

Anatomy and Histology of a New Species of *Enotepteron* (Cephalaspidea: Gastropteridae) from Tropical Northeastern Australia

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Abstract. The anatomy and histology of a new species of gastropterid cephalaspidean, *Enotepteron heikeae*, sp. nov., from tropical Australia is described. *Enotepteron* is the least documented of the gastropterid genera with only two previously recorded species, from the Yellow Sea (North Pacific) and the Seychelles (Indian Ocean). The unique features of *E. heikeae*, within the genus, are the long thin tail (posterior end of the foot), cuticular penial armature, and a bilobed prostate. The investigation also reveals the presence of a very large anal gland. This gland maybe a useful taxonomic and phylogenetic character not previously recognized. This is the first record of *Enotepteron* from the South Pacific region, and its discovery considerably broadens the previously known geographical occurrence of the genus. Documentation and investigation of this species improves our knowledge of the morphological variation across the genus, and allows reassessment of the generic features to show that the presence of spheres to the posterior edge of the parapodia may be the only unifying character.

INTRODUCTION

The cephalaspidean family Gastropteridae Swainson, 1840, consists of four genera—*Gastropteron* Meckel in Kosse, 1813, *Sagaminopteron* Tokioka & Baba, 1964, *Enotepteron* Minichev, 1967, *Siphopteron* Gosliner 1989—which are distinguished by differences in siphonal and visceral hump formation, the gill, radular teeth, and the male genital complex (Gosliner, 1989; Burn & Thompson, 1998).

The genus *Enotepteron* was established by Minichev (1967) to accommodate a species from the Yellow Sea that was distinct from other described gastropterids. At that time, the generic features were a pair of stalked spheres on the posterior end of the parapodia, inner lateral teeth with a few large denticles, and a lack of penial papilla (Gosliner, 1989). With the addition of a second species to the genus, Gosliner (1988) modified the generic characters to the presence of spheres on the parapodia and the presence of large denticles on the inner lateral teeth. A phylogenetic review of the Gastropteridae (Gosliner, 1989) supported recognition that *Enotepteron* is a valid genus and that further generic apomorphies include the absence of a shell and an appressed cerebral ganglion.

Therefore only two species of *Enotepteron* have previously been described, *E. flavum* Minichev, 1967, from

the Yellow Sea, and *E. rosewateri* Gosliner, 1988, from Aldabra Atoll in the Seychelles. This present paper describes a new species of *Enotepteron* from tropical Australia. This is the first record of a member of this genus from the South Pacific region. Organ systems of this species are examined by macroscopic dissection as well as detailed histological investigation.

MATERIALS AND METHODS

Specimens of *Enotepteron heikeae* were collected by plankton tow in Cleveland Bay, a shallow, sheltered coastal bay along the northeastern coast of Queensland, Australia. Animals may have been swimming in the lower water column after being disturbed, or accidentally scraped from the muddy benthos. Five specimens in total from Cleveland Bay were examined. Live animals were videotaped before two specimens were preserved in 8% formalin in seawater, and three specimens in 70% alcohol. One alcohol-preserved specimen was dissected; one formalin-preserved specimen was sectioned (2.5 μ m) using Kulzer methyl-methacrylate resin and toluidine blue stain. The radula was scanned using a Hitachi Scanning Electron Microscope. Terminology used in anatomical descriptions follows Wägele & Willan (2000).

RESULTS

Enotepteron heikeae

Brodie, Klussmann-Kolb & Gosliner, sp. nov.

(Figures 1–3)

Type material: Total of five specimens, all 5 mm preserved length, Cleveland Bay, Queensland, Australia (19°18'S, 146°58'E) 3 August 1994 (1) Holotype: 1 specimen (Queensland Museum Townsville [QMT], Australia Reg. No. MO40196), (2) Paratypes: 1 specimen (Queensland Museum Townsville, Australia Reg. No. MO40197); 1 specimen, histological sections (methacrylate resin) (Queensland Museum Townsville, Australia Reg. No. MO40198); 2 specimens, 1 dissected (California Academy of Sciences, San Francisco, USA Reg. No. CASIZ 121556); 1 specimen, intact (California Academy of Sciences, San Francisco, USA Reg. No. CASIZ 121557).

Etymology: This species is named in honor of PD Dr. Heike Wägele of the Ruhr-Universität Bochum (previously of the University of Bielefeld) for her contributions to opisthobranch systematics and phylogeny, particularly with respect to encouragement and support to graduate students.

Distribution: To date, this species is only known from Cleveland Bay, Townsville, Australia.

External morphology: The living animals at rest (Figure 1A) are 3–6 mm in length, and 6–7 mm in diameter when their parapodia are spread. The body color is translucent off-white with small brownish orange, and larger black, irregular markings. Anteriorly the cephalic shield is broad. When raised, the posterior of this shield produces a “siphon,” the edges of which form an open groove. This “siphon” is often held upright when the animal is crawling but held forward and flattened when the animal is swimming. A siphonal crest or papillae is absent. No flagella are present on the body, but a pair of flexible stalked spheres, with variable patches of black pigment on the rounded apex, is present on the inside posterior of the parapodia. These spheres are folded in beneath the parapodia when the animal is at rest. A long, very thin “sting-ray-like” tail is also present as a posterior extension of the foot. The gill of the dissected specimen consists of nine simple plicae. No shell was found in any of the specimens examined.

Internal morphology:

Digestive system. A schematic diagram of the relatively simple digestive system is shown in Figure 1B. The small rounded mouth opens into the short oral tube. The epidermal tissue of the mouth opening is folded and heavily ciliated. Numerous pear-shaped subepidermal glandular cells are present with small dark-blue-staining nuclei. The content of these cells is probably mucus. Dark-blue-stain-

ing glandular cells containing small granules are also visible subepidermally.

The oral tube expands into a relatively large pear-shaped muscular pharynx. The epithelium of the oral tube is folded, surrounded by muscle, and composed of barely discernible cuboidal cells. A few subepidermal glandular cells are visible. These cells contain light-red-staining mucus secretions.

The pharynx (as defined by Wägele & Willan, 2000) is elongate anteriorly, but becomes wider toward its posterior end. At the transition between the oral tube and the pharynx the epithelium is covered by a very thin cuticle, which is barely visible in some parts (Figure 2A).

Two small jaw plates, bearing numerous irregular rodlets (Figure 3A) are located at the anterior end of the pharynx. The radular formula of the dissected specimen is $18 \times 4.1.0.1.4$. The inner lateral teeth are broad with seven to nine irregular denticles (maximum height $6 \mu\text{m}$) on the inside of the large cusp (Figures 3B,C). The outer laterals have a prominent cusp but lack denticles along the masticatory margin (Figure 3D).

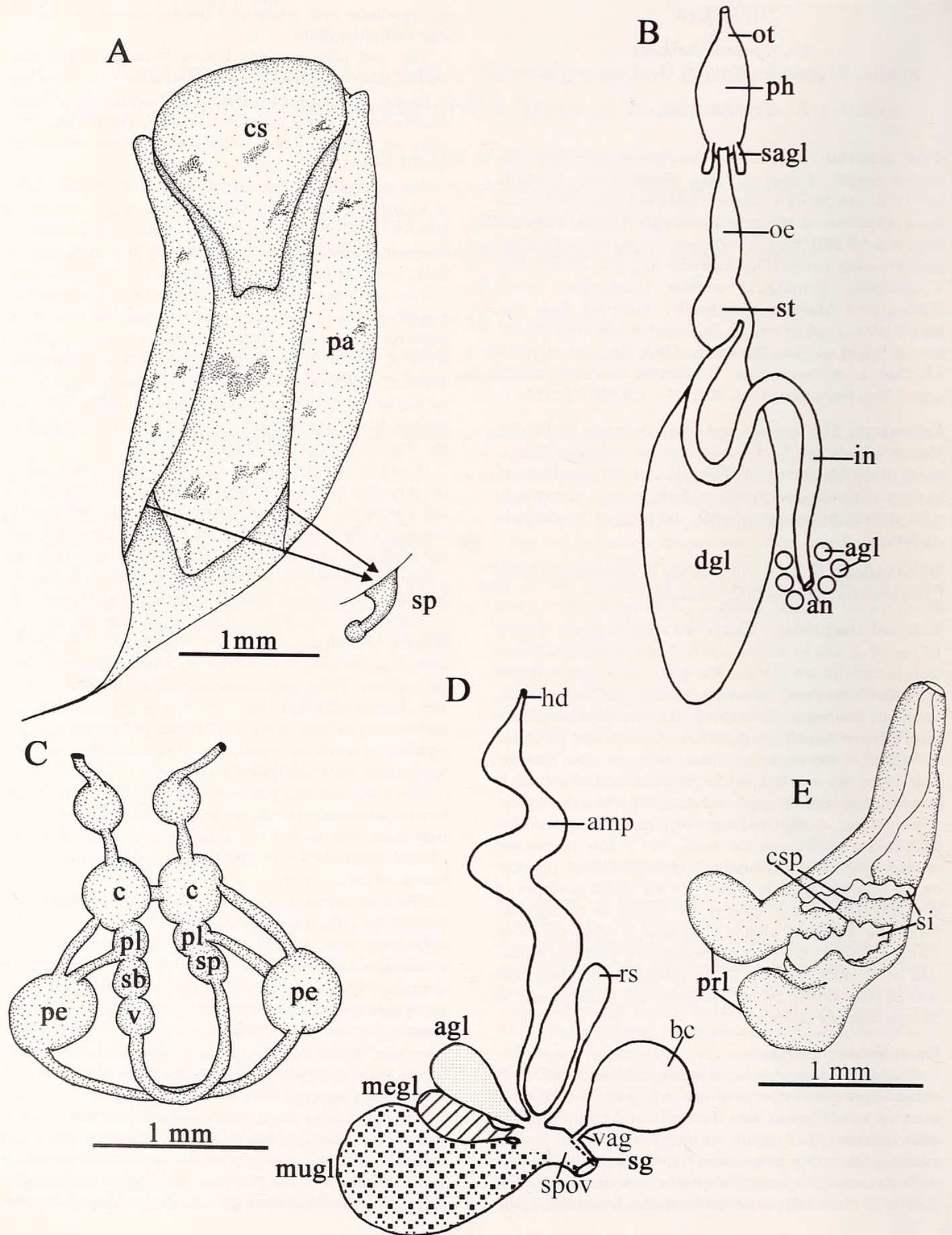
A pair of salivary glands emerges, one on each side of the posterior pharynx, at the transition of the pharynx into the esophagus, and runs posteriorly along the anterior portion of the esophagus (Figure 1B). Salivary gland cells are ciliated, with light staining granules and a large nucleus. A nucleolus is sometimes also visible. A few columnar cells surround a common central duct (Figure 2B).

The tubular esophagus is narrower than the pharynx (Figure 1B) but has a relatively large lumen. The epithelium is composed of columnar glandular cells with elongate apices. These cells contain large nuclei, and in some cells mucus secretions are visible. The epithelium is surrounded by a muscle layer. The rounded stomach is differentiated from the esophagus by possession of a thin epithelium without glandular cells.

The long uniform intestine leaves the stomach at the latter's junction to the digestive gland and emerges on the right side. The folded intestinal epithelium is composed of cuboidal cells with centrally lying nuclei. These cells bear long cilia.

The anal opening is on the right-hand dorsal side just behind the gill. The epithelium of this opening is folded with long cilia. Within the connective tissue the anal opening is surrounded by a relatively large number of irregularly shaped glandular cells that contain numerous heterogeneous secretions and dark-blue-staining nuclei. A histological section of this large distinct anal gland is shown in Figure 2C. The presence of glandular secretions within the anal opening suggests that these glandular cells are discharging inside the anal opening.

The long unilobed digestive gland is composed of one main central canal, which is lined by glandular epithelium consisting of several cell types that are difficult to distinguish. Some cells are elongate and have a club-shaped apical tip, whereas others are columnar. Some cells con-



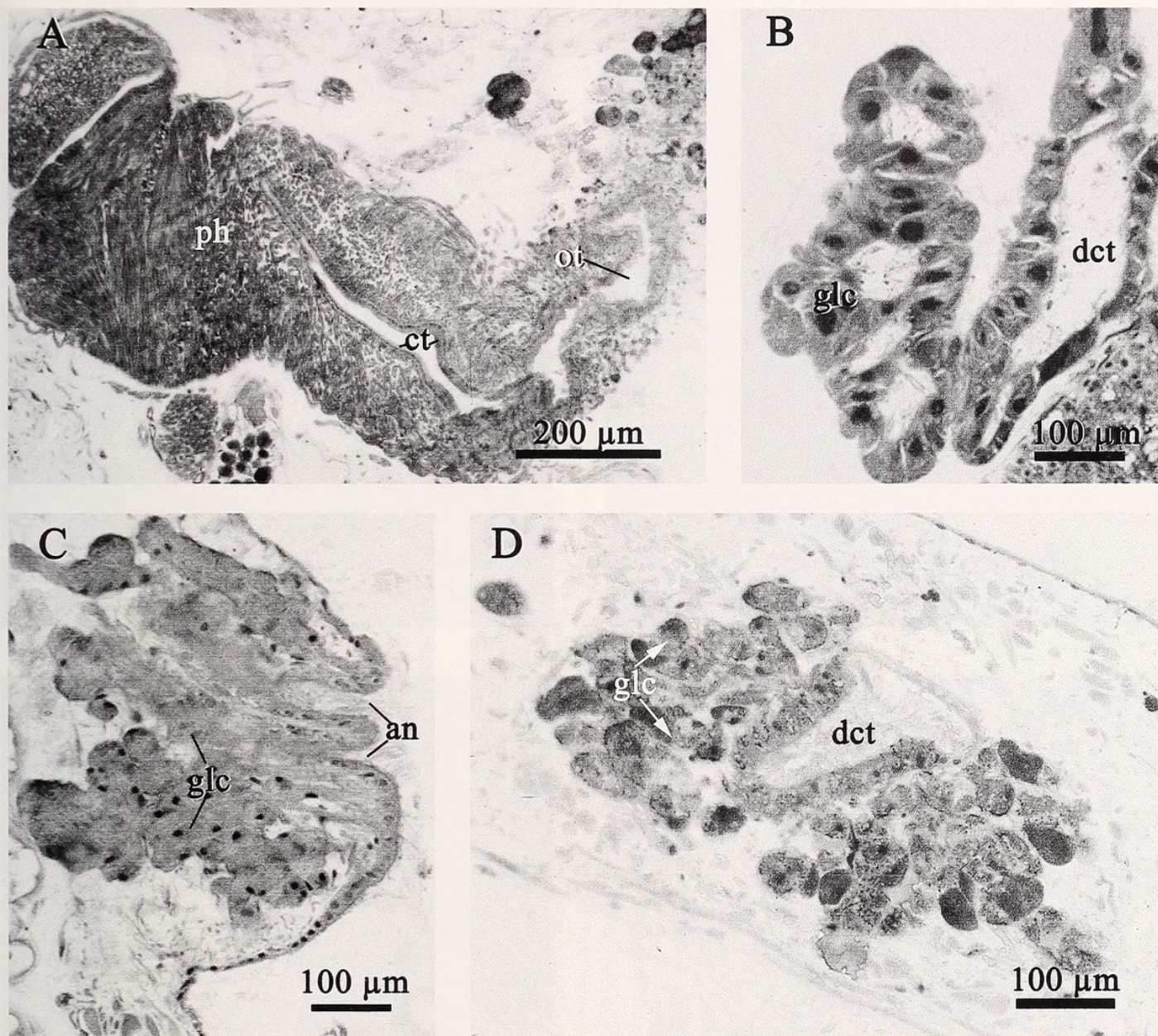


Figure 2. *Enotepterion heikeae* Brodie, Klussmann-Kolb & Gosliner, sp. nov. Histological sections of specimen QMT M040198. A. Transition between the oral tube and the pharynx showing a very thin cuticle covering the epithelium. B. Salivary gland showing central common duct and glandular cells. C. Anal gland and anus showing long cilia around the anal opening. D. Foot (pedal) gland showing pear-shaped glandular cells arranged around a large ciliated duct. an = anus, ct = cuticle, dct = duct, glc = glandular cell, ot = oral tube, ph = pharynx.

Figure 1. *Enotepterion heikeae* Brodie, Klussmann-Kolb & Gosliner, sp. nov. A. Composite drawing of live individual. cs = cephalic shield, pa = parapodia, sp = spheres. B. Schematic outline of the digestive system (QMT M040198). agl = anal gland, an = anus, dgl = digestive gland, in = intestine, oe = esophagus, ot = oral tube, ph = pharynx, sagl = salivary gland, st = stomach. C. Drawing of the central nervous system (CASIZ 121556). c = cerebral ganglion; pe = pedal ganglion; pl = pleural ganglion; sb = subintestinal ganglion; sp = suprainstestinal ganglion; v = visceral ganglion. D. Schematic outline of the anterior reproductive system (QMT M040198). agl = albumen gland, amp = ampulla, bc = bursa copulatrix, hd = hermaphroditic duct, megl = membrane gland, mugl = mucus gland, rs = receptaculum seminis, sg = sperm-groove, spov = spermoviduct, vag = vagina. E. Drawing of the copulatory organ (penis) (CASIZ 121556). csp = cuticular spines, prl = prostatic lobes, si = sinuses.

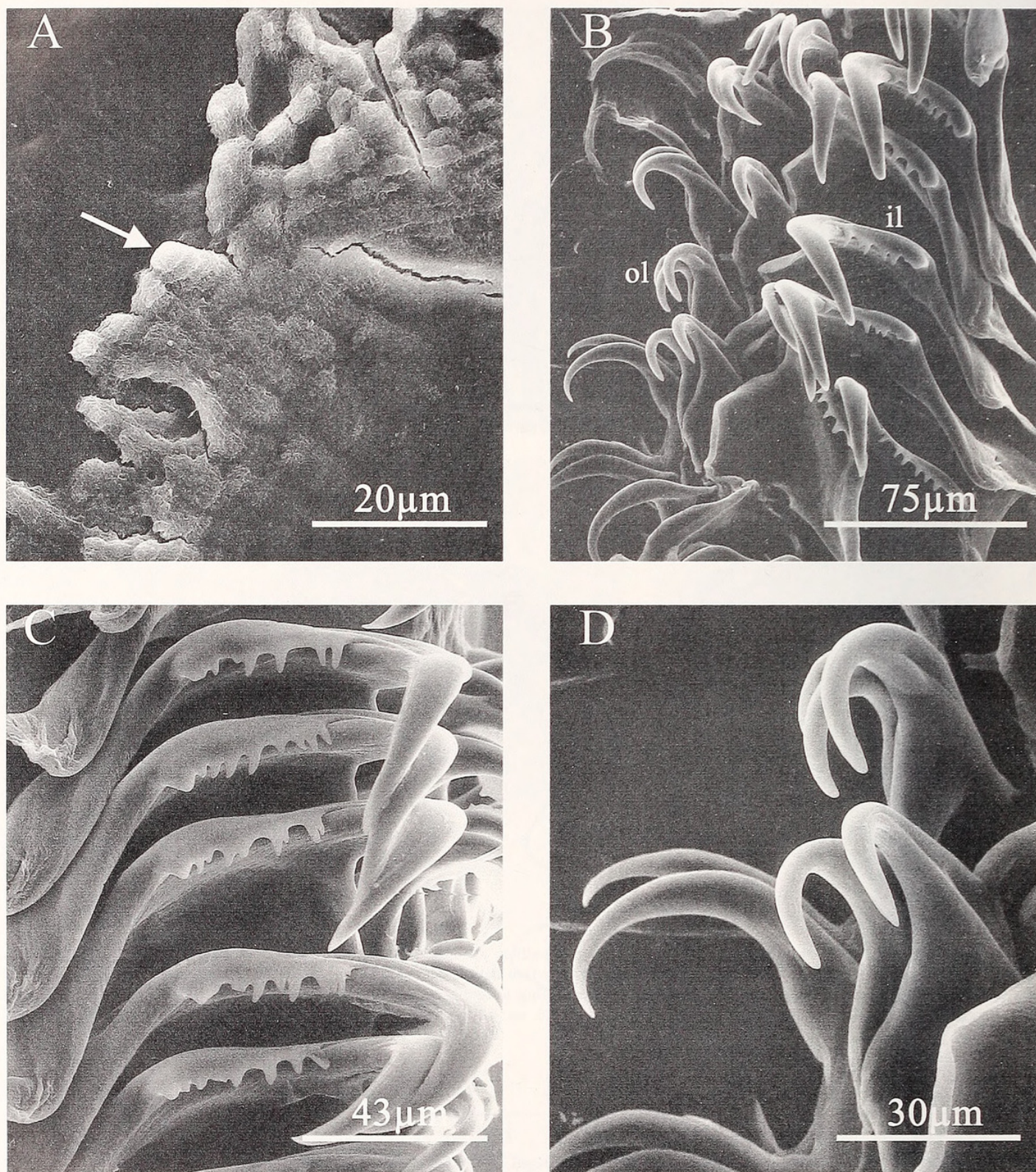


Figure 3. *Enotepterion heikeae* Brodie, Klussmann-Kolb & Gosliner, sp. nov. Scanning electron micrographs of jaws and radula teeth (CASIZ 121556). A. Jaw plate showing irregular rodlets (see arrow). B. Several rows of radular teeth showing the difference between the inner and outer lateral teeth across a row. ol = outer lateral, il = inner lateral. C. A close-up of the inner lateral teeth showing seven to nine irregular denticles on the inner border. D. Close-up of the outer lateral teeth showing absence of denticles on the smoothly curved cusp.

Table 1

Features of *Enotepteron heikeae* in comparison with all other known members of the genus *Enotepteron* and *Gastropteron bicornutum* which displays similar coloration.

Species	Distribution	Depth found	Body color	Shell	Flagellum	Gill plicae	Spheres	Tail	Jaws
<i>Enotepteron heikeae</i>	northern Australia	<4 m	Translucent off-white, with small brownish orange and larger black irregular markings	absent	absent	9 simple	stalked	long, very thin, tapering	well developed
<i>Enotepteron flavum</i>	Yellow Sea	28 m	Uniform yellow (preserved material only)	absent	present	8–10 simple	stalked	short pointed	well developed
<i>Enotepteron rosewateri</i>	Seychelles	intertidal	Translucent white, with orange and brown markings	absent	variable, short or absent	3–4 simple	sessile	short rounded	poorly developed
<i>Gastropteron bicornutum</i>	Japan & Papua New Guinea	6.8 m	Translucent white with black, opaque white, and yellow pigment	present	2 present	12–18 bipinnate	absent	long, thin, elongate	well developed

Species	Radula formula	Inner lateral teeth	Anal gland	Cerebral commissure	Visceral ganglion	Penial papillae	Prostate	Reference
<i>Enotepteron heikeae</i>	4.1.0.1.4	7–9 irregular denticles	present large	short	distinct	not distinct, cucullary armature	two separate glandular lobes	This study
<i>Enotepteron flavum</i>	3.1.0.1.3	regular denticles	absent	short	fused	absent	simple	Minichev 1967; Carlson & Hoff 1974; Gosliner 1988, 1989
<i>Enotepteron rosewateri</i>	3.1.0.1.3	3–6 irregular denticles	?	short	distinct	simple, unarmed	thick, simple, curved, glandular	Gosliner 1988
<i>Gastropteron bicornutum</i>	4.1.0.1.4	5–11 regular elongate denticles	?	short*	distinct	simple, short, unarmed	simple, curved	Baba & Tokioka 1965; Gosliner 1989

* incorrectly scored "long" in Gosliner (1989) Table 2

tain non-staining vacuoles, while others contain blue-green or dark-blue-staining granules. In some cells, mucus droplets are visible. The epithelial lining of the central digestive canal is not glandular throughout. Some areas, mainly the ventral anterior portion, are composed of cuboidal cells.

Gill. The simple gill plicae have a very thin epithelium of cuboidal cells with central nuclei; the epithelium is ciliated and encloses large cavities, which appear to be empty.

Foot (Pedal) Gland. A gland is present at the posterior of the foot below the base of the tail. The pear-shaped glandular cells, with pink staining contents, are arranged around a ciliated duct (Figure 2D), which opens to the outside of the foot.

Nervous System. All the ganglia are contained within a circum-esophageal nerve ring (Figure 1C). The cerebral ganglia are appressed with a very short commissure. The visceral ganglion is distinct.

Reproductive System. The anterior part of the gonad lies on top of the digestive system and extends to the far end of the body cavity. The gonad, which is surrounded by connective tissue, is composed of follicles with sperm acini separated from smaller oocyte follicles. Sperm acini are located centrally, surrounded by oocyte follicles. Oocyte follicles are subdivided into cells containing nucleus, yolk granules, and non-staining vacuoles. Sperm acini contain both immature spermatogonia and mature sperm. The heads of the mature sperm face the epithelial lining, and some nursing cells are present.

A schematic diagram of the monaulic reproductive system is shown in Figure 1D. The hermaphroditic duct is short and hardly differentiated from the ampulla. *In situ*, the tubelike ampulla is coiled and runs from the ventral part of the gonad on the right side of the digestive gland toward the anterior reproductive system. The ampulla itself is lined by an epithelium composed of cuboidal cells with central nuclei of elliptical shape. This epithelium is heavily ciliated in certain areas. Within the ampulla, sperm are arranged irregularly, i.e., not aligned, with heads facing the epithelium.

The seminal receptacle has an elongate club shape. The thin duct leading to it is relatively long. The epithelium of the receptacle is weakly folded and surrounded by a layer of muscle. The epithelium consists of ciliated cuboidal cells with small hardly visible nuclei. Sperm are present in the seminal receptacle of the specimen sectioned, and these are arranged in the usual way with heads facing the epithelium. The duct leaving the receptacle is also lined by a ciliated epithelium of small cuboidal cells. The sectioned animal has probably copulated, since sperm is visible in the receptacle.

The bursa copulatrix (= gametolytic gland) is globular and connects to the distal section of the spermoviduct, close to the genital opening, via a short thin vagina (all-sperm receiving duct). The vaginal epithelium consists

of cuboidal cells, with small nuclei, bearing long cilia. Nucleoli are also visible in these cells. The bursa copulatrix is lined by an epithelium of cuboidal cells with basally lying nuclei. This epithelium bears short cilia and contains numerous non-staining vacuoles. The epithelium of the spermoviduct consists of cuboidal cells containing small nuclei and long cilia.

The nidamental glandular system is divided into three separate parts (Figure 1D). The small proximally lying albumen gland consists of one lobe. Like the membrane gland and the distally lying mucus gland, the albumen gland joins the spermoviduct at its distal end. The albumen gland is composed of high columnar glandular cells (which are smaller than those seen in the mucus gland) containing numerous small dark-blue-staining granules and a basally lying nucleus. Supporting cells are not visible, but cilia are present. Following the albumen gland is a small membrane gland, composed of columnar cells containing heterogeneous mucous fibers, which stain pink. The supporting cells in the membrane gland bear long cilia. The distally lying mucus gland is the largest of the nidamental glands. It is widely folded and consists of highly columnar glandular cells with different mucus contents. The staining properties range from red to violet. The supporting cells in the mucus gland bear short cilia.

A sperm-groove leads from the spermoviduct to the prostate and penis. The sperm-groove is a fold in the outer epithelium, which is lined by long cilia. No glands are associated with this groove. The penis opens to the outside at the anterior of the body next to the mouth. There are two separate glandular prostatic lobes (Figure 1E). The penial papilla is not distinct. Some unusual cuticular spines are arranged around two sinuses. These spines are not well developed nor are they arranged in distinct rows.

Excretory System. The kidney is located on top of the digestive gland and anterior portion of the gonad. It is lined by pavement epithelium with basal nuclei and large non-staining vacuoles with unknown contents. The epithelium forms internal folds lining a large lumen. The reno-pericardial duct is small, narrow, and ciliated. It leads to the nephropore, which is located on the right side of the body underneath the very posterior end of the gill.

Circulatory System. The pericard is lined by very thin pavement epithelium. The atrium and ventricle are composed of loose connective tissue, and located left of the kidney on top of the digestive gland.

Behavior: This species is an active swimmer. The swimming action involves rapid beating of the parapodia in a very "batlike" manner. The posterior of the cephalic shield is flattened during this swimming behavior.

DISCUSSION

Within the genus, *Enotepteron heikeae* is unique in having a long, very thin tail, cuticular penial armature, and

a bilobed prostate. Table 1 presents a comparison of *E. heikeae* with other *Enotepteron* species and *Gastropteron bicornutum* Baba & Tokioka, 1965, which it resembles in color.

Enotepteron flavum differs from *E. heikeae* in that it has a short pointed tail, regular denticles on the inner lateral teeth, a fused visceral ganglion, no penial papillae, a simple prostate, and quite possibly no anal gland. *Enotepteron rosewateri* differs from *E. heikeae* in that it has sessile parapodial spheres, a short rounded tail, poorly developed jaws, unarmed penial papillae, and a simple prostate.

Enotepteron heikeae resembles *E. flavum* in that the parapodial spheres are stalked, whereas in *E. rosewateri* they are sessile. Burn (1980) considered that the right-hand sphere probably functions to hold a partner's penial papilla in place during copulation, whereas the left-hand sphere is the result of bilateral symmetry. Gosliner (1989) however, considered this unlikely because *E. flavum* lacks a penial papilla. Such a hypothesis needs to be substantiated by observation of living animals during mating. Our histological investigations reveal no internal structural components that suggest any particular function to these appendages.

In coloration *E. heikeae* closely resembles *Gastropteron bicornutum*. However, unlike *G. bicornutum*, our species has no shell, lacks hornlike protuberances (flagella) on the dorsal hump, has simple rather than bipinnate gill plicae, carries spheres on the inner posterior of the parapodia, and has a tapering tail and irregular denticles on the inner lateral teeth. Also, *G. bicornutum* has a simple short, unarmed penial papilla and a simple curved prostate, whereas *E. heikeae* has an indistinct penial papilla, unusual cuticular spines around two sinuses, and two separate prostatic lobes.

Minichev (1967) conducted a histological study of *Enotepteron flavum*. He found that *E. flavum* has subepithelial basophilic and acidophilic glands surrounding the oral tube and a stomach not distinctly separated from the esophagus. A foot gland is also present in *E. flavum*. It is notable that Minichev did not report an anal gland. Considering the very conspicuous nature of this gland in *H. heikeae*, its presence may well be an additional unique character of the current species. According to Wägele & Willan (2000), anal glands are not widespread within the Opisthobranchia.

According to Gosliner (1989), the presence of spheres on the parapodia and the presence of large denticles on

the inner lateral teeth characterize *Enotepteron*. Other apomorphies are stated to include an absence of shell and an appressed cerebral ganglion. Our investigations confirm that a characteristic feature of the genus is the spheres on the posterior parapodia but show that the denticles on the inner lateral teeth are not particularly large. In fact the inner lateral denticles of *E. heikeae* (this study Figure 3C) and *E. rosewateri* (see Gosliner, 1988: figure 14A) are smaller than those found in *Gastropteron bicornutum* (see Gosliner, 1989: figure 24). Thus, the only remaining unique generic character for *Enotepteron* appears to be the presence of spheres to the posterior edge of the parapodia.

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