because of the fusion of the dentaries and premaxillae with their contralateral members. In our *Parahollandia* material, the jaws were very fragile, and accordingly, we left them attached to the neurocranium.

For analysis of the character evolution of the rostral cartilage, the ethmoid region, the autopalatine and its connection

to the ectopterygoid, and the ethmopalatine articulation, a simple taxa/character matrix was created and mapped onto the topology of Tyler and Holcroft (2007).

## Institutional abbreviations

BMNH, The Natural History Museum, London; NSMT, The National Museum of Science and Nature, Tokyo; SEAMAP, Southeast Area Monitoring and Assessment Program Ichthyoplankton Archiving Center, Fish and Wildlife Research Institute; USNM, National Museum of Natural History, Smithsonian Institution.

## Material examined

Perciformes. Moronidae. *Dicentrarchus labrax* (Linnaeus), BMNH 2009.3.16. 16–24, 28 mm standard length (SL), c&s.

Tetraodontiformes. Triacanthodidae. *Atrophacanthus japonicus* (Kamohara), BMNH 1987.1.23, one specimen, 58 mm, c&s; one specimen, uncatalogued (Chiba Institute of Technology), 18 mm SL, c&s; *Parahollandia* sp. (Fraser-Brunner), one specimen, CA 89144605, 3.9 mm notochord length (NL), c&s. Triacanthidae. *Tripodichthys oxycephalus* (Bleeker), two specimens, BMNH 2006.3.280, 16 and 33 mm SL, c&s. Balistidae. *Balistapus undulatus* (Park), two specimens, uncatalogued (NSMT), 2.7 & 4.9 mm NL, c&s; one specimen, BMNH 1974.2.25, 29.0 mm, c&s. Monacanthidae. *Stephanolepis* sp. (Gill), one specimen, SEAMAP 10741, 5.1 mm SL, c&s; two specimens, uncatalogued (NSMT), 3.4 and 14.4 mm SL, c&s. Ostraciidae. *Lactophrys* sp. (Swainson), one specimen, SEAMAP 25817, 2.3 and 3.5 mm NL, c&s; one specimen, SEAMAP 22682, 11.3 mm SL, c&s. Molidae. *Ranzania laevis* (Pennant), two specimens, uncatalogued (USNM), 2.5 and 22.0 mm SL, c&s. Tetraodontidae. *Monotretu suwatii* (Sontirat), four specimens, uncatalogued, 3.7 mm NL – 16.4 mm SL, c&s. Adult specimens were kept and spawned in captivity. Larvae were preserved on a daily basis in 4% formalin (not buffered) and 2 days later transferred into 70% ethanol. Diodontidae. *Diodon hystrix* (Linnaeus), one specimen, uncatalogued (NSMT), 2.7 mm NL, c&s; one specimen, SEAMAP 19379, 5.9 mm SL, c&s; one specimen, SEAMAP 22672, 15 mm SL, c&s.

## Figure abbreviations

Autopalatine	ap
Angular	ang
Dentary	d
Ectopterygoid	ectpt
Endopterygoid	enpt
Ethmoid	eth
Ethmoid plate	epl

Frontal	f
Hyomandibular	hy
Internasal septum	sint
Interopercle	iop
Lamina orbitonasalis	lorb
Lateral ethmoid	leth
Meckelian cartilage	mc
Maxilla	mx
Metapterygoid	mpt
Opercle	op
Parasphenoid	psph
Pars autopalatina	pap
Preopercle	pop
Preopercular spinules	spop
Premaxilla	pmx
Quadrate	q
Retroarticular	ra
Rostral cartilage	rc
Subopercle	sop
Symplectic	sy
Vomer	v

**Results**

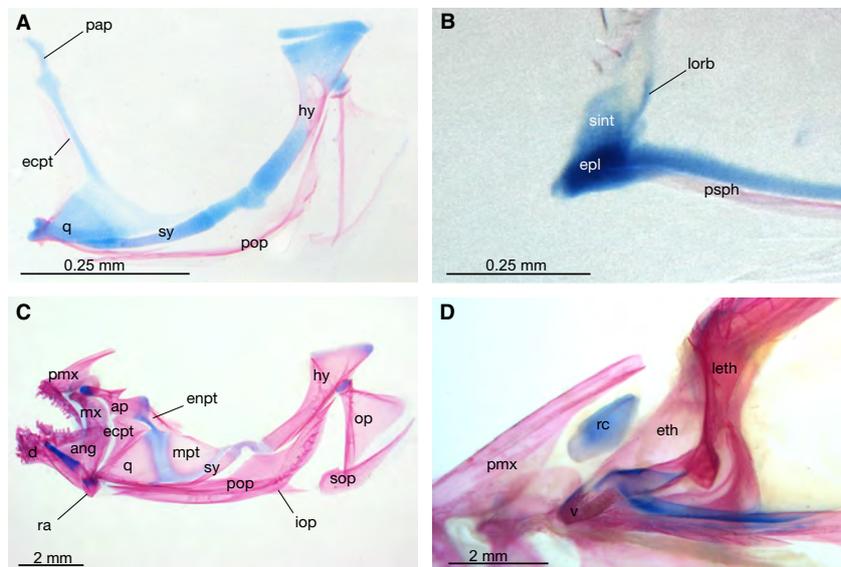
Triacanthodidae – *Parahollardia* sp. (3.9 mm; Fig. 1A,B): In this larval stage of *Parahollardia* sp., the suspensorium consists of the palatoquadrate and the pars hyomandibularis. The quadrate and the autopalatine have started to ossify within the pars quadrata and the pars autopalatina, respectively. The posteroventral process of the quadrate is fully developed and attached to the symplectic and preopercle. The pars metapterygoidea defines the posterior end of the palatoquadrate and tapers caudally, and its posterior tip is positioned at about the same level as the posterior margin of the symplectic. The premaxilla and maxilla are slender, well-ossified elements. The dentary has two teeth on each side of the symphysis. The hyomandibular consists of a thin perichondral layer of bone. A

foramen, serving as a passage for the mandibular branch of the facial nerve, pierces the hyomandibular. A crest of membrane bone extends the dorsal part of the hyomandibular anteriorly. The opercular head is oriented ventrally. The opercular series is present. The horizontal arm of the preopercle is longer than the vertical arm.

The autopalatine articulates with a laterally expanded ethmoid plate. The lamina orbitonasales and the internasal septum are very close together. The lateral ethmoid and the ethmoid have started to ossify in the lamina orbitonasalis and the internasal septum, respectively.

*Atrophacanthus japonicus* (18.0 and 58.0 mm; Fig. 1C,D): All ossifications of the suspensorium are present. The z-shaped autopalatine bears a prominent processus maxillaris. The dorsoposterior margin of the autopalatine houses an indentation for the lateral ethmoid. The quadrate has shifted its position and is now located roughly below the autopalatine. The pars autopalatina persists posteroventrally to the autopalatine. The posteroventral process of the quadrate covers the anterior part of the symplectic laterally. The pars metapterygoidea has become larger, and the metapterygoid is present.

The triangular ectopterygoid is in loose contact with the autopalatine and the processus pterygoideus. The anterior end of the endopterygoid is covered by the autopalatine laterally, while the posterior two-thirds of the endopterygoid covers the metapterygoid dorsally. The premaxilla has a long ascending process that is extended at its proximal base and housed in a groove formed by the dorsomedial and dorsolateral processes of the maxilla. The dentary is a stout and triangular element with conical teeth. A large coronameckelian is present at the posterior end of the meckelian cartilage, and medial to the dentary. A small retroarticular at the caudoventral end of the articular points ventrally.



**Fig. 1**—Triacanthodidae. —**A** and **B**. *Parahollardia* sp. —**A**. Suspensorium, jaws removed, and —**B**. Ethmoid region of a 3.9 mm SL specimen. —**C** and **D**. *Atrophacanthus japonicus*. —**C**. Suspensorium of a 18 mm SL specimen. —**D**. Ethmoid region of a 58 mm SL specimen. All figures in lateral view.

The dorsal margin of the hyomandibular articulates along its entire edge with a facet on the otic capsule formed by the sphenotic, prootic, and autopterotic. The cartilaginous connection between the symplectic and the hyomandibular is arched dorsally, where the dorsal tip of the interhyal articulates.

The triangular opercle has a dorsoventrally oriented ridge at its anterior margin that extends dorsally beyond the opercular head of the hyomandibular. The subopercle is broad anteriorly and tapers posterodorsally. The interopercle reaches from the anterior end of the subopercle to the anterior end of the preopercle.

The autopalatine articulates with the lateral expansion of the vomer and the anteroventral part of the lateral ethmoid. Anterior to the ethmoid a large oval rostral cartilage articulates with the ascending processes of the premaxillae.

**Triacanthidae – *Tripodichthys oxycephalus*** (16.0 and 33.0 mm; Fig. 2): The two individuals do not differ remarkably, and both show juvenile to adult characters. The autopalatine is a squarish element with a well-developed processus maxillaris. The posterior margin of the autopalatine has an indentation for articulation with the vomer. The processus pterygoideus is a short curved bar, forming the only connection between the autopalatine and the suspensorium. The autopalatine articulates with the maxilla anteriorly and the vomer posteriorly. Posteriorly, the triangular ectopterygoid does not reach the ventral margin of the autopalatine. The metapterygoid has a blunt posterior cartilaginous end and reaches to the level of the ventral end of the pars hyosymplectica. Posterodorsally, the metapterygoid bears a crest of membrane bone.

The shaft of the hyomandibular is roughly as wide as the head, of which the dorsal margin forms a single articular condyle articulating with a groove formed by the prootic, sphenotic, and pterotic of the neurocranium. The opercular head is oriented dorsoventrally. In both specimens, the pars hyomandibular is separated from the pars symplectica.

A dorsally oriented process from the opercle covers the opercular head of the hyomandibular laterally. Anteriorly, the subopercle bears a process and tapers posterodorsally. The preopercle is slender and consists mainly of the ridge where the adductor mandibulae is attached. The thin interopercle is pointed anteriorly and broadened posteriorly.

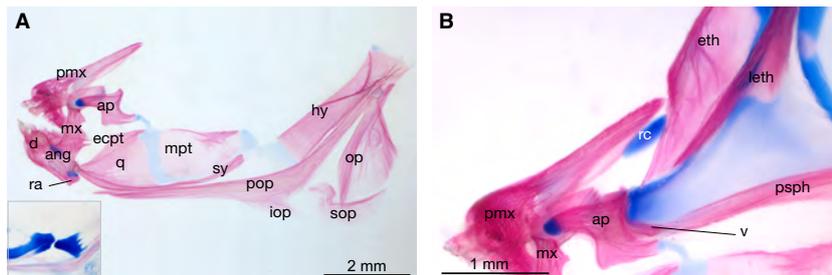
The ovoid rostral cartilage is situated between the ethmoid and the ascending processes of the premaxilla. The ethmoid is

a massive block-like bone flanked by the lateral ethmoids. The lateral ethmoid itself is roughly vertically oriented and in these specimens does not reach the anterior end of the ethmoid plate and does not contact the vomer.

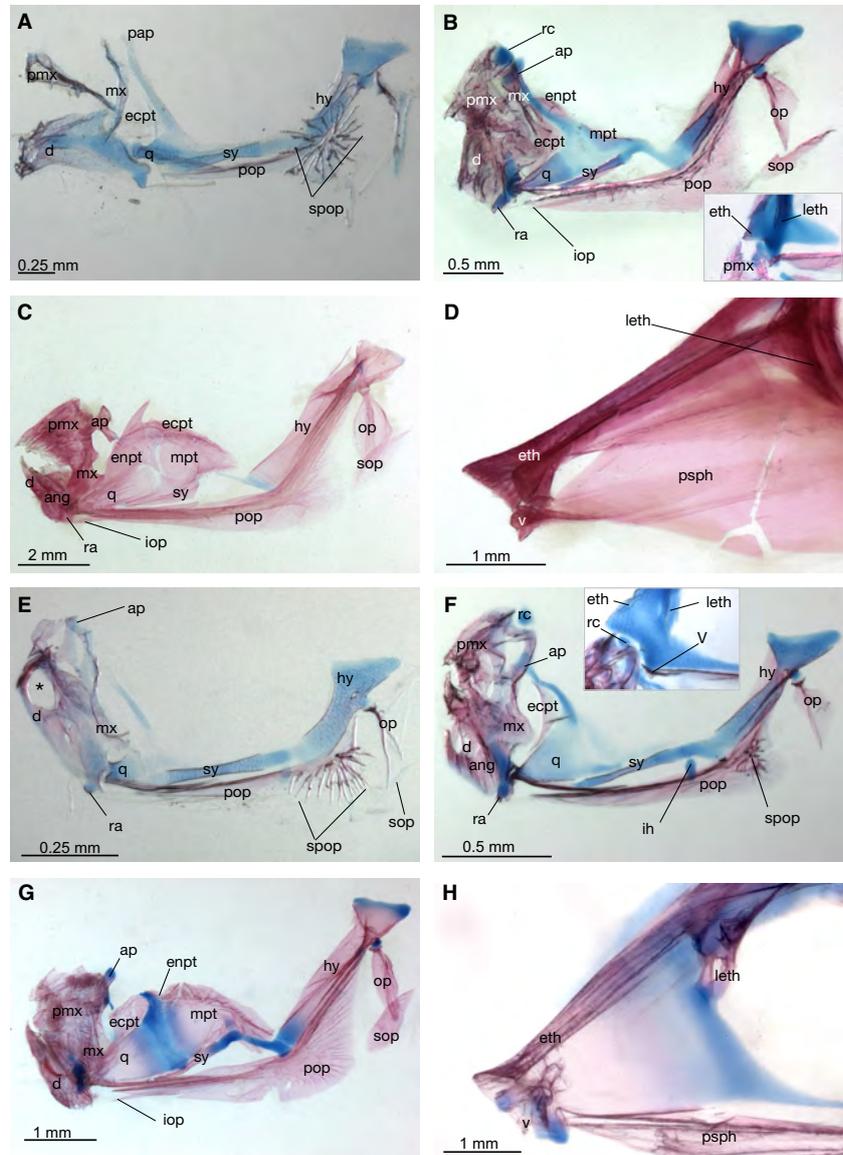
**Balistidae – *Balistapus undulatus*** (2.7 mm; Fig. 3A): The quadrate is the only ossification present in the palatoquadrate at this stage. The posteroventral process of the quadrate is fully developed and embraces the anterior tip of the symplectic. The pars autopalatina is slightly curved and pointed anterodorsally. As in the triacanthodids, the pars metapterygoidea tapers caudally to a point and ends in the region of the posterior margin of the symplectic. The ectopterygoid has started to ossify as a small strip of bone anterior to the processus pterygoideus. The dentary is a massive element that embraces the articular caudally. The retroarticular at the posterior tip of Meckel's cartilage points ventrally. Both the dentary and the premaxilla bear conical teeth.

The posterior end of the symplectic is only slightly higher than its anterior tip. The perichondrally ossified hyomandibular is discernable with the opercular head projecting posteroventrally. All elements of the opercular series are present. The preopercle bears about thirty ossified, segmented spinules at the angle of the vertical and horizontal arm.

***Balistapus undulatus*** (4.9 mm; Fig. 3B): All ossifications in the suspensorium are present. The pars autopalatina now appears as an oblique-oriented 'T'. As a perichondral ossification, the autopalatine surrounds the pars autopalatina except for the most distal tip on either side of the crossbar. The processus pterygoideus is slightly curved and more massive than in the previous stage. It is now embraced by the ectopterygoid (anteroventrally) and endopterygoid (posterodorsally). The pars quadrata and the associated quadrate are elongated caudally. The metapterygoid covers the pars metapterygoidea, and a small crest of membrane bone has started to develop at its dorsal margin. The posterior tip of the pars metapterygoidea is closely associated with the posterior end of the pars hyosymplectica. The maxilla is now firmly attached to the premaxilla. The teeth now have the incisiform appearance of the adults. The pars hyosymplectica is arched, and the posterior part of the symplectic is now oriented more dorsally and is no longer in line with the shaft of the hyomandibular. The spinules on the lateral face of the preopercle are reduced. The distal tip of the triangular opercle projects ventrally and covers the subopercle laterally (displaced in this specimen).



**Fig. 2**—Triacanthidae. —**A** and **B**. *Tripodichthys oxycephalus*. —**A**. Suspensorium and —**B**. Ethmoid region of a 33 mm SL specimen. Close up in **A**. Close up of the separate pars symplectica and pars hyomandibular of a 16 mm SL specimen. All figures in lateral view.



**Fig. 3**—Balistidae and Monacanthidae. —**A–D.** *Balistapus undulatus*. —**A.** Suspensorium of a 2.7 mm NL specimen. —**B.** Suspensorium and close up of the ethmoid region of a 4.9 mm SL specimen. —**C.** Suspensorium and **D.** Ethmoid region of a 29 mm SL specimen. —**E–H.** *Stephanolepis* sp. —**E.** Suspensorium of a 3.4 mm NL specimen. Asterisk marks the foramen in the dentary. —**F.** Suspensorium and close up of the ethmoid region of a 5.1 mm SL specimen. —**G.** Suspensorium and **H.** Ethmoid region of a 14.4 mm SL specimen. All figures in lateral view.

In the ethmoid region, all elements are present although not yet fully developed. The lamina orbitonasalis and the internasal septum are close together on the dorsal surface of the ethmoid plate. The posterior end of the ethmoid is partially covered by the frontals. The vertical oriented lateral ethmoid is fully formed. A conical rostral cartilage is closely attached and embraced by the premaxillae.

*Balistapus undulatus* (29.0 mm; Fig. 3C,D): This stage closely resembles the adult condition. All bones are present and well ossified. The T-shaped autopalatine is connected to the rest of the suspensorium only by a persisting part of the processus pterygoideus of the palatoquadrate, which is enclosed proximally by the ectopterygoid. The ectopterygoid bears a long dorsoposteriorly oriented process. A second process of the ectopterygoid extends ventrally between the

quadrate and metapterygoid, medial to the palatoquadrate. The metapterygoid has a blunt posterior end and does not reach the hyomandibular. The ventral margin of the metapterygoid covers the persisting pars hyosymplectica dorsally. Crests of membrane bone broaden the symplectic dorsally and ventrally. The dorsal crest bears a projection directly approaching the ventral projection of the ectopterygoid. In the opercular series only the opercle has changed its shape. It is now an oval element of which its ventral end covers the subopercle laterally.

The ethmoid region has become greatly elongated, and the ethmoid has moved well anterior to the lateral ethmoid. The anterior margin of the ethmoid forms a concave surface and together with the vomer forms a socket for the rostral cartilage. The ethmoid is expanded laterally to form a socket that

articulates with the posterodorsally oriented tip of the crossbar of the autopalatine.

Monacanthidae – *Stephanolepis* sp. (3.5 mm; Fig. 3E): A distinct pars metapterygoidea is absent at this stage, and the palatoquadrate therefore consists only of the pars quadrata, processus pterygoideus, and the pars autopalatina. The quadrate has started to ossify, surrounding the socket that articulates with the lower jaw. The posteroventral process of the quadrate is attached to the symplectic and to the preopercle. The processus pterygoideus projects anterodorsally, ending in an ill-defined pars autopalatina. The dentary is well ossified and pierced by a large foramen. The maxilla is a needle-shaped ossification located posterior to the premaxilla, which bears a single tooth next to the symphysis. The symplectic anteriorly and the hyomandibular posteriorly have started to ossify in the pars hyosymplectica. All elements of the opercular series are present. The preopercle has around 20 bony spinules, which are located roughly at the angle between the horizontal and vertical arms.

*Stephanolepis* sp. (5.1 mm; Fig. 3F): The pars quadrata has become enlarged relative to the processus pterygoideus. As in the balistids, the pars autopalatina appears as an obliquely oriented ‘T’. The autopalatine has started to ossify close to the shaft of the ‘T’ and at the center of the crossbar. The ectopterygoid fills the indentation between the autopalatine and the quadrate anteriorly. A small pars metapterygoidea is now present, tapers posteriorly, and ends at about the same level as the posterior margin of the symplectic. The elements of the jaws are similar in general appearance to those of a 4.9 mm specimen of *Balistapus undulatus*. The shape of the teeth has now changed to incisiform. Between the head and shaft, the hyomandibular has a crest of membrane bone on the anterior margin.

The opercle articulates with the ventrally oriented opercular head of the hyomandibular. The subopercle is a teardrop-shaped bone just ventral to the opercle (not shown). The preopercular spinules are restricted to the broadened part of the preopercle. The interopercle is a short needle-shaped element medial to the anterior portion of the preopercle. The stout ethmoid region resembles that in *B. undulatus* at around 4.9 mm. A small cone-shaped rostral cartilage is embraced by the premaxillae.

*Stephanolepis* sp. (14.4 mm; Fig. 3G,H): All elements of the suspensorium are present at this stage. The shaft of the pars autopalatina consists only of a thin strip of cartilage that connects the highly reduced autopalatine to the suspensorium. The processus pterygoideus is embraced by the endopterygoid and ectopterygoid. Neither element approaches the autopalatine. The metapterygoid has a large crest of membrane bone that encloses the pars hyosymplectica caudoventrally. All jawbones are well ossified, and the rostral cartilage is embraced by the premaxillae posteriorly. The persisting pars hyosymplectica is strongly arched, resulting in a less horizontal position of the symplectic. All elements of the

opercular series are well ossified. The preopercle has lost the spinules entirely.

The ethmoid region is elongated, and the ethmoid occupies a large area of the ethmoid cartilage. The lateral ethmoid lags behind relative to the anterior tip of the ethmoid.

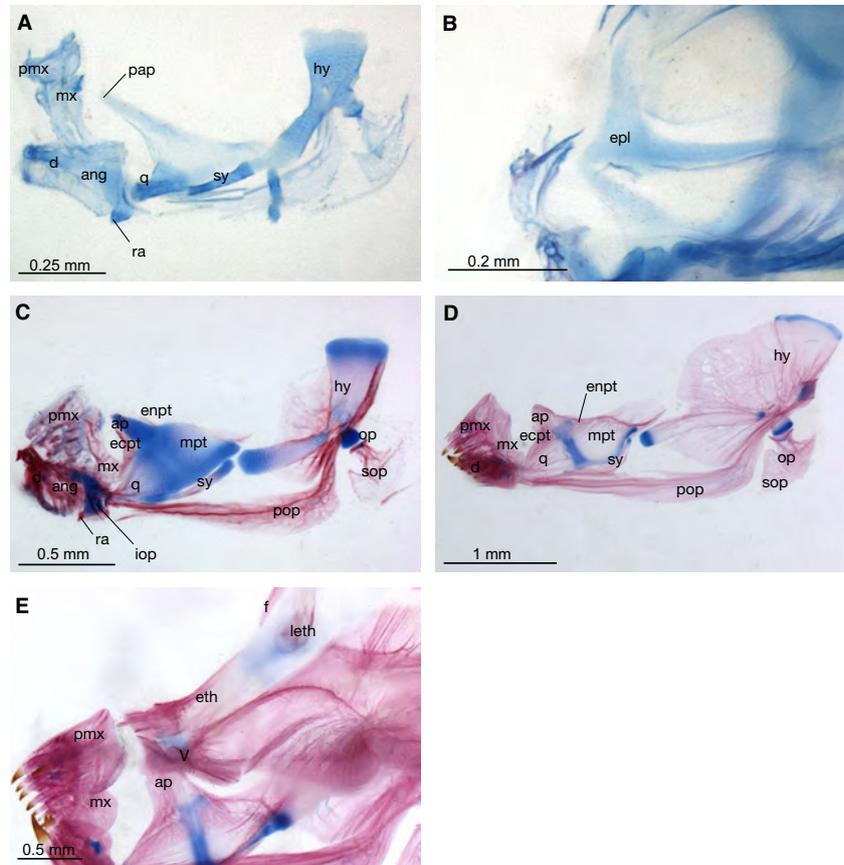
Ostraciidae – *Lactophrys* sp. (2.3 mm; Fig. 4A,B): The processus pterygoideus of the palatoquadrate is a massive dorsoanteriorly oriented bar with a blunt end. The pars autopalatina is not yet differentiated from the processus pterygoideus. The pars metapterygoidea has a blunt end, extending posteriorly to the level between the hyomandibular and the symplectic. The quadrate is present and has a large posteroventral process. The premaxilla, maxilla, and all elements of the lower jaw are present. The rectangular Meckel’s cartilage bears an anteroventrally oriented retroarticular. Both the symplectic and hyomandibular are beginning to ossify. The opercular head of the hyomandibular faces posteroventrally and articulates with a small opercle. All elements of the opercular series are present. The anteroventral edge of the ethmoid plate articulates with the blunt end of the pars autopalatina.

*Lactophrys* sp. (3.5 mm; Fig. 4C): The processus pterygoideus has broadened, and the anterior tip of the autopalatine has started to ossify. The metapterygoid is present and has a lamina of membrane bone at the posterodorsal margin. The endopterygoid has formed at the dorsal margin of the pars autopalatina and the pars quadrata. The symplectic is slightly curved anteroventrally and now separated from the hyomandibular. The shaft of the hyomandibular has slightly shifted dorsally, and its distance to the preopercle has increased. Two crests of membrane bone have enlarged the hyomandibular, the larger anteriorly between the head and the shaft and the smaller caudoventrally to the shaft.

The vertical arm of the narrow preopercle is shorter than the horizontal arm. The opercle is the smallest element in the opercular series. The subopercle bears a posterodorsal process, which is covered by the opercle laterally. The interopercle is needle shaped and its anterior tip closely approaches the retroarticular.

*Lactophrys* sp. (11.3 mm; Fig. 4D,E): The autopalatine lacks the processus maxillaris, and an articulation with the maxilla is not established. Proximally, the autopalatine interdigitates with the ectopterygoid and endopterygoid. The small endopterygoid covers the autopalatine proximally and the metapterygoid anterodorsally. Its extension contacts the ectopterygoid on the medial side of the palatoquadrate. The crest of membrane bone of the metapterygoid approaches the shaft of the hyomandibular closely. Ventrally, the symplectic is extensively enlarged by membrane bone. The anterior crest of membrane bone of the hyomandibular is greatly enlarged. The opercular series does not differ significantly from the previous stage, described before.

The ethmoid region is elongated, and the lateral ethmoid lags behind relative to the anterior tip of the ethmoid. The vomer forms a massive block that covers the ethmoid ventrally. The anterior part of the vomer is aligned with the anterior part



**Fig. 4**—Ostraciidae. —**A–E.** *Lactophrys* sp. —**A.** Suspensorium —**B.** Ethmoid region of a 2.3 mm NL specimen. —**C.** Suspensorium of a 3.5 mm NL specimen. —**D.** Suspensorium and **E.** Ethmoid of a 11.3 mm SL specimen. All figures in lateral view.

of the ethmoid, and together, they form an indentation. A shallow, anterolaterally oriented indentation on the vomer provides the articulation surface for the autopalatine.

Molidae – *Ranzania laevis* (2.5 mm; Fig. 5A): The processus maxillaris of the autopalatine bears two wing-shaped crests of membrane bone. The one that projects dorsocaudally is tightly bound to the lateral ethmoid, while the more posteriorly oriented crest is closely attached to the parasphenoid.

The maxilla is closely attached to the premaxilla (not shown). The premaxilla and the dentary bear several small distinct teeth. The posteroventral process of the quadrate covers the symplectic laterally. An endopterygoid is developed on the dorsal surface of the processus pterygoideus. The metapterygoid has started to ossify. The opercular head of the hyomandibular is posteroventrally oriented. The slender symplectic is horizontally oriented. The opercle is a ventrally oriented slender element. The subopercle and interopercle are slender elements. The preopercle bears a large crest ventrally. The lamina orbitonasalis and the internasal septum are positioned at the same plane. A small vomer is present ventral to the ethmoid plate.

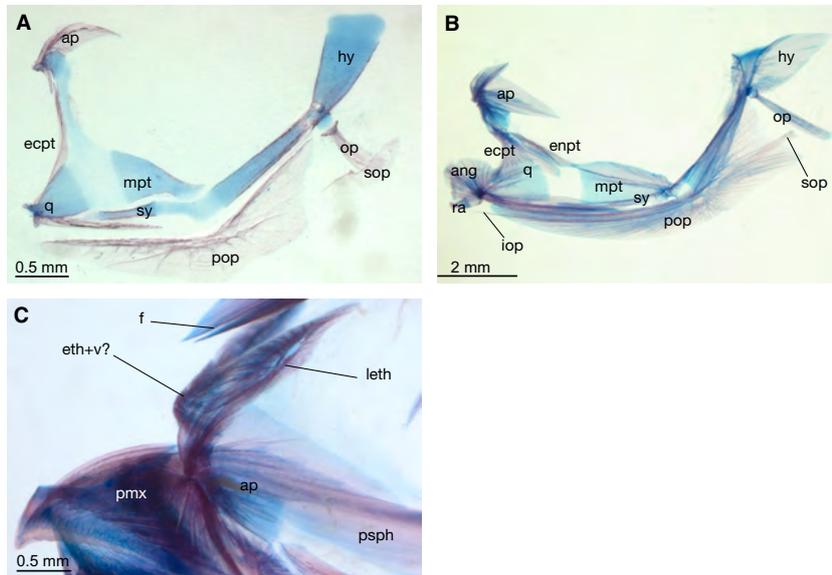
*Ranzania laevis* (22 mm; Fig. 5B,C): The crests of membrane bone of the autopalatine are greatly enlarged. The ectopterygoid now covers the dorsal part of the quadrate

laterally. Ventrally, the autopalatine interdigitates with the ectopterygoid and is also attached to the endopterygoid. The caudal part of the metapterygoid articulates with the shaft of the hyomandibular and at the same time covers the persisting pars hyosymplectica laterally. The hyomandibular bears two laminae of membrane bone of which the anterior is smaller than the posterior.

All elements of the opercular series have become elongated. The subopercle has shifted its position and is now in a more anterior position than in the previous stage. It has lost its connection to the opercle. Most of its length is now covered by the preopercle. The horizontal arm of the preopercle has elongated and is now longer than the vertical arm.

It is not clear to us whether the anterodorsal extension of the vomer represents the ethmoid. However, a development of an ethmoid could not be observed in any of the stages.

Tetraodontidae – *Monotretes suwattii* (3.7 mm; Fig. 6A,B): The processus pterygoideus of the palatoquadrate ends in a slightly angled pars autopalatina. The quadrate has started to ossify. The pars metapterygoida tapers caudally and ends roughly at about the level where the interhyal articulates with the pars hyosymplectica. A faintly stained maxilla is present anterior to the processus pterygoideus. At about the anterior



**Fig. 5**—Molidae. —**A–C.** *Ranzania laevis*. Interopercle entirely covered by the preopercle laterally. —**A.** Suspensorium, jaws removed, of a 2.5 mm NL specimen. —**B.** Suspensorium, jaws removed, and **C.** Ethmoid region of a 22 mm SL specimen. All figures in lateral view.

tip of Meckel's cartilage, two teeth are present. The symplectic and the hyomandibular are ossified within the pars hyosymplectica. Of the opercular series only the opercle and the subopercle are present.

The ethmoid plate is laterally expanded, and the tips are slightly ventrally curved. The internasal septum of the ethmoid plate is not separated from the lamina orbitonasalis.

*Monotretes suvattii* (4.7 mm; Fig 6C,D): The processus pterygoideus appears shorter and more massive than in the previous stage. The pars autopalatina is covered by the autopalatine. The processus maxillaris of the autopalatine bears a small posterodorsally oriented process of membrane bone that contacts an anterolateral projection of the vomer. The quadrate is now located more anteriorly than in the previous stage. The ectopterygoid has started to ossify. Seven teeth are present on the dentary and a single one on the premaxilla. The maxilla is closely attached to the premaxilla. The metapterygoid has started to ossify in the posterior region of the palatoquadrate. At this stage, the hyomandibular and symplectic are fully formed. The persisting cartilage between the symplectic and hyomandibular is slightly arched.

All elements of the opercular series are fully formed. The opercle is triangular in shape. The pointed caudal end of the subopercle projects dorsally. The interopercle is needle shaped and bears a ventrally oriented projection. A crest enlarges the preopercle at its ventral edge. The horizontal arm of the preopercle is larger than the vertical.

*Monotretes suvattii* (5.4 mm; Fig. 6E,F): Only slightly notable differences exist between this stage and the 4.7 mm larva. The processus pterygoideus has broadened. The posterodorsal process of the quadrate is enlarged and attached to the symplectic and preopercle. The endopterygoid is ossified on the posterior margin of the processus pterygoideus.

The lateral ethmoid and the ethmoid are now ossified and located in the same vertical plane. The vomer covers the ethmoid plate ventrally and bears a rostrrolateral projection.

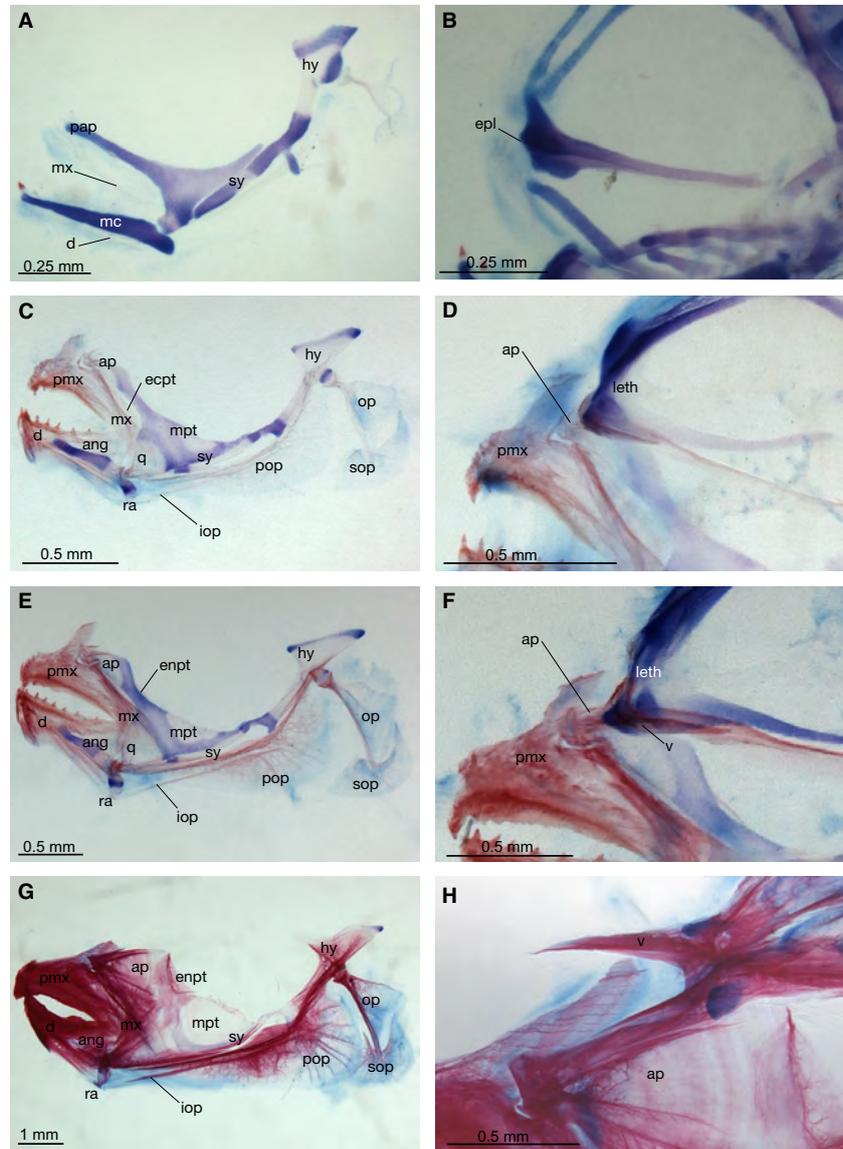
*Monotretes suvattii* (16.9 mm; Fig. 6G,H): This stage resembles the adult closely, and all elements are fully developed. The dorsal process of membrane bone of the autopalatine has become elongated and interdigitates with the vomer. Ventrally, the autopalatine interdigitates with the ectopterygoid and is closely attached to the endopterygoid. The metapterygoid is enlarged and has a small crest of membrane bone at its dorsal margin. The jaw elements have a beak-like appearance in which individual teeth are still visible. The opercle has a triangular appearance, and its ventral margin is embraced by two dorsally oriented projections of the subopercle. The interopercle is a needle-shaped element with a ventrally oriented extension.

The rostrrolateral projection of the vomer is enlarged and interdigitates with the autopalatine. The ethmoid region has become more elongated, and the ethmoid and the lateral ethmoid are no longer vertically aligned.

Diodontidae – *Diodon hystrix* (2.7 mm; Fig. 7A,B): The short processus maxillaris of the autopalatine has a dorsally oriented splint-like process of membrane bone. The palatoquadrate has a short and wide processus pterygoideus. The ectopterygoid extends from the shaft of the pars autopalatina to the dorsal margin of the quadrate.

The pars hyosymplectica is a broad element in which the symplectic and the hyomandibular have started to ossify. The opercular head of the hyomandibular is pointed posterodorsally.

All four elements of the opercular series are present. The opercle is triangular with a very narrow shaft that leads to the articular facet for the opercular head of the hyomandibular. The subopercle is larger than the opercle, and the interopercle



**Fig. 6**—Tetraodontidae. —**A–H.** *Monotrete suvattii*. —**A.** Suspensorium and **B.** Ethmoid region of a 3.7 mm NL specimen. —**C.** Suspensorium and **D.** Ethmoid region of a 4.7 mm NL specimen. —**E.** Suspensorium and **F.** Ethmoid region of a 5.4 mm SL specimen. —**G.** Suspensorium and **H.** Ethmoid region of a 16.4 mm SL specimen. All figures in lateral view.

is triangular in shape. The preopercle is obliquely oriented, and its dorsal margin is roughly a straight line.

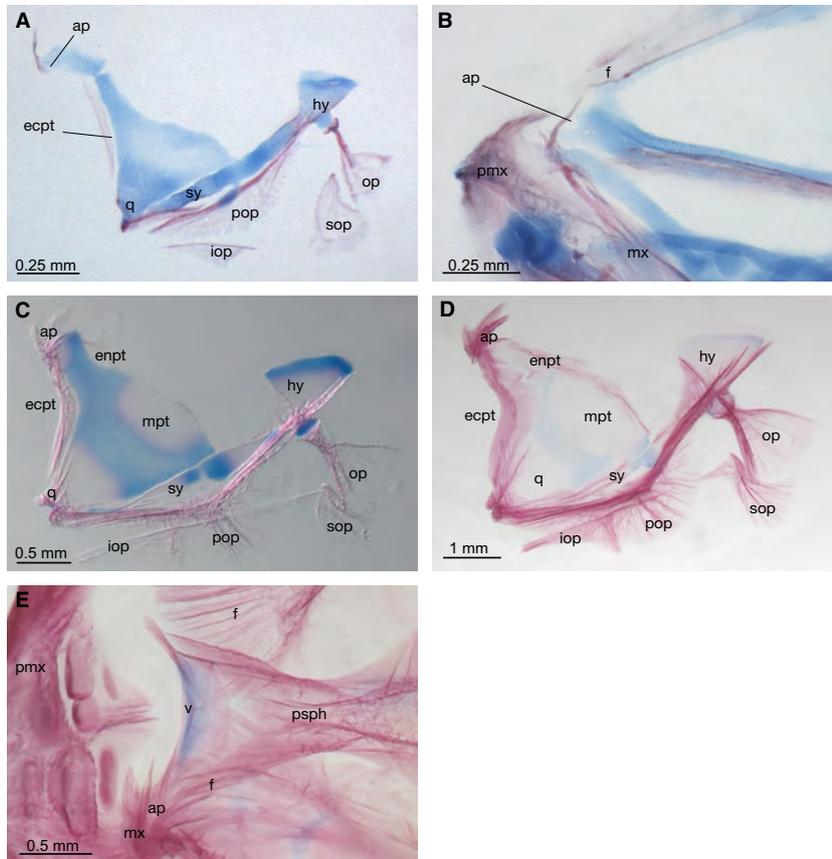
The process of membrane bone of the autopalatine surrounds the ethmoid plate. The frontal reaches far anteriorly, and its most anterior tip contacts the dorsally oriented process of the autopalatine. No ossifications within the ethmoid region are present at this stage.

*Diodon hystrix* (5.9 mm; Fig. 7C): The processus pterygoideus has become broader and shorter compared to the previous stage, and the palatoquadrate is more massive. Three processes of membrane bone are developed on the processus maxillaris of the autopalatine. The quadrate has shifted its position and is now located below the autopalatine. The endopterygoid appears at the posterodorsal edge of the shortened processus pterygoideus. The quadrate is enlarged, and the metapterygoid covers the pars metapterygoidea, which

extends to the anteroventral margin of the hyomandibular. A crest of membrane bone extends the hyomandibular anteriorly. The opercle is triangular in shape. The subopercle bears an anterior process that is covered laterally by the preopercle. The interopercle has a large ventrally oriented crest.

*Diodon hystrix* (15.0 mm; Fig. 7D,E): The autopalatine is in contact and interdigitates with the ectopterygoid and endopterygoid. The membrane bone processes of the autopalatine are now more distinct, and two of them project dorsally, while the third projects medially. The metapterygoid has a crest of membrane bone at its dorsal margin. The symplectic, hyomandibular, and the opercular series are as described for the previous stage.

The lateral ethmoid is separated from the anterior tip of the ethmoid region. The ethmoid is still absent, and the vomer is only a small, thin element embraced by the anterior part of



**Fig. 7**—Diodontidae. —**A–E**. *Diodon hystrix*. —**A**. Suspensorium, jaws removed, and **B**. Ethmoid region of a 2.7 mm NL specimen. —**C**. Suspensorium, jaws removed of a 5.9 mm SL specimen. —**D**. Suspensorium, jaws removed, and **E**. Ethmoid region from a 15 mm SL specimen. All figures but **E** are in lateral view.

the parasphenoid. The frontal and part of the lateral ethmoid are closely attached to the two dorsally projecting processes of the autopalatine.

## Discussion

The Tetraodontiformes are well known for their robust jaws adapted to a non-elusive and hard-shelled (durophagous) diet (Tyler 1968; Targett 1978; Lauzanne 1988; Turingan and Wainwright 1993; Duncan and Szelistowski 1998). Although able to engulf prey by producing negative pressure in the buccal cavity, it plays only a minor role in feeding in tetraodontiforms. Suction feeding is described for *Balistes vetula*, when it feeds on soft items (Turingan and Wainwright 1993) and for *Chylomycterus schoepfi*, where it is related not to feeding but to inflation of the body (Wainwright *et al.* 1995).

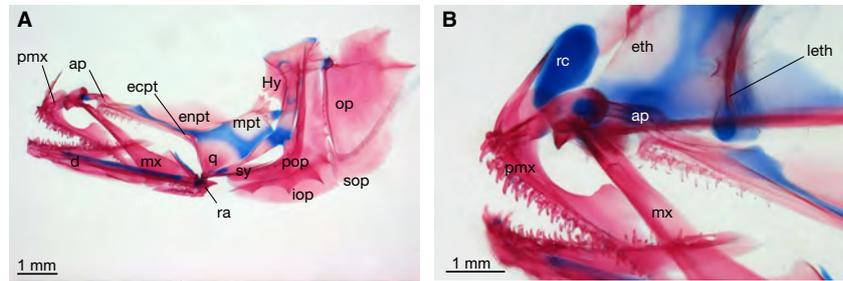
Authors of many functional studies have attempted to understand the evolution of muscular control of the highly derived jaws (Turingan and Wainwright 1993; Turingan 1994; Turingan *et al.* 1995; Ralston and Wainwright 1997; Friel and Wainwright 1998, 1999; Wainwright and Friel 2000). In these studies, the skeletal adaptations of the jaws and suspensorium have been simplified and treated as identical among representatives of the order. As we discuss below, adaptations of the jaw and suspensorium for durophagy differ

remarkably among the Tetraodontiformes and follow two different modulations.

### *Ontogenetic transformation of the suspensoria*

Early tetraodontiform larvae have a palatoquadrate and jaws identical to that of many other teleost larvae (de Beer 1937; Fritzsche and Johnson 1980; Cabbage and Mabee 1996; Hunt von Herbing *et al.* 1996) (Fig. 8). Larval *Dicentrarchus labrax* and tetraodontiforms have an elongate processus pterygoideus, and the anterior tip of the pars autopalatina/autopalatine is located far beyond the level of the quadrate. Meckel's cartilage reaches from the quadrate anteriorly to beyond the level of the anterior tip of the pars autopalatina/autopalatine. In *D. labrax*, the shape of the jaws and suspensorium do not change drastically during subsequent development, but in tetraodontiforms, there is a characteristic and significant shape change in which the quadrate becomes much more anteriorly placed, and the processus pterygoideus becomes short and robust.

Although all adult tetraodontoids lack individual teeth (Pflugfelder 1930; Andreucci *et al.* 1982), early larval stages of the Tetraodontidae (Fig. 6), Diodontidae (Fig. 7) and Molidae (personal observation) have them (unknown for *Triodon*).



**Fig. 8**—Moronidae. —**A.** and **B.** *Dicentrarchus labrax*. —**A.** Suspensorium and —**B.** Ethmoid region of a 28 mm SL specimen. All figures in lateral view.

In concert with the ontogenetic shape change of the palatoquadrate is an elongated horizontal arm of the preopercle, which is characteristic for all adult tetraodontiforms. We interpret this unusual shape of the suspensorium and the concomitant elongated horizontal arm of the preopercle as an autapomorphy of the order.

#### Character evolution

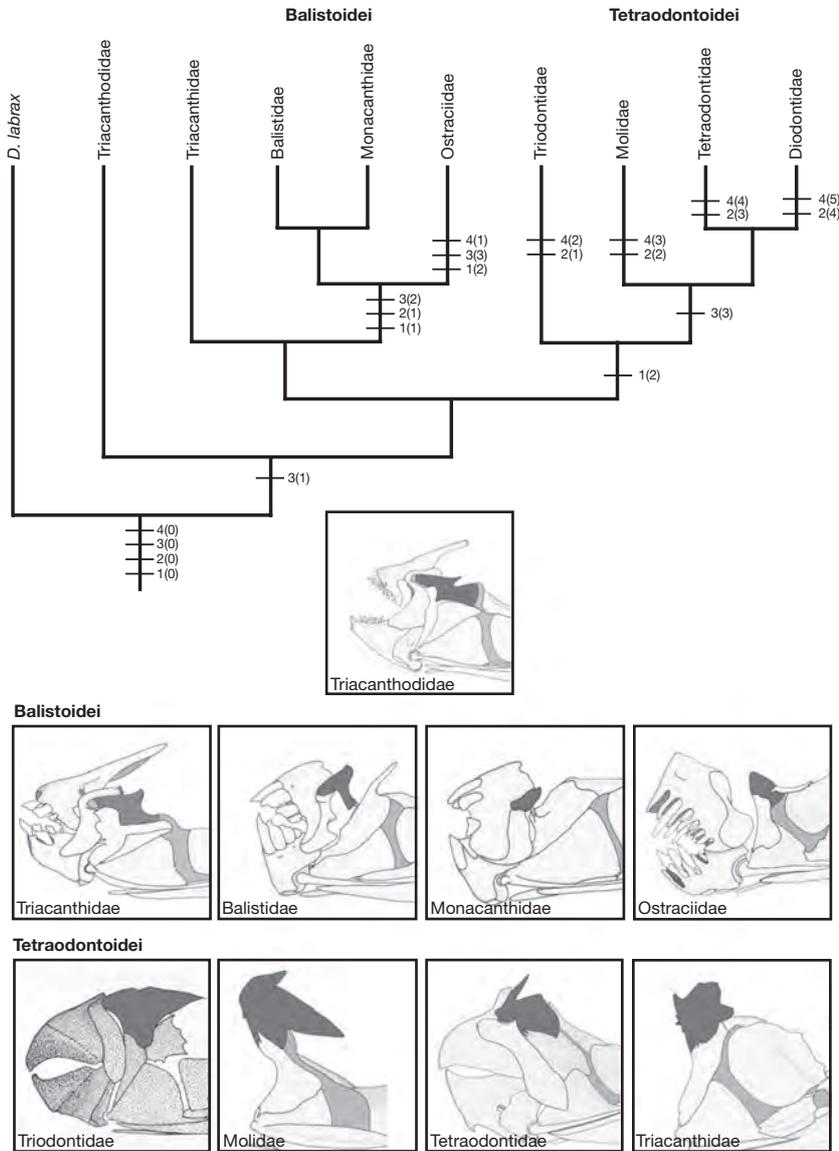
There is no general consensus about the phylogenetic intrarelationship of the Tetraodontiformes (Fig. 9). Herein, we discuss the evolution of the rostral cartilage, autopalatine, and ethmoid region within the context of the phylogenetic hypothesis of Tyler and Holcroft (2007). In that hypothesis, the triacanthodids are the sistergroup of the remaining eight families, which are divided into two suborders: the Balistoidei, in which the Triacanthidae are the sistergroup to the Balistidae, Monacanthidae, and Ostraciidae. In contrast to Tyler and Holcroft, we treat the Aracanidae as a subgroup of the Ostraciidae, Balistidae, and Monacanthidae; and the Tetraodontoidei, comprising Triodontidae (*Triodon*) as the sistergroup to a clade formed by the Molidae, Tetraodontidae, and Diodontidae.

We consider the jaws of the Triacanthodidae as the most plesiomorphic condition within the Tetraodontiformes because: (1) the large ascending process is able to glide over the ovoid rostral cartilage, suggesting upper jaw protrusion similar to that described by Liem (1980) for cichlids with a similar jaw anatomy, (2) the shape and attachment of the autopalatine indicate the possibility of a lateral movement of the suspensorium, (3) characters listed elsewhere and not necessarily involving the jaws (Winterbottom 1974; Tyler 1980; Leis 1984; Rosen 1984; Santini and Tyler 2003).

**Rostral cartilage.** The Triacanthodidae and Triacanthidae have a primitive rostral cartilage [1(0)], similar in configuration to that of *Dicentrarchus labrax*, reported previously only by Winterbottom (1974) and Rosen (1984) (Fig. 9; [1]). Although several studies have dealt with the osteology of the Tetraodontiformes extensively (Matsuura 1979; Tyler 1980; Santini and Tyler 2003), they have failed to report a rostral cartilage in the Balistidae and Monacanthidae, wherein it is specialized in being conical in shape and fully embraced by the premaxillae and maxillae [1(1)]. The Ostraciidae and the Tetraodontoidei have convergently lost the rostral cartilage [1(2)] (Table 1).

**Ethmoid region.** In the Triacanthodidae and Triacanthidae, the ethmoid is placed slightly dorsoposterior to the vomer, and its anterior, oblique margin forms a concavity for the rostral cartilage (Fig. 9; [2]). Because a similar configuration of the ethmoid region characterizes *Dicentrarchus labrax* and other generalized percomorphs, we consider this situation to be plesiomorphic for all Tetraodontiformes [2(0)]. In the Balistidae, Monacanthidae, Ostraciidae, and *Triodon* (Tyler 1980: Fig. 184), the anterior end of the ethmoid overlaps the vomer anteriorly [2(1)]. In the Balistidae and Monacanthidae, both elements together form an anteroventrally oriented concavity that abuts the rostral cartilage. The ethmoid region of the Molidae, Tetraodontidae, and Diodontidae is extremely different, making a meaningful comparison between the families impossible. In tetraodontids, the vomer is the prominent element of the ethmoid region and has a forked anterior margin [2(3)]. In contrast, the vomer is reduced to a small plate in molids, where it is fused to the ethmoid [2(2)] and diodontids, which lack the ethmoid entirely [2(4)].

**Autopalatine and its contact to the suspensorium.** Because of the shape change of the palatoquadrate during ontogeny, the connection between the palatoquadrate and the ectopterygoid in adult Triacanthodidae is specialized (the autopalatine is broad and in loose contact with the ectopterygoid) compared to the generalized percomorph configuration [3(0)] (Fig. 9; [3]). Nonetheless the triacanthodid configuration [3(1)] is more primitive than the other two configurations within the order. According to Tyler's (1980) description, in *Triodon*, the ectopterygoid is loosely attached to the autopalatine and resembles the Triacanthodidae closely. Two more derived configurations characterize the remaining families of the order: the autopalatine becomes removed from the ectopterygoid and therefore is detached from the suspensorium [3(2)]; or the autopalatine interdigitates with the ectopterygoid and therefore becomes tightly attached to the suspensorium [3(3)]. Loss of the bony connection of the autopalatine to the suspensorium in the Triacanthidae, Balistidae, and Monacanthidae is accompanied by a reduction in size of the autopalatine. In the Monacanthidae, where this reduction is greatest, the processus maxillaris is still complete. The Ostraciidae, in contrast, have the processus maxillaris of the autopalatine reduced and an interdigitation pattern of the autopalatine to



**Fig. 9**—Character evolution. The four major elements in the caudal skeleton of the Tetraodontiformes mapped onto Tyler and Holcroft’s (2007) (only recent taxa are shown) phylogenetic hypothesis. Rostral cartilage 1. Plesiomorphic 1(0); modified 1(1); absent 1(2). Ethmoid region 2. Plesiomorphic 2(0); modified 2(2–4). Autopalatine and its contact to the suspensorium 3. Acanthomorph condition 3(0); plesiomorphic for Tetraodontiformes 3(1); autopalatine detached from suspensorium 3(2); autopalatine interdigitates with ectopterygoid 3(3). Autopalatine and the ethmopalatine articulation 4. Plesiomorphic 4(0); modified 4(1–5). For an explanation about plesiomorphic conditions and modification, see text. Drawings below present the different modifications of the autopalatine. The drawing of *Triodon* is modified after Tyler (1980).

the ectopterygoid identical to the members of the Tetraodontoidae [3(3)] (Table 2).

*Autopalatine and ethmopalatine articulation.* As in generalized percomorphs, the autopalatine in the Triacanthodidae forms an articulation with the vomer and the lateral ethmoid that enables the suspensorium to move laterally [4(0)] (Fig. 9; [4]). In the Triacanthidae, the ethmoid is excluded from the ethmopalatine articulation, and the autopalatine articulates exclusively with the vomer. In the Balistidae and Monacanthidae, the autopalatine articulates only with the ethmoid. Although the arrangement of articular elements of the ethmoid region differs between the balistids and monacanthids on the one hand and triacanthids on the other, both cases represent the plesiomorphic state for the order. Exclusion of the vomer from the articulation in the former two families may

result from reduction in the autopalatine [4(0)]. The Ostraciidae are unique within tetraodontiforms in having the distal rather than the proximal part of the autopalatine reduced [4(1)], as is the case in the remaining balistoids.

The fixation of the ethmopalatine articulation differs substantially among the four families of the Tetraodontoidei (Table 3). We therefore coded the immobilization of the ethmopalatine articulation with four different states [4(2–5)] and conclude that this fixation cannot be used to support the monophyly of the suborder as has been previously suggested (Fraser-Brunner 1943; Santini and Tyler 2003).

*Conflicts and problems with various phylogenetic hypotheses*

Since Cuvier (1817) first recognized the fish order Tetraodontiformes (‘Plectognathi’), the intrarelationships of this

**Table 1** Rostral cartilage

Taxa	Rostral cartilage
<i>Dicentrarchus</i>	Ovoid
<i>Atrophacanthus</i>	Ovoid
<i>Tripodichthys</i>	Ovoid
<i>Balistapus</i>	Conical
<i>Monacanthus</i>	Conical
<i>Lactophrys</i>	Absent
<i>Triodon</i>	Absent
<i>Ranzania</i>	Absent
<i>Monotretete</i>	Absent
<i>Diodon</i>	Absent

**Table 2** The autopalatine and its association with the ectopterygoid (suspensorium)

Taxa	Contact autopalatine to the ectopterygoid
<i>Atrophacanthus</i>	Loose contact
<i>Tripodichthys</i>	Detached
<i>Balistapus</i>	Detached
<i>Monacanthus</i>	Detached
<i>Lactophrys</i>	Interdigitates
<i>Triodon</i>	Loose contact
<i>Ranzania</i>	Interdigitates
<i>Monotretete</i>	Interdigitates
<i>Diodon</i>	Interdigitates

**Table 3** The autopalatine and its association with different elements of the ethmoid region

	Vomer	Ethmoid	Lateral Ethmoid	Parasphenoid	Frontal
<i>Triodon</i>	Sutured	Sutured	Sutured		
<i>Ranzania</i>			Attached	Attached	
<i>Monotretete</i>	Interdigitated				
<i>Diodon</i>					Interdigitated

morphologically highly specialized group have been a continuous subject of discussion. Winterbottom (1974) was the first to publish a phylogenetic hypothesis based on cladistic principles applied to morphological characters (Hennig 1950). His work on the phylogenetic systematics of the Tetraodontiformes was followed by several others that re-evaluated his conclusions, based on additional morphological characters and taxonomic data sets (Tyler 1980; Leis 1984; Rosen 1984; Tyler and Sorbini 1996; Santini and Tyler 2003). In recent years, with the rapid development of molecular systematics, additional studies aiming to elucidate the interrelationship of the Tetraodontiformes with molecular data sets were added to the existing turmoil (Holcroft 2005; Alfaro *et al.* 2007; Yamanoue *et al.* 2008).

Despite the considerable attention given to the intrarelationships of the Tetraodontiformes over the years, no consensual phylogenetic hypothesis has come to the fore. Among other things, authors continue to disagree on the position of the ostraciids relative to members of the suborder Tetraodontoidae and on the position of *Triodon* (e.g. on the exclusion of *Triodon* from the Tetraodontoidae). To date, neither morphological nor molecular characters have provided unambiguous answers to these problems (Dareste 1849, 1850; Regan 1902; Winterbottom 1974; Tyler 1980; Leis 1984; Rosen 1984; Tyler and Sorbini 1996; Holcroft 2005; Alfaro *et al.* 2007; Yamanoue *et al.* 2008). One reason for the phylogenetic intractability of the tetraodontiforms may be their confusing combination of reductive and highly specialized features. Another is that, in the absence of an ontogenetic perspective, previous studies have sometimes misinterpreted or misidentified skeletal elements (Britz and Johnson 2005a,b; Johnson and Britz 2005; Konstantinidis and Johnson 2011).

As one example, beak-like jaws have been used in various earlier studies to define the suborder Tetraodontoidae (Cuvier 1817, 1829; Fraser-Brunner 1943; Tyler 1980; Santini and Tyler 2003). Although the configuration of this beak has often been interpreted to be the same in all tetraodontoids, a few (mostly ignored) studies shed some doubt on its homology. Several of these comparatively investigated its ultrastructure in the four families (Andreucci 1968; Andreucci and Blumen 1971; Britski and Andreucci 1975; Andreucci *et al.* 1982; Britski *et al.* 1985). Britski *et al.* (1985) summarized the results and concluded that the beak of *Triodon* resembles more closely the jaws of parrotfishes (Scaridae), that the Molidae show no evidence of the incorporated teeth found in the other three families, and that only the beaks of Tetraodontidae and Diodontidae have a cogently similar ultrastructure. In other words, the beaks of *Triodon*, molids, and tetraodontids/diodontids differ enough to invalidate this shared structure as a synapomorphy of the suborder. It is likely that fixation of the ethmo-palatine articulation is related to the beak-like jaws, and, as we concluded above, seems also to have arisen independently, also invalidating earlier hypotheses (e.g. Fraser-Brunner 1943; Santini and Tyler 2003) that it is a unifying character of tetraodontoids.

Other examples of misinterpreted characters can be found in the phylogenetic hypothesis of Santini and Tyler (2003) based on 210 morphological characters. The authors coded fusion of the anterior vertebrae to the basioccipital in the Ostraciidae [127(1)] as originally described by Tyler (1963). Britz and Johnson (2005b) demonstrated that the anteriormost vertebra also fuses to the occiput in the Molidae. Santini and Tyler misinterpreted this character (character 127) for molids, instead describing the molid basioccipital (character 9) as 'prolonged dorsally behind the exoccipital to border the foramen magnum to the exclusion of the exoccipitals'. This prolongation is actually the result of the first vertebra having fused to the basioccipital. Konstantinidis and Johnson (2011) showed that two to three epurals are present in larval stages of

triacanthodids, whereas Santini and Tyler observed only a single epural (character 182) in adult triacanthodids they used in their study.

Molecular data sets have also proved incongruent. Holcroft (2005) published the first molecular phylogenetic hypothesis of the Tetraodontiformes based on mitochondrial 12S and 16S genes and the nuclear RAG1 gene. Alfaro *et al.* (2007) re-analyzed Holcroft's data set and added sequences of the enigmatic *Triodon* and a second triacanthid species. The two studies indicate similar relationships, but Alfaro *et al.*'s analysis shows a higher resolution, possibly because of the inclusion of *Triodon*. In their analysis, *Triodon* forms, together with the Molidae and Ostraciidae, the basal sistergroup of the remaining families, suggesting a convergent evolution of the parrot beak-like jaws within the order. Yamanoue *et al.* (2008) analyzed the entire mitochondrial genome and reached a quite different conclusion, which conflicts with previous morphological and molecular hypotheses. Yamanoue *et al.* (2008) recovered a close relationship between the Ostraciidae and *Triodon* that forms together with the Triacanthodidae the basal sistergroup of the remaining families, among which the interrelationships are mostly unresolved. Yamanoue *et al.* discussed most of their findings in light of statistic parameters that makes it difficult for us to interpret and evaluate their findings.

Holcroft (2005) and Alfaro *et al.* (2007) recovered a clade formed by molids and ostraciids and, in the latter analysis, including *Triodon*. A closer relationship of ostraciids to some taxa within the Tetraodontoidei was also proposed by Rosen (1984) and Leis (1984). Rosen placed the ostraciids in a polytomy with the Tetraodontoidei based on one character (character 20; 'dorsal fin and radials remote from occipital region of skull'). Leis placed the ostraciids in a trichotomy with diodontids and molids based on 23 of what he called 'larval' characters (actually, a number of them, e.g. vertebral and fin-ray numbers also characterize adults). *Triodon* was unavailable for both studies.

As noted above, Britz and Johnson (2005b) also presented evidence in support of a close relationship between the Ostraciidae and one tetraodontoid family, the Molidae, i.e. the shared fusion of one or more vertebrae to the basioccipital. This rare fusion is known elsewhere among acanthomorphs only in males of the distantly related Cetomimidae (Johnson *et al.* 2009) and among other teleosts, only in the osteoglossomorph *Heterotis* (Patterson and Johnson 1995; Johnson and Britz 2010), and the elopomorph *Megalops* (Johnson and Britz 2010).

We anticipate that more ontogenetically focused studies will facilitate resolution of some of the phylogenetic conundra of teleost taxa, particular those involving highly specialized taxa, like the Tetraodontiformes, in which the larvae still show more plesiomorphic conditions than their adult congeners (for examples see Johnson 1984 and citations herein).

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