Zootaxa 4903 (2): 275–284
https://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4903.2.7
http://zoobank.org/urn:lsid:zoobank.org:pub:7F6F65B9-A5A2-498A-AD62-03F0CBDD85B5

A new species of *Diplotaxodon* (Cichliformes: Cichlidae) from Lake Malaŵi

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Abstract

A species of haplochromine cichlid fish of the genus *Diplotaxodon* Trewavas, endemic to Lake Malaŵi is described: *Diplotaxodon dentatus*, new species. All eight type specimens were trawled together off Thumbi East Island in the Southeastern arm of the lake at 73 meters in 1985. They were initially identified as *D. argenteus* because the teeth on the oral jaws were fully exposed with a closed mouth. The shorter snout length of *D. dentatus* (26.6–29.2 % HL) clearly separates it from *D. argenteus* (31.7–34.2 % HL). A plot of a principal components analysis further supports the separation of *D. dentatus* from *D. argenteus*.

Key words: Bentho-pelagic cichlids, Ndunduma, commercial fisheries

Introduction

The freshwaters of Africa harbor between 70– 80% of all the described cichlid fishes (Stauffer *et al*., 2007). Many of these species are found in the Great Lakes (Lake Victoria, Lake Tanganyika, and Lake Malaŵi). It is estimated that some 850 species of cichlids are endemic to Lake Malaŵi (Konings, 2016). Currently overfishing constitutes the biggest threat to Malaŵian fishes. Data from commercial fisheries in Malaŵi show that some of the collected fishes are identified to genus, while others received no identification at all. Management from commercial vessels stated they do not have a specialist to identify fishes (see Stauffer *et al*. 2018). A number of cheironyms were given to unrecognizable and undescribed species of the genus *Diplotaxodon*. Many of these names referred to the same species or the same name referred to different species. Thus, it was extremely difficult to retrieve reliable information until recently. When Stauffer *et al*. (2018) described two species of *Diplotaxodon* and taught managers how to delimit the species in their catches, data became much more reliable and could be incorporated into a data base compiled by the Department of Fisheries in Malaŵi (Titus Phiri, Malaŵi Fisheries Department.). Species descriptions are needed to accurately monitor fish biodiversity in the future and to create management strategies for the protection of selected stocks.

The genus *Diplotaxodon* was diagnosed by Trewavas (1935) as cichlids with short inferior apophyses (of the third or third and fourth vertebra) retractor muscles of the pharyngeal jaws that do not approach each other below the aorta, with conical teeth in two series, in the oral jaws, and with non-beak-like premaxillaries. Initially the genus was monotypic with *Diplotaxodon argenteus* as the type species. Subsequently, *Diplotaxodon eccelsi* Burgess & Axelrod, 1973 and *Diplotaxodon greenwoodi* Stauffer & McKaye, 1986 were described. Eccles & Trewavas (1989) revised the diagnosis of the genus to include an oblique mouth, a prognathic lower jaw, a small knob at the synthesis of the dentaries, and the absence of distinct bars or stripes. Turner (1994) described *Diplotaxodon limnothrissa* and Turner & Stauffer (1998) described *Diplotaxodon aeneus*, *Diplotaxodon apogon,* and *Diplotaxodon macrops*. Recently, Stauffer *et al*. (2018) described *Diplotaxodon longimaxilla* and *Diplotaxodon altus*. Many additional *Diplotaxodon* species are thought to occur in the lake (Turner *et al*. 2004, Genner in Konings, 2007). The latter author classifies the various *Diplotaxodon* species in three main groups: The *D. macrops* group, the *D. argenteus* group, and the *D. limnothrissa* group.

Accepted by J. Armbruster: 26 Nov. 2020; published: 7 Jan. 2021

The *D. macrops* group, characterized by a relatively small size and large eye, includes the described taxa *D. macrops, D. ecclesi,* and *D. aeneus*, and three undescribed species, *D.* sp. 'macrops black-dorsal', *D.* sp. 'macrops north', and *D.* sp. 'macrops ngulube'. *Diplotaxodon ecclesi* has a lake-wide distribution, while all three undescribed species are restricted to the northern half of the lake, north of Nkhata Bay, and *D. macrops* occurs only in the southern part of the lake and has never been found north of Tukombo. *Diplotaxodon aeneus* has never been relocated after initial collection. The members of the *D. macrops* group are small species and may be specialized in feeding on plankton rather than on *Engraulicypris sardella* (Günther), a cyprinid found in Lake Malaŵi and usually referred to as the lake sardine which appears to be the most common food source for *Diplotaxodon* species (Turner & Stauffer, 1998).

The *D. argenteus* group, characterized by a relatively large size and a "standard" body (neither slender nor deep-bodied), includes *D. argenteus* (with a lake-wide distribution), *D. altus* (found near Chipoka and in the southeastern arm of the lake), and *D. longimaxilla* (known only from near Domira Bay in the southern part of the lake), plus the undescribed taxa *Diplotaxodon* sp. 'holochromis' (with a lake-wide distribution), *Diplotaxodon* sp. 'similis white-back north' (as yet found only north of Nkhata Bay), and the new species described herein which has not knowingly been encountered in catches since its collection in 1985 (Stauffer *et al*. 2018).

The *D. limnothrissa* group, characterized by a very slender body, contains *D. limnothrissa*, which has a lake-wide distribution, and the following undescribed species: *Diplotaxodon* sp. 'limnothrissa black-dorsal' (with a lake-wide distribution), *Diplotaxodon* sp. 'limnothrissa black-pelvic' (as yet found only north of Nkhata Bay), and *Diplotaxodon* sp. 'limnothrissa msaka' (to date collected only in the southwestern arm of the lake at Msaka) (Genner in Konings, 2007).

D. greenwoodi does not seem to belong to any of these groups. It is a paedophage which steals fry from the mouths of brooding females (Stauffer & McKaye, 1986). It has a characteristic oblique mouth with a protruding lower jaw. When the mouth is closed there is still a small round opening between the jaws. This species is occasionally caught by hook and line, which may indicate that it is not restricted to its feeding specialization. It has been found all over the lake. The purpose of this paper is to describe another species of *Diplotaxodon* collected near Monkey Bay (Fig. 1).

Materials and methods

We obtained specimens deposited into the Penn State University Fish Museum (IACUC#: 46589-1, Preserved Animals) and transferred to the South African Institute for Aquatic Biodiversity (SAIAB), where they were assigned the SAIAB collection numbers recorded herein. We examined the lectotype (BMNH 2017.8.24.1) and paralectotypes of *D. argenteus* (BMNH 1935.6.14.2281-2282) and compared them with specimens of the new species. Additionally, we compared the new species to *D. aeneus* (BMNH 1996.4.30:16, BMNH 1996.4.30:17–20, PSU 3026; n=6), *D. altus* (PSU 12501, SAIAB 203929; n=5), *D. apogon* (BMNH 1996.4.30:21, BMNH 1996,4,30:22–25, BMNH 1996.4.30:31, BMNH 1996.4.30:32—38, PSU 3025; n=21), *D. argenteus* (BMNH 1935.6.14.2281–2282; n=3), *D. ecclesi* (USNM 210696; n=1), *D. greenwoodi* (USNM 207847, USNM 207248; n=4), *D. limnothrissa* (SAIAB 203932; n=11), *D. longimaxilla* (PSU 12499, SAIAB 203930, SAIAB 203935; n=12), and *D. macrops* (BMNH 1996.4.30:1–15, PSU 3024; n=21). Counts and measurements follow Konings & Stauffer (2006). All counts and measurements were taken from the left side of the body except for gill-raker counts, which were taken on the right side.

Morphometric data were analyzed using a sheared principal component analysis, which factors the covariance matrix and restricts size variation to the first principal component (Humphries *et al*. 1981, Bookstein *et al*. 1985). Meristic data were analyzed using a principal component analysis in which the correlation matrix was factored. Differences among the new species and *D. argenteus* were illustrated by plotting the sheared second principal components (SPC2) of the morphometric data against the first principal components (PC1) of the meristic data (Stauffer & Hert 1992).

The holotype of *D. dentatus* was scanned on the high-resolution x-ray computed tomography (HRCT) system in the Center for Quantitative X-Ray Imaging (CQI) at Penn State University. The specimen was scanned with target pixel and slice resolutions of approximately 32 µm. Scan data were reconstructed as 16-bit TIFF images with a 1024×1024 pixel grid. The entire body was scanned. The volumetric image datasets were used to create a threedimensional isosurface reconstruction to study bone tissue. The upper and lower pharyngeal bones were segmented using Dragonfly (Object Research Systems (ORS) Inc., www.theobjects.com.)

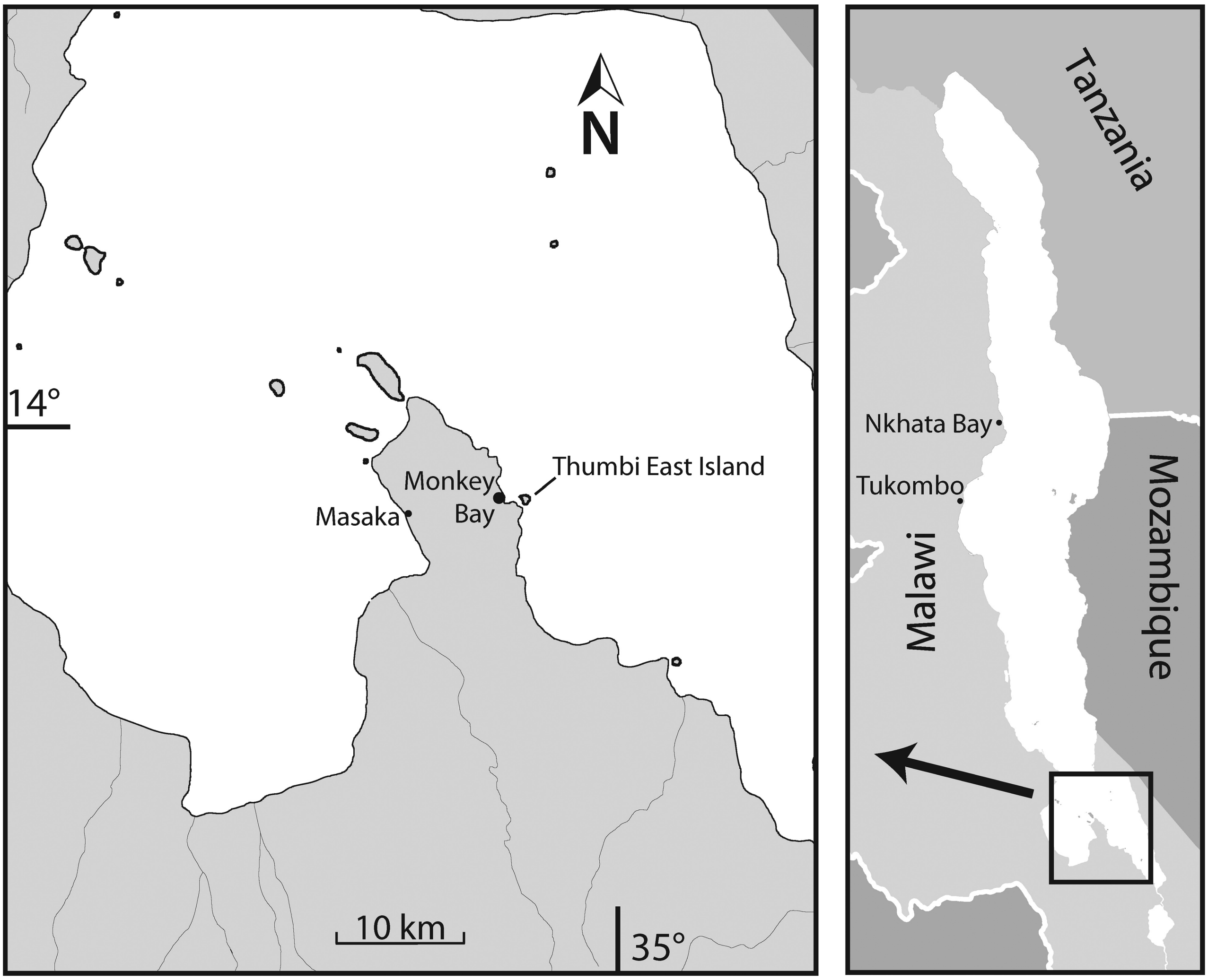

FIGURE 1. Map of Lake Malaŵi with localities mentioned in text indicated.

Results

Diplotaxodon dentatus, new species

Figs. 2, 3, 4; Table 1.

Holotype. SAIAB 209443 (male), 108.7 mm SL, collected by trawl off Thumbi East Island, Monkey Bay, Malaŵi, Africa at 73 m depth, J. R. Stauffer, 27 March 1985.

Paratypes. SAIAB 209441, 7, 96.9–119.7 mm SL, data as for holotype.

Diagnosis. The oblique mouth, a prognathic lower jaw, a small knob at the synthesis of the dentaries, the absence of distinct bars or stripes (Eccles & Trewavas, 1989), the closely-spaced teeth, and lack of beak-like premaxillaries (Trewavas, 1935; Turner, 1994) place this species in *Diplotaxodon*. *Diplotaxodon dentatus* has a smaller body depth (26.4–28.4 % SL) than *D. altus* (35.1–37.8% SL) (Stauffer *et al*., 2018), *D. greenwoodi* (34.2–36.5% SL) (Stauffer and McKaye, 1986), *D. macrops* (33.9–37.6 % SL), *D. apogon* (32.4–37.3 % SL), *D. aeneus* (34.3–37.1 % SL), and *D. ecclesi* (35.5 % SL) (Turner and Stauffer, 1998). There are more gill rakers on the first ceratobranchial in *D. dentatus* than in *D. longimaxilla* (23–27 vs. 16–21). *Diplotaxodon dentatus* has fewer teeth in the outer row of the left lower jaw (17–25) that are exposed (Fig. 3) when the mouth is closed and more widely spaced than those of *D. limnothrissa* (36–46), which are close together and embedded (Turner, 1994). *Diplotaxodon dentatus* has a shorter snout length (26.6–29.2 % HL) than *D. argenteus* (31.7–34.2 % HL), a longer post-orbital head length

(39.0–41.7 vs. 37.7–38.8 % HL), a narrower cheek depth (10.6–15.2 vs. 15.3–17.0 % HL), generally more gill-rakers on the first ceratobranchial (23–27 vs. 20–23), and a greater distance between the anterior origin of the dorsal fin to the posterior insertion of the anal fin (50.3–53.1 vs. 49.6–51.2 % SL).

Description. Morphometric ratios and meristic data in Table 1. Body fusiform, slender, and laterally compressed, deepest at origin of dorsal fin (Figs. 2 & 3). Dorsal-fin origin posterior to operculum, above insertion of pectoral fin, dorsal-fin spines increasing to maximum length over 8-10 spines. Caudal peduncle relatively long, 4.8–5.6 times SL. Holotype with 16 abdominal and 18 caudal vertebrae (CT scan Fig. 3), typical of *Diplotaxodon* spp. Caudal fin emarginate. Anal-fin, below vertical through first dorsal-fin ray; anal-fin rayed section rounded not reaching to caudal-fin base. Pectoral-fin origin close behind gill slit; pectoral fin in mature males to anal-fin origin. Pelvic fin, short, and not to anal-fin origin. Ctenoid scales small, 32–38 in lateral line. Upper lateral line with slight upward curve anteriorly, to before posterior insertion dorsal fin; lower lateral line straight through mid-caudal peduncle; 0–1 pored scales posterior to hypural plate.

FIGURE 2. *Diplotaxodon dentatus*, Holotype SAIAB 209443 (male), 108.7 mm SL, collected by trawl off Thumbi East Island, Monkey Bay, Malaŵi, Africa, 27 March 1985.

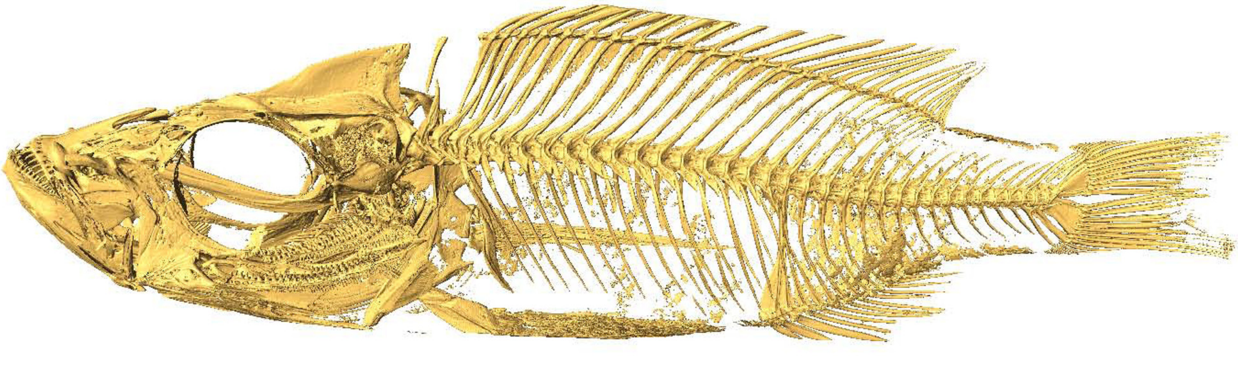

FIGURE 3. CT scan of the lateral view of the holotype of *Diplotaxodon dentatus* SAIAB 209443 (male), 108.7 mm SL.

FIGURE 4. The head of the holotype of *Diplotaxodon dentatus* SAIAB 209443 (male), 108.7 mm SL showing the exposed teeth (enlarged in inset)

TABLE 1. Morphometric and meristic values of *Diplotaxodon dentatus* (n=8). The mean, standard deviation and range include holotype and paratypes.

Variable	**Holotype**	**Mean**	**SD**	**Range**
Standard length, mm	108.7	105.5	7.0	96.9–119.7
Head length, mm	37.6	36.6	2.2	34.1–40.4
Percent of standard length				
Head length	34.6	34.7	0.75	33.8–36.0
Body depth	27.0	27.5	0.77	26.4–28.4
Snout to dorsal-fin origin	35.5	36.0	1.5	34.5–39.2
Snout to pelvic-fin origin	38.7	39.8	1.8	37.7–43.4
Dorsal fin base length	46.6	47.5	1.0	46.2–49.3
Anterior dorsal to anterior anal	41.2	41.8	1.4	39.6–44.2
Anterior dorsal to posterior anal	51.1	51.4	1.1	50.3–53.1
Posterior dorsal to anterior anal	27.1	26.0	1.2	24.2–27.9
Posterior dorsal to posterior anal	15.0	14.1	0.9	12.4–15.2
Posterior dorsal ventral caudal	21.6	22.0	1.3	20.1–24.0
Posterior anal to dorsal caudal	25.5	23.5	1.4	21.5–25.5
Anterior dorsal to pelvic-fin origin	27.8	27.8	0.7	26.8–29.2
Posterior dorsal to pelvic-fin origin	46.8	48.3	1.4	46.4–50.1
Caudal peduncle length	20.4	19.3	1.0	17.7–20.7
Least caudal peduncle depth	12.0	11.2	0.6	10.1–12.0
Percent of head length				
Snout length	27.9	27.9	0.7	26.6–29.2
Postorbital head length	40.8	40.1	0.9	39.0–41.7
Horizontal eye diameter	31.9	32.0	1.3	29.9–33.9
Vertical eye diameter	30.1	31.0	1.8	28.4–33.6
Pre-orbital depth	18.2	18.3	1.5	15.7–20.0
Cheek depth	13.3	12.9	1.4	10.6–15.2
Lower jaw length	41.2	3q9.8	1.2	38.0–41.2
Head depth	71.6	67.8	3.9	62.8–73.1
Counts		**Mode**	**Freq**	**Range**
Dorsal-fin spines	16	15	50	14–16
Dorsal-fin rays	13	13	50	11–13
Anal-fin spines	3	3	100	
Anal-fin rays	10	11	50	10–12
Pelvic-fin rays	5	5	100	
Pectoral-fin rays	14	13	87.5	13–14
Lateral line scales	35	35	37.5	32–38
Pored scales posterior to LL	1	0/1	50	0–1
Cheek Scales	2	3	75	2–3
Gill-rakers on first epibranchial	6	7	62.5	6–8
Gill-rakers on first ceratobranchial	24	25	37.5	23–27
Teeth outer row of left lower jaw	22	22/26	25	17–25
Tooth rows on upper jaw	2	2	100	
Tooth rows on lower jaw	2	2	100	

Head elongate (33.8–36.0 % SL), length greater than body depth, with lower jaw at oblique angle (Fig. 2 & 4). Eye large (horizontal eye diameter 29.9–33.9 % HL, vertical eye diameter 28.4–33.6 % HL), greater than pre-orbital depth (15.7–20.0 % HL). Snout smaller than orbit diameter, 26.6–29.2 % HL, with premaxillary pedicel to vertical through anterior orbit. Cheek shallow (10.6–15.2 % HL) with 2–3 scale rows. Mouth large and superior, lower jaw 38.0–41.2 % HL; teeth on lower and upper jaw caniniform, with space between them about width of tooth (17–25 in outer row of left lower jaw) and exposed (Fig. 4). Teeth on pharyngeal jaws unicuspid (Fig. 5). First ceratobranchial with 23–27 gill-rakers and first epibranchial with 6–8 rakers.

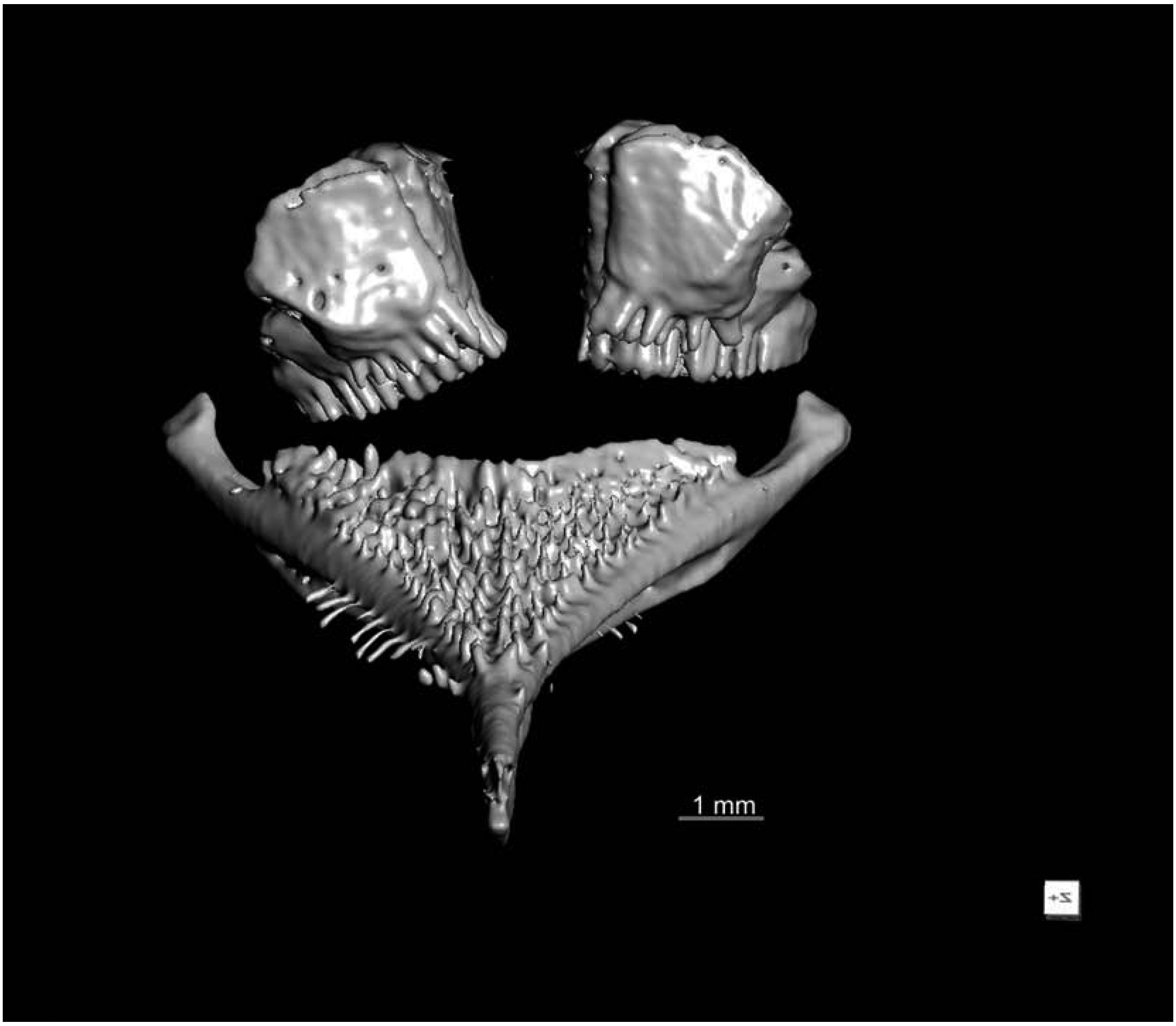

FIGURE 5. CT scan of the upper and lower pharyngeal bones of the holotype of *Diplotaxodon dentatus*, SAIAB 209443 (male), 108.7 mm SL.

Coloration. Preserved males with dark snout. Flank dark dorsally, fading lighter ventrally. Dorsal fin with black lappets; caudal fin with 5–6 central rays black; anal fin with distal portion of membranes dark gray to black and without egg spots; pelvic fins black and pectoral fins clear. Head with black gular region. Coloration of preserved females similar to males, but lighter overall. Live coloration not recorded.

Remarks. In general appearance *Diplotaxodon dentatus* is most similar to *D. argenteus* and also shares the character of exposed teeth when the mouth is closed. When the morphometric and meristic data for *D. dentatus* were compared to that of the lectotype and paralectotypes of *D. argenteus* the first principal component (size variable) of the morphometric data explained 94.6% of the observed variance and the sheared second principal component explained 39.4% of the remaining 5.4%. Variables that had the highest loadings on the sheared second principal components of the morphometric data were distance between the posterior insertion of the dorsal fin and origin of the pelvic fin (0.55), distance between the anterior insertion of the dorsal fin and origin of the pelvic fin (-0.39), and caudal peduncle depth (0.33). The first principal component of the meristic data explained 45.8% of the variance. Variables with the highest loadings on the first principal components of the meristic data were number of gill-rakers on the ceratobranchial of the first arch (-0.56), pored scales posterior to the hypural plate (0.55), and number of gill-rakers on the epibranchial (-0.41). A plot of the second sheared principal component of the morphometric data versus the first principal component of the meristic data shows that *D. dentatus* is clearly separated from *D. argenteus* (Fig. 6).

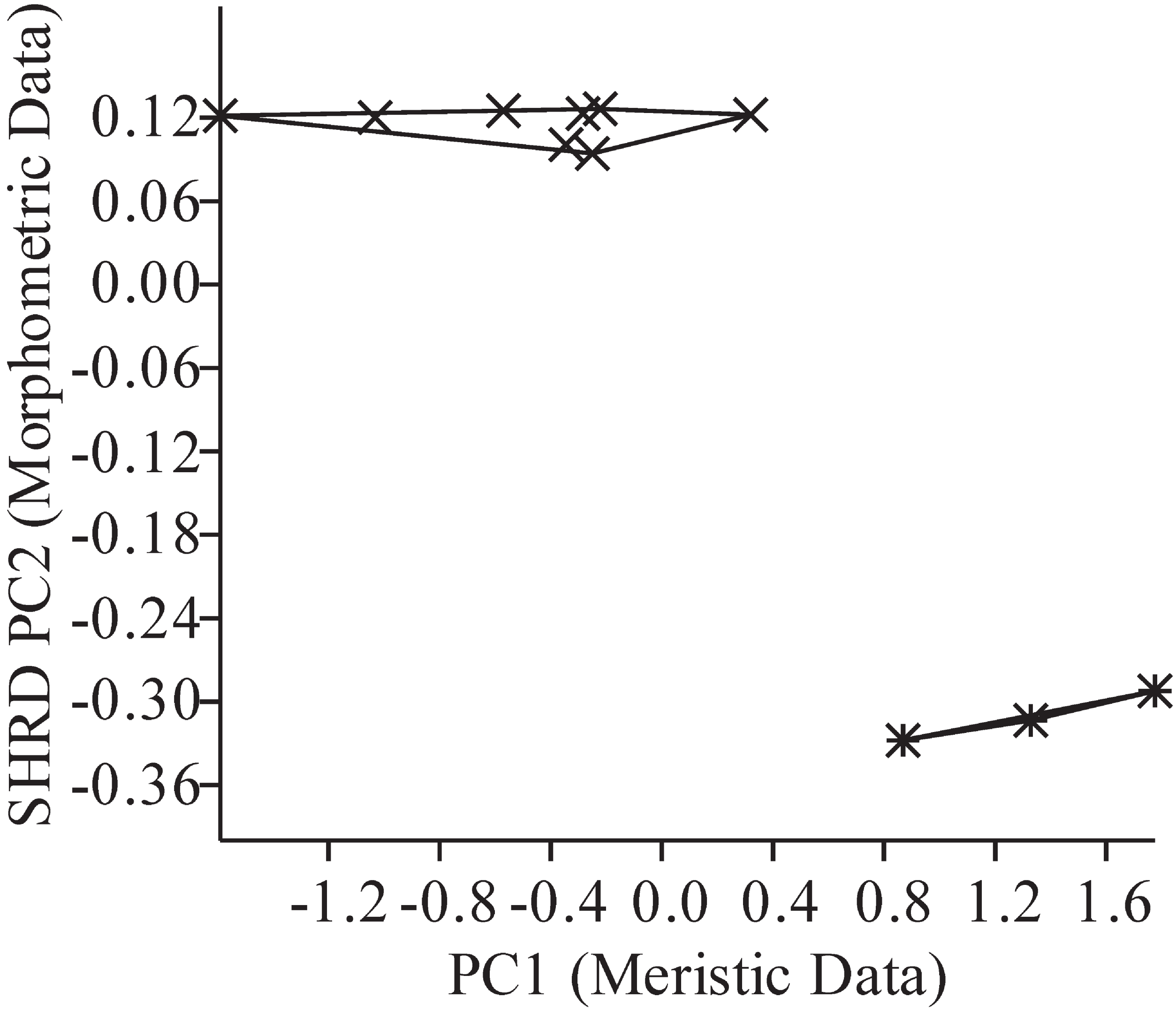

FIGURE 6. First principal components (meristic data) plotted against the sheared second principal components (morphometric data) of *Diplotaxodon dentatus* (x) and *Diplotaxodon argenteus* (*).

Ct scans revealed that the stomachs of the type series were empty, however, based on the exposed teeth in the oral jaws and the unicuspid teeth of the pharyngeal jaws (Fig. 5) it is suggested that *D. dentatus* is a piscivore.

Etymology. *Dentatus* from Latin meaning toothed or having teeth alluding to the caniniform teeth on the outer margin of the dentary and premaxilla which are exposed when the mouth is closed.

Discussion

There are now ten species described in the genus *Diplotaxodon*. Turner *et al*. (2004) recognized species in the genus that were not described including *Diplotaxodon* sp. 'holochromis', *Diplotaxodon* sp. 'similis', *Diplotaxodon* sp. 'deep', *Diplotaxodon* sp. 'offshore', and *Diplotaxodon* sp. 'brevimaxillaris'. *Diplotaxodon dentatus* differs from ‘holochromis’, which has males that are uniformly black, from ‘similis’, which has less than 20 gill-rakers on the ceratobranchial of the first arch and shallower directed gape, from ‘deep’ and brevimaxillaris, which are deep-bodied species, and from ‘offshore’, which has dark pelvic, caudal, and anal fins (Turner *et al.*, 2004). Additionally, there are 12 forms that were tentatively recognized and listed as “dubious status” or “deep” (Turner *et al.*, 2004). Clearly additional taxonomic work is needed in order to formulate an effective management plan for this group of fishes, many of which are commercially important.

Artificial key to the species of *Diplotaxodon*

(based on examination of specimens listed in Materials and methods)

1a.	Body depth greater than 33 % standard length	2
1b.	Body depth less than 33% standard length	8
2a.	Gape inclination greater than 55º	*D. greenwoodi*
2b.	Gape inclination less than 55º	3
3a.	21 or more gill-rakers on ceratobranchial	4
3b.	Fewer than 21 gill-rakers on ceratobranchial	5
4a.	Body depth greater than 35% SL	*D. altus*
4b.	Body depth less than 35% SL	*D. macrops* (part)
5a.	Length lower jaw more than 42 % HL	6
5b.	Length lower jaw less than 42 % HL	7
6a.	Pectoral-fin length less than 34.5% SL	*D. aeneus* (part)
6b.	Pectoral-fin length greater than 34.5% SL	*D. apogon* (part)
7a.	Length snout to dorsal fin more than 40 % SL	*D. aeneus* (part)
7b.	Length snout to dorsal fin less than 40 %SL	*D. macrops* (part)
8a.	Outer row oral teeth prominent when mouth closed	9
8b.	Oral teeth not obvious when mouth closed	10
9a.	Snout length shorter than 31 % HL	*D. dentatus*
9b.	Snout length longer than 31 % HL	*D. argenteus*
10a.	Teeth deeply embedded in tissue of lower jaw	*D. limnothrissa*
10b.	Teeth not deeply embedded	11
11a.	More than 21 gill-rakers on ceratobranchial	*D. ecclesi*
11b.	Fewer than 22 gill-rakers on ceratobranchial	12
12a.	Cheek depth more than 22 % HL	*D. apogon* (part)
12b.	Cheek depth less than 22 % HL	*D. longimaxilla*

Acknowledgements

We thank Josh Wisor and Sara Mueller who completed the CT scans and digitally segmented the pharyngeal bones. This study was funded in part by Agriculture Experiment Station Project 04585 (Penn State University).

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