

A description of the smallest *Triodon* on record (Teleostei: Tetraodontiformes: Triodontidae)

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Abstract The smallest known specimen (20 mm standard length: SL) of *Triodon macropterus* Lesson is described and illustrated. It is easily distinguished from superficially similar tetraodontid and diodontid larvae or early juveniles of comparable size by the following characters: separate premaxillae in conjunction with the fused dentaries; the presence of multicuspoid spinoid scales; the jet-black mark in front of the soft dorsal fin; the developing pelvis, which is visible through the distended skin of the belly; and the presence of a number of procurent caudal fin rays. The small *Triodon* differs from the adult in possessing a huge head that measures 45% SL (vs. 28.5–32.7% in adult), the absence of the characteristic deltap with the conspicuous lateral ocellus, and the structure of the scales and nostrils.

Key words *Triodon* · Early juvenile · External anatomy · Tetraodontiformes

The rare pelagic *Triodon macropterus* Lesson is the only extant member of the family Triodontidae in the percomorph order Tetraodontiformes and is currently considered the most basal gymnodont (Tyler, 1962, 1967, 1980; Santini and Tyler, 2003). Because of its phylogenetic position, it has been of special interest to tetraodontiform workers, but due to its rareness in collections only a few studies have described its anatomy (Dareste, 1849; Hollard, 1860; Breder and Clark, 1947; Tyler, 1962, 1967, 1980; Winterbottom, 1974). For a long time, only specimens of 270–463 mm were available for study (Tyler, 1967, 1980; Winterbottom, 1974), and smaller specimens of 89–103 mm were caught and investigated only recently (Tyler and Patterson, 1991).

Leis (1984) summarized the early life history information on tetraodontiforms but was unable to include triodontids because of lack of information. During a visit at the Muséum Nationale d'Histoire Naturelle in Paris in September 2003, we discovered, unexpectedly and with considerable excitement, a specimen of *Triodon* measuring only 20 mm standard length (SL), representing by far the smallest specimen on record. We use this opportunity to provide a description of its external anatomy and structure of its internal organs, to be followed by a detailed description of its skeletal anatomy.

Material and Methods

The 20 mm SL *Triodon macropterus* is housed in the ichthyological collections of the Muséum Nationale d'Histoire Naturelle in Paris (MNHN 1998–1145, collected by Campagne Musorstom 7 on 11 May 1992 at Wallis and

Futuna, French territory, 14°19'8" S; 178°4'8" W at a depth of 245–440 m by beam trawl).

All measurements except SL were taken with an ocular micrometer to 0.1 mm; SL was measured with digital calipers. Head length is measured from the tip of the upper jaw to the rim of the gill opening. Internarial width is measured between interior rims of anterior nostrils. All other measurements are self-explanatory and follow Hubbs and Lagler (1958).

Results

External anatomy. Morphometric and meristic information on the 20 mm specimen of *Triodon* are summarized in Table 1. The rotund body tapers posteriorly, both in dorsal and lateral view, with its widest part at the level of the pectoral fin (Figs. 1B,C, 2). The head is very large, contributing to almost half of the standard length. It is rectangular in dorsal view and slopes anterior to the eyes, with the snout tapering toward the tip. There is a browlike ridge above each eye with a more shallow area between them. The large eye is more than one-third of the head length. The anterior nostril projects as a tube beyond the surface of the skin, and the posterior nostril is a round orifice with a flap of skin covering most of the opening (Figs. 1E, 2).

The prominent beak is formed by coalesced tooth units of the two separate premaxillae in the upper and the fused dentaries in the lower jaws (Fig. 1D,E). Tooth units in both jaws are arranged in transverse proximal to distal rows. The proximal rows of the lower jaw feature rounded tooth units with clear limits that are less apparent distally and absent from the two most distal rows. The beak is surrounded by

upper and lower lips bearing numerous papillae, densest at the angle of the lips (Fig. 1D).

The small, semicircular gill opening is located in front of the base of the pectoral fin (Figs. 1C, 2A). Its rim extends as a ridge of skin that covers the proximal part of the base of the pectoral fin.

The sac-like belly is distended, not laterally compressed as in the adult (compare Fig. 1A with Fig. 1B,C), its original shape impossible to determine due to extensive wrinkling (contortion) of the skin, apparently an artifact of preservation. The pelvic girdle is relatively shorter compared to the size of the belly than in the adult, so that it seems unlikely that it could be used to effectively distend the belly sac.

The adult complement of fins and fin rays is present. The dorsal fin has two short slender spines and 11 soft rays. The anal fin has 10 soft rays. The caudal fin has 12 principal rays and 9 dorsal and 8 ventral procurent rays, of which the anteriormost are vestigial. The pectoral fin has 17 rays. The pelvic fin is absent.

The scales are spinoid with one to five spines (Fig. 3A,B).

Pigmentation. The back and upper sides are yellowish-brown due to the musculature beneath the skin, and the belly is pale white (Fig. 1B,C). The head and body are densely covered dorsally and dorsolaterally with tiny (1.2–2.5 μm) circular melanophores that become more sparse ventrally at the level of the pectoral fin and are absent from most of the belly (Fig. 1B–F). However, the peritoneum in that area shows a similar pattern of dense circular melanophores (Fig. 3C,D). The only distinctive (and diagnostic) mark is the jet-black streak in front of the soft dorsal fin (Fig. 1F), which is in the exact position of the black mark in the adult that characterizes the spinous dorsal fin.

Table 1. Selected morphometric information on 20mm *Triodon* and comparative data for adults

	20 mm	307–480 mm ^a	
	mm	% SL	% SL
SL	20		
Post head length (HL)	11	55	
HL	9	45	28.5–32.7
Snout length	3.4	17	17.0–18.8
Eye diameter	3.6	18	6.0–8.9
Interorbital width	4.6	23	9.2–11.1
Internarial width	1.6	8	
Mouth opening width	2.5	12.5	
Height of gill opening	1.1	5.5	5.6–7.6
Pectoral fin length	3.3	16.5	9.7–11.0
Length of base of dorsal fin	1.8	9	
Length of base of anal fin	1.2	6	
Greatest length of caudal fin	3.8	19	17.2–19.2
Caudal peduncle depth	1.6	8	2.8–3.8
Caudal peduncle length	2.5	12.5	21.4–27.4
Pelvis length	8	40	
Tip of upper jaw to tip of pelvis	9	45	40.7–58.1

SL, standard length

^aData from Tyler (1967)

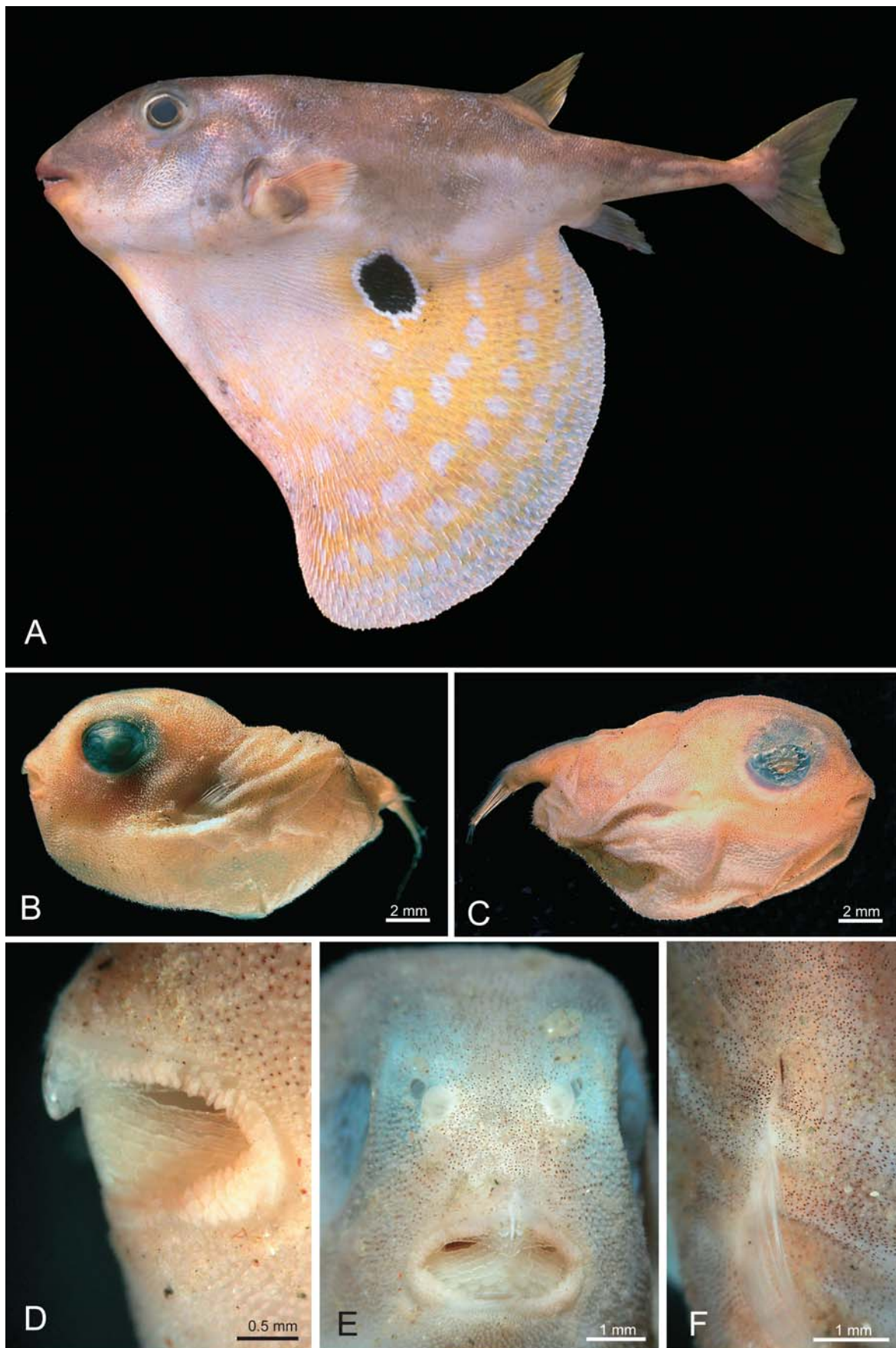
Anatomy of the viscera. The oesophagus opens into the anterodorsal side of the very large, translucent, and elastic stomach, the most prominent organ in the abdominal cavity (Fig. 3C). Its inner surface contains rows of widely spaced papillae that converge toward the pylorus (Fig. 3F). The stomach contained numerous fragments and particles, of which only some could be identified (Fig. 3G). Among them were the skeletons of pelagic foraminifera, spines of echinoids, spicules of sponges, and the exoskeleton of a crustacean (most likely a mysid). The pyloric opening is located on the anteroventral side of the stomach, shifted slightly to the left (Fig. 3F). The remainder of the alimentary tract lies dorsal to the stomach and has one S-shaped loop (Fig. 3E,F). The internal wall of the anterior portion of the intestine bears numerous short papillae (Fig. 3H). Between the loop and the rectum, the intestine is expanded into a sac-like compartment that we term Tyler's pouch (Fig. 3E,F,I), packed with unidentified items (Fig. 3I). The papillae in the internal wall of this compartment are larger (0.4 mm) and more compressed than the more anterior ones (0.2 mm). The trilobate liver surrounds the anterior end of the stomach (Fig. 3C,E). Preceding the intestinal loop, the hepatic duct expands to form the gallbladder (Fig. 3E), and the spleen lies ventral to the loop (Fig. 3F). A small swim bladder with a relatively large rete mirabile occupies the anterior third of the abdominal cavity dorsal to the stomach (Fig. 3D). A thin-walled translucent sac close to the rectum appears to represent the urinary bladder (Fig. 3D).

Discussion

Diagnostic features of early juvenile *Triodon*. Our early juvenile *Triodon* bears a superficial resemblance to larvae and early juveniles of tetraodontids or diodontids in its general body shape and distended belly. It is, however, easily distinguished by the separate premaxillae in conjunction with the fused dentaries. Additional features that clearly differentiate the 20mm *Triodon* from tetraodontids or diodontids of a comparable size are: the presence of tricuspid spines, the jet-black mark in front of the soft dorsal fin, the developing pelvis, which is visible through the distended skin of the belly, and the presence of a number of procurent caudal fin rays (unique among extant Tetraodontiformes).

Differences between early juvenile and adult *Triodon*. One of the most conspicuous features of the 20mm *Triodon* is its relatively gigantic head, which measures 45% SL versus 28.5–32.7% in the adult fishes studied by Tyler (1967) and its huge eye of 18% SL versus 6.0–8.9% SL in the adults.

The early juvenile differs further from the adults by a much shorter peduncle, which measures only 12.5% SL versus 21.4–27.4% SL. Another clear difference is the absence of the dewlap and its striking ocellus characteristic of larger specimens. Additional distinctive features that require observation at higher magnification are the structure of the scales and that of the nostrils. The scales of the early juvenile are unicuspid to pentacuspid, whereas those of the adult have a rhombic base with a median ridge that bears several



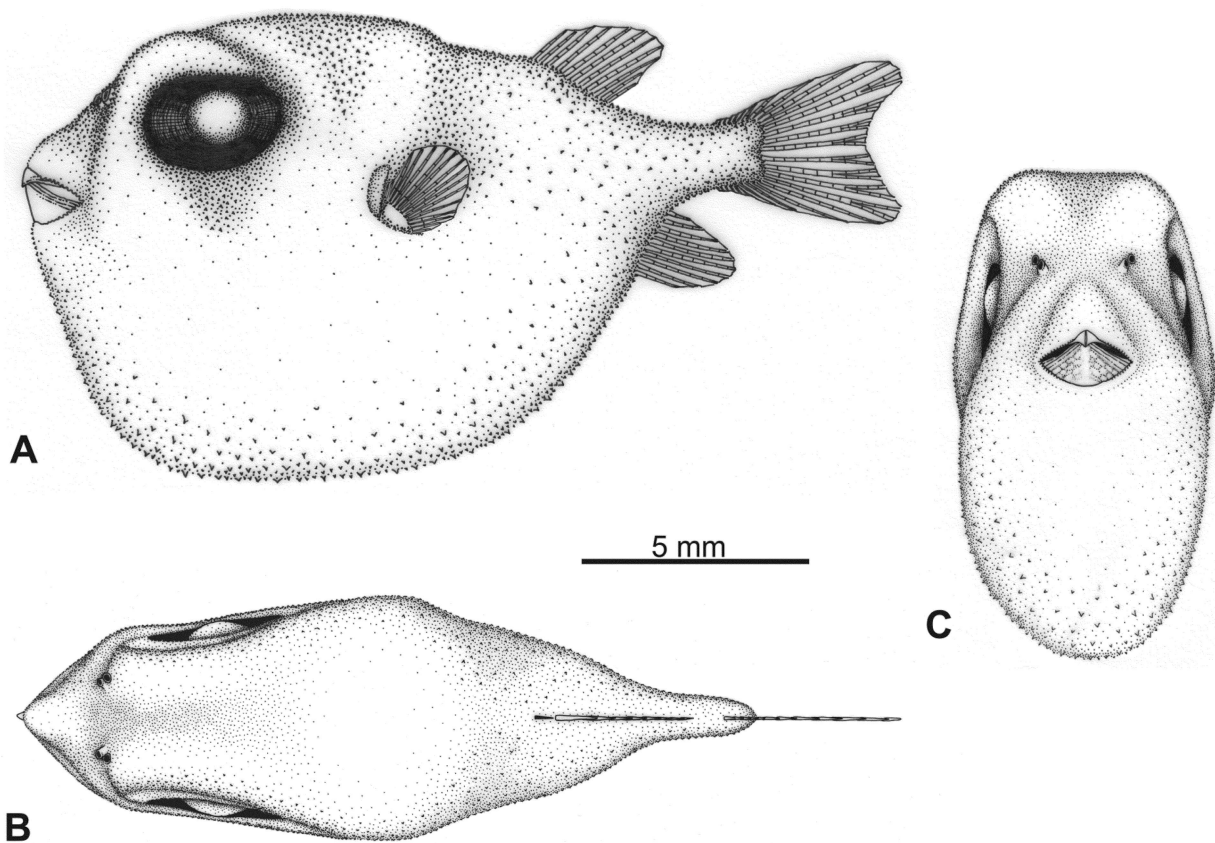


Fig. 2. *Triodon macropterus*, MNHN 1998–1145, 20 mm SL: **A** left lateral view; **B** dorsal view; **C** frontal view. Note that the degree of distension and shape of the belly is estimated

spines (see Tyler, 1980). The anterior and posterior nostrils are relatively more widely separated in the early juvenile, with the anterior nostril elongated into a short tube and the posterior nostril flush with the surface of the body and guarded by a skin flap. The adult has “the anterior nostril with an upraised flap posteriorly and the posterior nostril with an upraised flap anteriorly” (Tyler, 1980: 244, fig. 181).

The 20 mm *Triodon* also differs from the adult in the structure of its viscera, most strikingly by the presence of the very large distended stomach, lacking in the adult (see Breder and Clark, 1947). We do not know the function of this modified stomach and what biological role it may play during early development, nor can we discount the possibility that it is an artifact. Unfortunately, Breder and Clark’s (1947) brief description of visceral structures in *Triodon* does not allow any more detailed comparison. Another

striking modification of the early juvenile gut, absent in the adult, is Tyler’s pouch, an expansion of the intestine preceding the rectum, likewise a structure of unknown function.

We believe that our ongoing detailed studies of this and other early developmental stages of tetraodontiform will offer important new insights into the familial relationships of this diverse group of fishes.

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Fig. 1. **A** *Triodon macropterus*, Pelahakan Ratu, south coast of Java, not preserved, ca. 360 mm SL. **B–F** MNHN 1998–1145, 20 mm SL: **B** left side; **C** right side; **D** beak, left lateral view; **E** beak, frontal view; **F** spinous dorsal fin, dorsal view

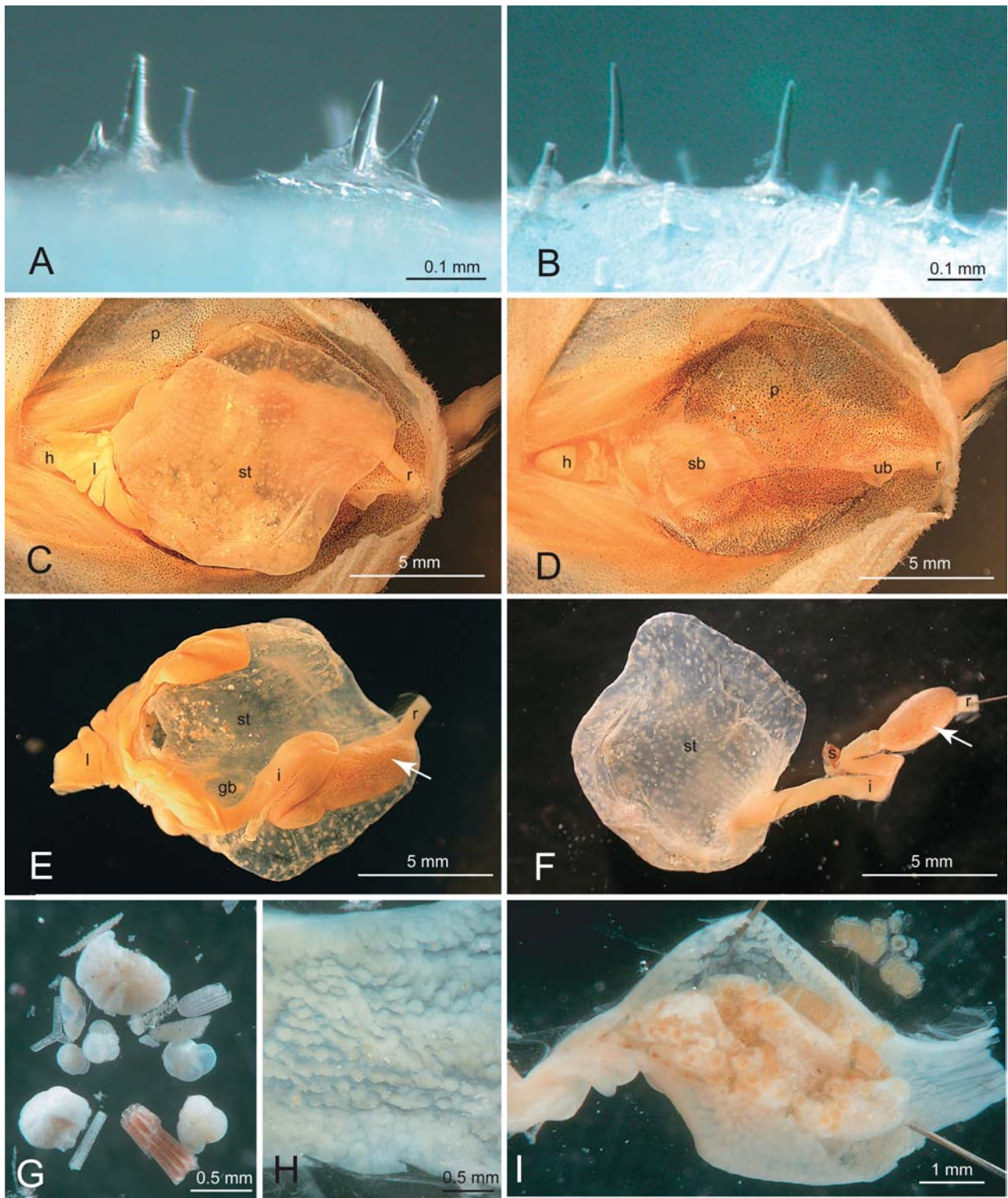


Fig. 3. *Triodon macropterus*, MNHN 1998-1145, 20mm SL. **A** bi- and tricuspid scales; **B** unicuspid scales; **C** abdominal cavity, viscera in situ, ventral view; **D** abdominal cavity, viscera removed, ventral view; **E** viscera, dorsal view (arrow points to Tyler's pouch); **F** viscera, intestine pulled away from stomach and liver removed (arrow points to Tyler's pouch); **G** stomach contents; **H** closeup of intestinal papillae; **I** Tyler's pouch, split open longitudinally and contents exposed. *gb*, gallbladder; *h*, heart; *i*, intestine; *l*, liver; *p*, peritoneum; *r*, rectum; *s*, spleen; *sb*, swim bladder; *st*, stomach; *ub*, urinary bladder

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