Copeia

founded in 1913 by John Treadwell Nichols

Osteology Identifies *Fundulus capensis* Garman, 1895 as a Killifish in the Family Fundulidae (Atherinomorpha: Cyprinodontiformes)

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***Fundulus capensis* Garman, 1895 was described from the unique holotype said to be from False Bay, Cape of Good Hope, South Africa. Largely ignored by killifish taxonomists, its classification has remained ambiguous for over a century. Radiography and computed tomography of the holotype reveal skeletal details that have been used in modern phylogenetic hypotheses of cyprinodontiform lineages. Osteological synapomorphies confirm it is a cyprinodontiform killifish and allow us to identify it to species. The first pleural rib on the second vertebra and a symmetrical caudal fin with hypural elements fused into a fan-shaped hypural plate corroborate its classification in the cyprinodontiform suborder Cyprinodontoidei. The twisted maxilla with an anterior hook and the premaxilla with an elongate ascending process both place it in the family Fundulidae. The pointed neurapophyses of the first vertebra that do not meet in the midline and do not form a spine exclude it from the family Poeciliidae. Presence of discrete exoccipital condyles excludes it from the subfamily Poeciliinae. Overall shape, position of fins, and meristic data agree well with those of the well-known North American killifish, *F. heteroclitus*. *Fundulus capensis* Garman, 1895, redescribed herein, is considered a subjective synonym of *Fundulus heteroclitus* (Linnaeus, 1766). Provenance of the specimen remains a mystery.**

FUNDULUS capensis Garman, 1895 was described from one specimen said to be from False Bay, Cape of Good Hope, South Africa (Fig. 1). To Samuel Garman (1895:113), the new species was a ''Form resembling that of *F. heteroclitus*'', the abundant, well-known fundulid killifish of coastal eastern North America known by the common name Mummichog. Garman had just one, possibly immature, specimen, 21 mm SL, of his new species at hand precluding description of sexual dimorphism or secondary sexual characteristics. His description concludes (p. 113–114): ''It may be that with material in better condition, and a knowledge of the sexual peculiarities, a different disposition of this form will have to be made. This possibility is suggested by the shape of the teeth, which is not that of other Funduli, but rather an approach to that of *Heterandria formosa*.'' That species, known commonly as the Least Killifish, is a diminutive livebearer classified in the family Poeciliidae, not the Fundulidae (*sensu* Parenti, 1981). Thus, from its first description, classification of a little killifish thought to be from South Africa was equivocal: it could be either a fundulid or a poeciliine poeciliid (Table 1).

Provenance of the single, immature specimen was always suspect. *Fundulus* is a North American, not African, genus. This may explain why *Fundulus capensis* has been largely ignored in killifish classifications. It is absent from the list of North American species compiled by Jordan and Evermann (1896); its description just the year before could have skipped their attention. It was also omitted from the checklist of Jordan et al. (1930:175) in which, ironically, *Fundulus nisorius* Cope, 1870, described from West Africa, considered a ''wrong locality,'' was included as a synonym of *F. heteroclitus*, after Hubbs (1924) who referred *capensis* to *Fundulus*.

Fundulus capensis was omitted from other compilations of North American *Fundulus*, such as those of Hubbs (1926), Miller (1955), and Brown (1957). It may have continued to go unnoticed had Griffith (1972) not included it in his thorough treatment of the taxonomic history of *Fundulus*. Unfortunately, he could not resolve its classification (Griffith, 1972:253): ''The status of *F. capensis* Garman, described from the Cape of Good Hope, is obscure'' and it is (Griffith, 1972:261) '' . . . almost certainly not a species of *Fundulus* but not suitably allocated by later authors.''

The late George Sprague Myers, venerable killifish expert of the early and mid-20th century (Walford, 1970), could not abide this taxonomic loose end. Myers wrote in a letter to one of us (KEH), dated 29 August 1978:

> ''There is one cyprinodontoid type that I hope is still at the MCZ. That is the unique type of *Fundulus capensis* Garman (''The Cyprinodonts'') supposedly from the Cape of Good Hope. I looked at it rather superficially in 1930, although with a binocular. It has never been properly placed by anybody, in print at least, so far as I know. It is no Cyprinodontid. It is a female Poeciliid, probably a guppy, but after satisfying myself that it didn't belong to the Cyprinodontidae and did belong to the Poeciliidae, I did not carry the examination further. [Underlined in original]. Somebody should tack the identification down more specifically than I did.''

Although Myers could not place the species with certainty, he exercised considerable authority and others followed his conclusion that *F. capensis* was not a fundulid (then family Cyprinodontidae), but a poeciliid (Lazara, 1979; Lucinda, 2003; Eschmeyer, 2010). As far as we know, Myers was the last person to examine the specimen.

Small, immature specimens of the nine cyprinodontiform families (Table 1) are confused easily using solely external characters such as fin position and pigment pattern. Doubt over the identification and classification of one, small cyprinodontiform specimen is no surprise. Yet, now there are straightforward tools to distinguish a fundulid from a poeciliid: well-corroborated phylogenetic hypotheses (Parenti, 1981, 2005; Costa, 1996, 1998; Ghedotti, 2000; Lucinda and Reis, 2005; Fig. 2) present explicit osteological characters to diagnose cyprinodontiforms and distinguish among its hypothesized lineages. We redescribe *F. capensis*, combining newly recorded osteological characters with

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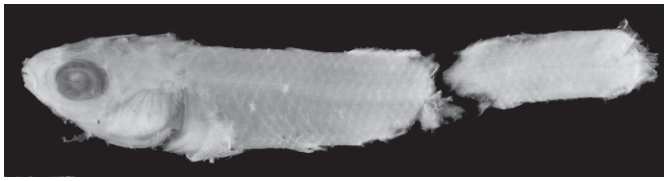

Fig. 1. *Fundulus capensis* Garman, 1895, MCZ 6454, holotype, 21 mm SL, in two pieces. Original photography © President and Fellows of Harvard College, reproduced with permission.

those of Garman, and compare the specimen with possible close relatives from North America and Africa. Radiographs and computed tomography (CT) micrographs of the holotype reveal critical osteological characters that allow us to identify it to species.

MATERIALS AND METHODS

Osteological data, counts, and measurements were recorded from film and digital radiographs and CT micrographs of the single specimen, the holotype of *F. capensis*. CT micrographs were prepared using the facilities of Harvard University's Center for Nanoscale Systems and the National Science Foundation's National Nanotechnology Infrastructure Network. During this study, the fragile, soft-bodied holotype fell into two pieces, bisected approximately just anterior to the dorsal and anal fins (Fig. 1). The poor condition of the holotype, including its relatively dis-articulated skeleton, obviated a complete, 3D CT reconstruction. Select micrographs are reproduced here as individual images. The redescription of *F. capensis* is based on our examination of the specimen, radiographs, and CT micrographs and Garman's (1895) original description. Comparative cyprinodontiform and atheriniform material cleared and counterstained for bone and cartilage following the protocols of Dingerkus and Uhler (1977) or Taylor and Van Dyke (1985), unless otherwise noted, and cleared and triple stained for bone, cartilage, and nerves following the protocol of Song

Table 1. Classification of Cyprinodontiformes (following Parenti [1981, 2005], Costa [1998], Ghedotti [2000]).

Order Cyprinodontiformes
- Suborder Aplocheiloidei
  - Family Aplocheilidae
  - Family Rivulidae
- Suborder Cyprinodontoidei
  - Superfamily Funduloidea
    - Family Profundulidae
    - Family Fundulidae
    - Family Goodeidae
  - Superfamily Valencioidea
    - Family Valenciidae
- Unranked category
  - Superfamily Cyprinodontoidea
    - Family Cyprinodontidae
  - Superfamily Poecilioidea
    - Family Anablepidae
    - Family Poeciliidae
      - Subfamily Aplocheilichthyinae
      - Subfamily Procatopodinae
      - Subfamily Poeciliinae

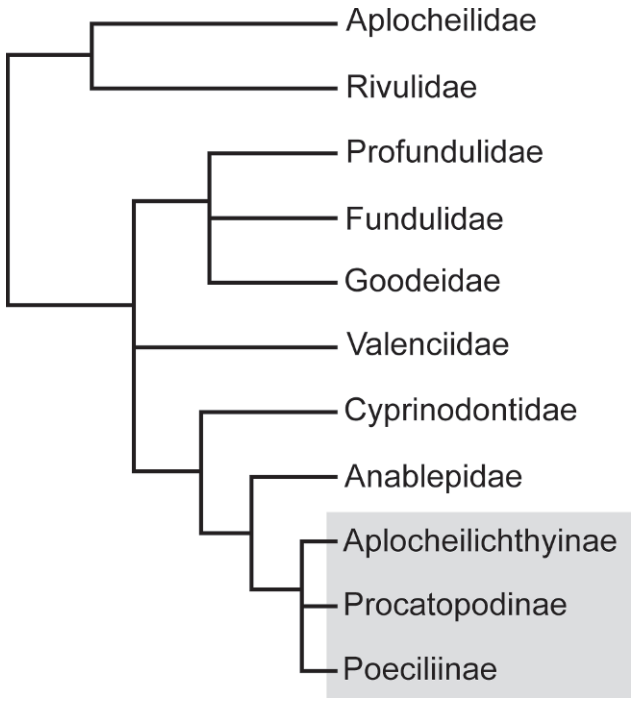

Fig. 2. Consensus cladogram of relationships among the families of cyprinodontiform fishes, following Parenti (1981, 2005), Costa (1996, 1998), and Ghedotti (2000). Subfamilies of the family Poeciliidae are in shaded box.

and Parenti (1995), was available in the collections of the Division of Fishes, USNM. Names of bones follow Parenti (1981). Institutional abbreviations are as listed at http://www.asih.org/node/204.

Fundulus capensis Garman, 1895

Figures 1, 3–8

Fundulus capensis Garman, 1895:113–114, pl. 3 (fig. 2), False Bay, Cape of Good Hope, South Africa.
Mollienesia sphenops?.—Lazara, 1979:34
Species inquirenda in Poeciliidae.—Lucinda, 2003:575.–Eschmeyer, 2010.

Holotype.—MCZ 6454, 21 mm SL, South Africa, Cape of Good Hope, False Bay, received at MCZ August 1872 (Fig. 1).

Description.—Only known specimen 21 mm SL, sex and maturity undetermined. Body compressed laterally, slender to somewhat deep-bodied. Mouth subterminal, lower jaw

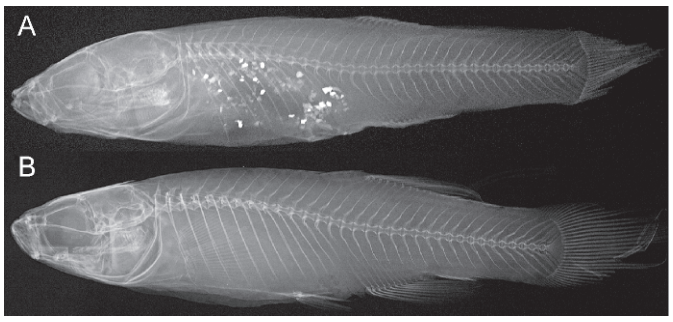

Fig. 3. Radiographs of (A) *Fundulus capensis* Garman, 1895, MCZ 6454, holotype, 21 mm SL, lateral view; (B) *Fundulus heteroclitus*, USNM 395762, 23.5 mm SL, lateral view.

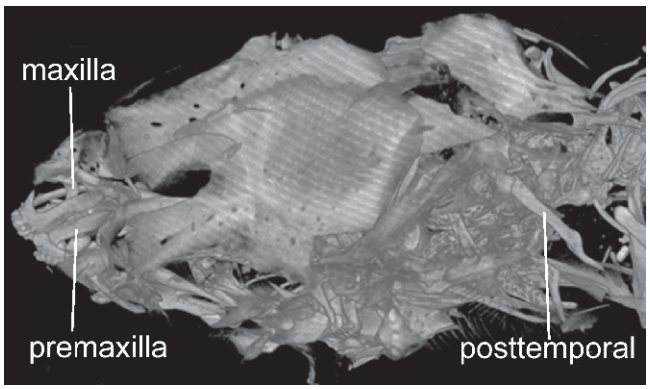

Fig. 4. Computed tomography micrograph of *Fundulus capensis* Garman, 1895, MCZ 6454, holotype, 21 mm SL, anterior portion of specimen from tip of snout through first three to four vertebrae. Original photography © President and Fellows of Harvard College, reproduced with permission.

extends slightly beyond upper jaw; upper jaw protractile. Dorsal and ventral body profile arched gently from head to dorsal- and anal-fin origins. Dorsal surface of head slightly convex just anterior to orbits. Head moderate, 6 mm long; snout 1 mm long; eye 2 mm wide, orbits do not project beyond dorsal surface of head (Fig. 3A). Basal portion of dorsal and anal fin do not project significantly beyond primary body profile. Scales of moderate size, cycloid, somewhat deciduous. Garman (1895:113) reported 36 scales in the lateral series; number could not be verified on holotype as most lateral scales have been lost. Ventrum covered with small, irregularly arranged cycloid scales. Dorsal and anal fins rounded. Caudal fin convex. Lacrimal with concave posterior border. Oral jaws short. Premaxilla with distinct, elongate ascending process (Fig. 4). Premaxillary and dentary teeth unicuspid. Medial arm of maxilla with pronounced anteriorly directed hook (Fig. 4). Lacrimal with concave posterior border. First pleural rib on parapophysis of second vertebra (Figs. 3A, 5A). Neural arches of first vertebra pointed, oriented vertically, open, not forming a neural spine (Fig. 6). Exoccipital condyles distinct (Figs. 5A, 7). Posttemporal bone straight, no ossified ventral arm (Figs. 4, 5A). No pleural ribs on hemal arches. Dorsal-fin origin above 16th vertebra. Anal-fin origin below 18th vertebra. Caudal skeleton symmetrical, one epural bone mirrored by parhypural. Hypural elements fused into fan-shaped plate. Fifth ceratobranchial toothplates subtriangular, separate, with pointed, unicuspid teeth anteriorly, molariform teeth posteriorly (Fig. 8).

Dorsal-fin rays 13. Anal-fin rays 13. Pelvic-fin rays 6. Total caudal-fin rays (principal and procurrent) approximately 40. Vertebrae 36 (15+21). Branchiostegal rays 5.

Color in alcohol.—Specimen faded to a uniform grayish green. Garman's (1895:113) description provides the only information available on pigmentation:

> ''Olivaceous, edges of scales darker. Top of head darker, crossed by a lighter band in front of the eyes. Opercle silvery, crossed by a darkish streak behind the eye. Belly whitish or silvery. A faint band of silvery from the operculum to the caudal along the middle of the side. Five or six broad blotches of brownish across the flanks, separated by rather wider spaces of the lighter color. A vertebral darkish streak, more distinct behind the dorsal; a similar line between anal and lower edge of caudal. A band crosses the caudal near its base. Darker color shows faintly through the silvery band on the flanks.''

Distribution and habitat.—The unique holotype is reported to be from False Bay, a marine inlet at the Cape of Good Hope, South Africa. This locality is probably wrong.

RESULTS AND DISCUSSION

The holotype of *Fundulus capensis*, maintained at the MCZ since 1872, is soft and flexible and has lost nearly all of its natural coloration. It is in two pieces and, because of its poor preservation, presents vague details of the relationship of one bone to another (Fig. 1). Fortunately, decalcification has been limited and radiographs and CT micrographs reveal critical osteological details that allow us to clarify the identification of this unique specimen and place the species in a classification with some conviction.

The holotype has the first pleural rib on the second vertebra and a symmetrical caudal fin with a single epural that mirrors the shape and position of the parhypural, two diagnostic characters that corroborate its classification in the order Cyprinodontiformes (Parenti, 1981; Table 1; Fig. 3A). The hypural elements are fused into a fan-shaped plate which further places it in the cyprinodontiform suborder Cyprinodontoidei (Parenti, 1981).

Character states of the first vertebra and its attachment to the skull vary among cyprinodontiforms and provide a set of phylogenetically informative data to distinguish among lineages. Cyprinodontiforms of the suborder Aplocheiloidei (families Aplocheilidae and Rivulidae) have a complete neural spine on the first vertebra (Parenti, 1981; Table 1). Within the suborder Cyprinodontoidei, in fundulids and goodeids and some other taxa, the pointed neurapophyses do not meet in the midline; therefore, the first neural arch is open and does not form a spine. The first vertebra attaches to the skull via well-formed basioccipital and exoccipital condyles in all the aforementioned taxa (Parenti, 1981; Fig. 9A).

Cyprinodontoid fishes in the poeciliid subfamilies Aplocheilichthyinae and Procatopodinae (Table 1; Fig. 2), with few exceptions (Ghedotti, 2000), have a closed first neural arch with a median, vertical flange. The first vertebra connects with the skull via the basioccipital and exoccipital condyles. An inferred further derived condition characterizes fishes in the subfamily Poeciliinae: the first neural arch encloses the spinal cord via a horizontal, bony flange. The neurapophyses are expanded anteriorly and enclose the back of the skull which lacks discrete exoccipital condyles (Parenti, 1981; Ghedotti, 2000; Fig. 9B).

The pointed neurapophyses of the first vertebra that do not meet in the midline to form a spine and the narrow, elongate premaxillary ascending processes exclude *F. capensis* from the family Poeciliidae. Presence of discrete exoccipital condyles exclude it from the subfamily Poeciliinae. The differences in these characters between fundulids and poeciliines can be demonstrated readily by comparison of the skeletons of *F. capensis* and *F. heteroclitus* with that of *Heterandria formosa*, the diminutive poeciliine species with which *F. capensis* was compared in Garman's (1895) description, abstracted above. Differences in the attachment of the first vertebra to the skull are striking (Fig. 9). In *Fundulus heteroclitus* and *F. capensis*, the first vertebra has

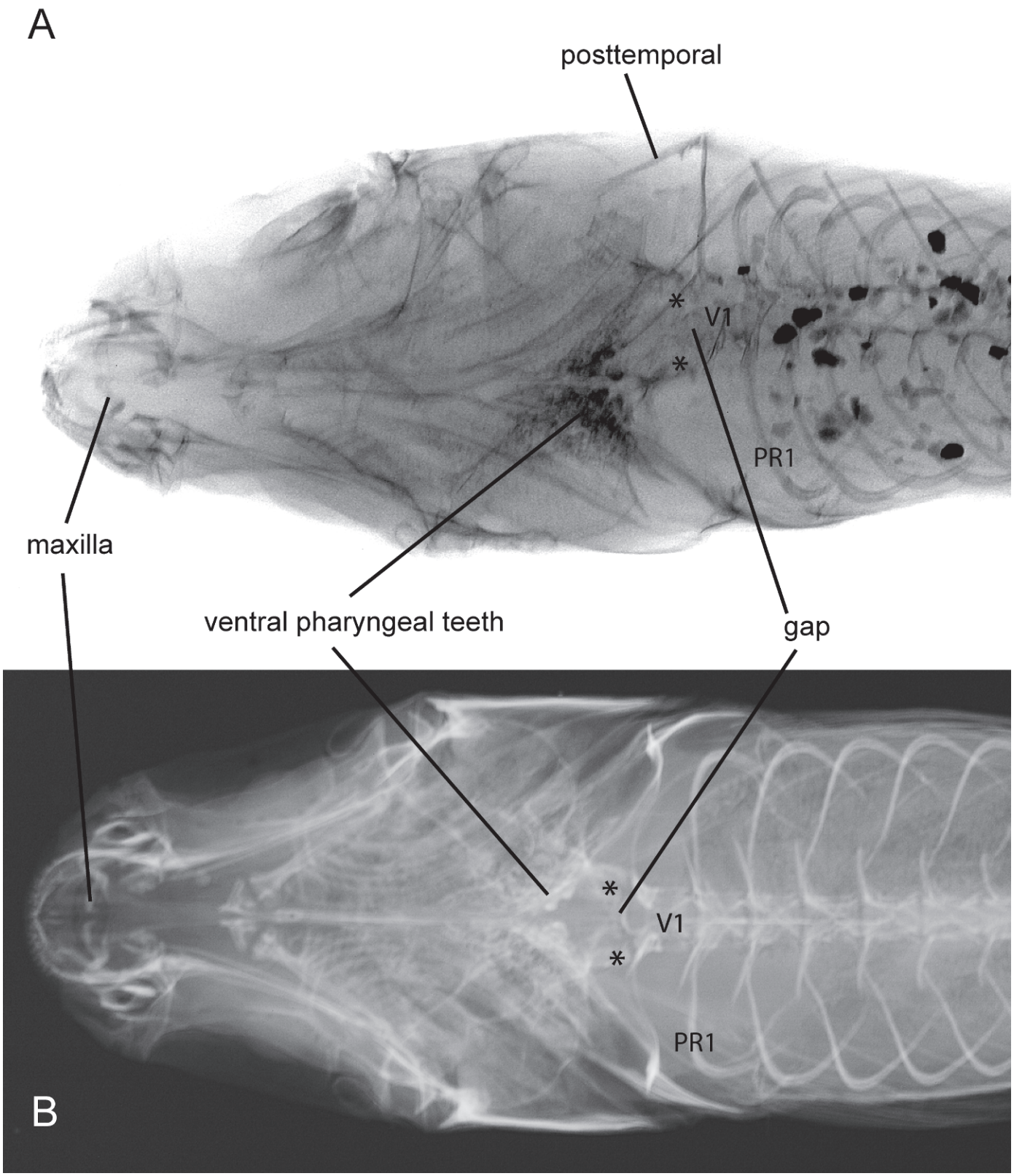

Fig. 5. Radiographs of *Fundulus capensis* Garman, 1895, MCZ 6454, holotype, 21 mm SL, inverted image, above; *Fundulus heteroclitus*, USNM 395762, 23.5 mm SL, below. Ventral view of skull and anterior portion of vertebral column. V1, first vertebra; PR1, first pleural rib. The gap is that between the first vertebra and the skull. Exoccipital condyles are starred (*).

well-formed medial and lateral condyles that attach to the basioccipital and exoccipital condyles, respectively. In *H. formosa*, the neurapophyses of the first vertebra are expanded anteriorly and applied to the back of the skull which lacks discrete exoccipital condyles, as in other members of the subfamily Poeciliinae. The teeth of *F. capensis* ''approach'' those of *H. formosa*, according to Garman (1895:114), rather than any other fundulids, and we conclude that similarity in shape and position of the outer jaw teeth may be due to small size of the specimens. Ventral pharyngeal teeth of *F.*

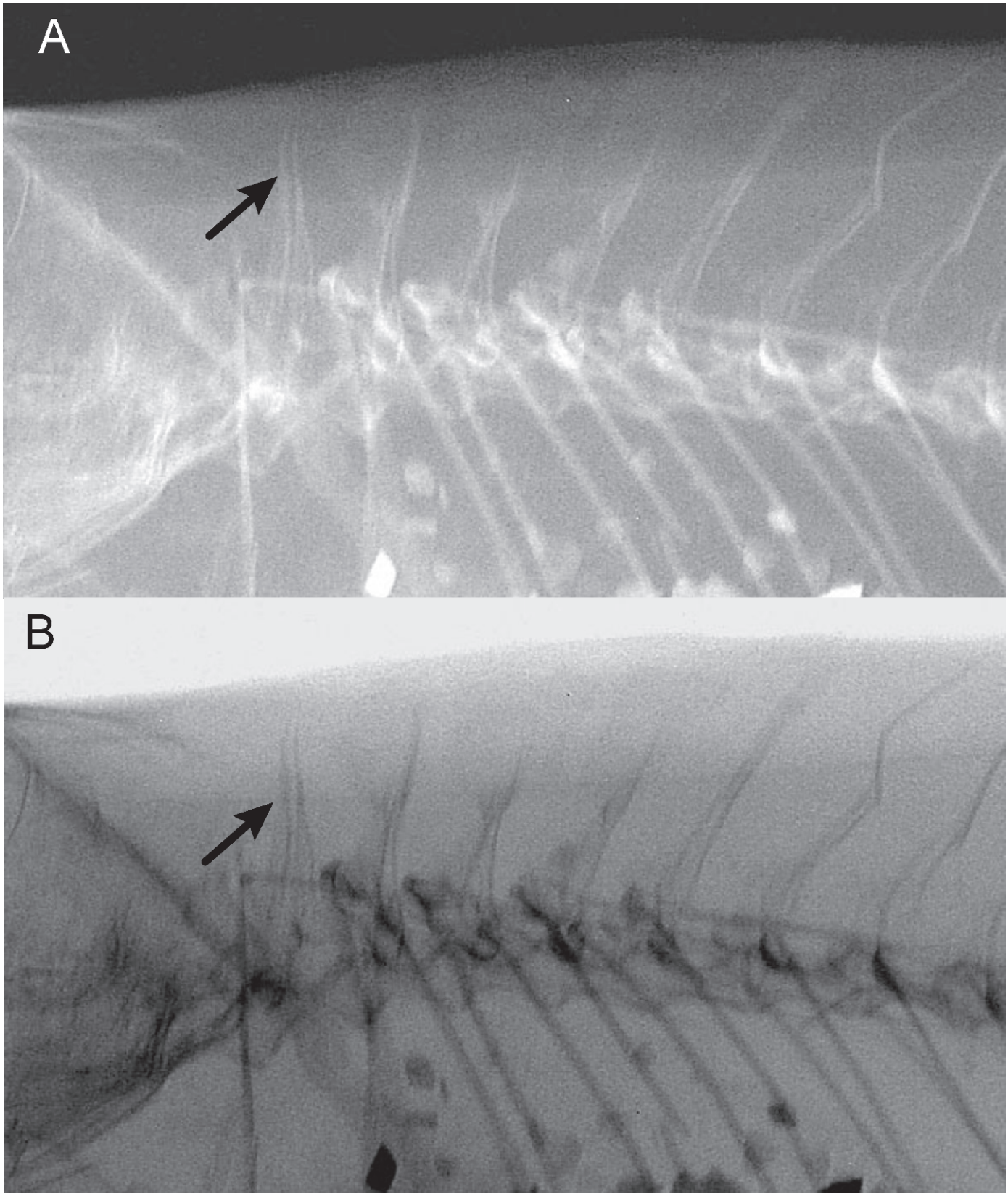

Fig. 6. Radiograph of *Fundulus capensis* Garman, 1895, MCZ 6454, holotype, 21 mm SL, lateral view of posterior region of skull and anterior portion of vertebral column, above; inverted image below. In both, arrow points to vertically oriented, pointed neural arches of first vertebra that do not form a neural spine.

capensis (Fig. 8) are relatively small and unicuspid anteriorly, molariform posteriorly, like other fundulids. In *H. formosa*, the ventral pharyngeal teeth are more uniform in size, without larger, molariform teeth posteriorly.

The twisted maxilla with anteriorly directed hook-like process of *F. capensis* (Fig. 4) is a synapomorphy of the family Fundulidae *sensu* Parenti (1981). Monophyly of the Fundulidae was corroborated by Wiley (1986) and Costa

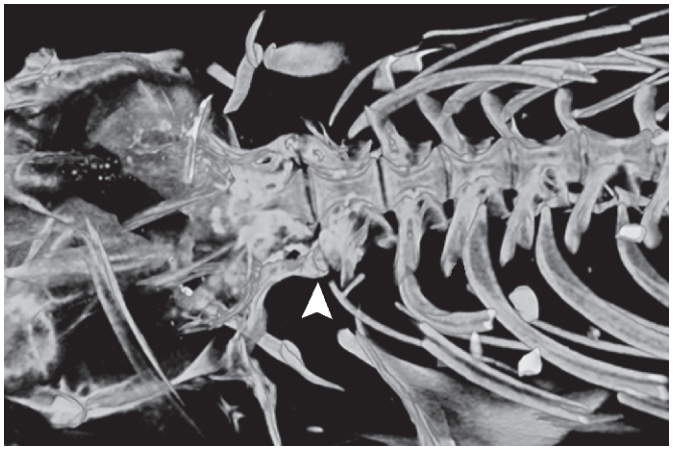

Fig. 7. Computed tomography micrograph of *Fundulus capensis* Garman, 1895, MCZ 6454, holotype, 21 mm SL, back of skull and anterior portion of vertebral column. White arrowhead points to exoccipital condyle. Original photography © President and Fellows of Harvard College, reproduced with permission.

(1998). Costa's (1998:555) nine morphological synapomorphies of the Fundulidae include the anteriorly directed maxillary process as well as an elongate premaxilla (Fig. 4). These two synapomorphies observed in the holotype of *F. capensis* corroborate the hypothesis that it is a fundulid.

Five recent genera were classified in the Fundulidae *sensu* Parenti (1981): *Fundulus*, *Plancterus*, *Lucania*, *Leptolucania,* and *Adinia*. Among these, only a species of *Fundulus* would have 36 scales in a lateral series, as reported for *F. capensis* by Garman (1895). *Plancterus* has 41–68 scales in a lateral series, and the three other genera have 32 or fewer (Rosen, 1973; Page and Burr, 1991).

Monophyly of *Fundulus* was supported by Parenti (1981), but rejected by Wiley (1986) and Cashner et al. (1993), among others. Nonetheless, Wiley (1986) classified most *Fundulus* species in four subgenera, *Fundulus*, *Xenisma*, *Fontinus,* and *Zygonectes*, which, in part, mirrors the classification of Farris (1968), and proposed preliminary

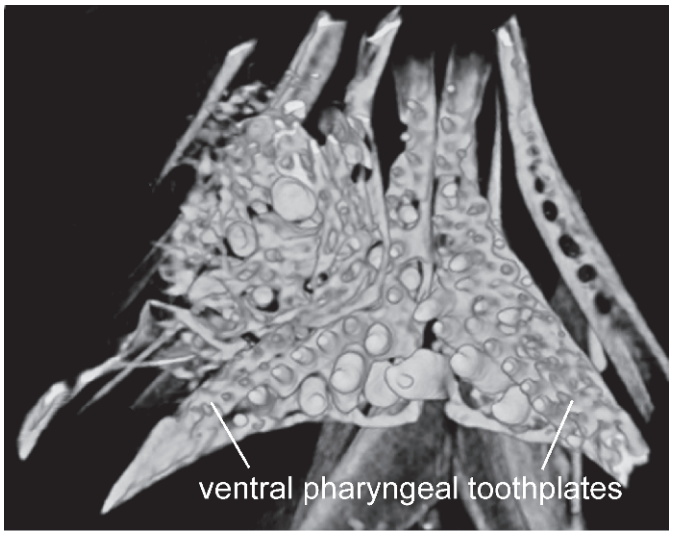

Fig. 8. Computed tomography micrograph of *Fundulus capensis* Garman, 1895, MCZ 6454, holotype, 21 mm SL, left dorsal and left and right ventral pharyngeal bones and toothplates. Note molariform posterior ventral pharyngeal teeth. Anterior is up. Original photography © President and Fellows of Harvard College, reproduced with permission.

morphological synapomorphies for each subgenus. *Fundulus capensis* may be rejected as a member of the subgenus *Zygonectes* because it does not have the synapomorphy of elongate and rectangular oral jaws. Likewise, it is not a member of the subgenus *Xenisma*, diagnosed by absence of vertical bars on the body; the ''five or six broad blotches across the flanks'' described by Garman (1895) are interpreted here as vertical bars. The subgenus *Fontinus* was diagnosed by Wiley (1986:124) using three osteological synapomorphies. We have been able to check only one of these, the posterior border of the lacrimal convex rather than concave, on the holotype, and it is rejected. The fourth subgenus, *Fundulus*, was diagnosed by one synapomorphy (Wiley, 1986:123–124): '' . . . maxilla with a posterior edge that is distinctly concave anteriorly . . . '' in medial view. We could neither confirm nor reject this character on the holotype of *F. capensis*. Yet, because we reject classification of *F. capensis* in the three other subgenera, we conclude that it is a member of the subgenus *Fundulus*.

Overall shape and position of fins agree well with those of *Fundulus heteroclitus* (Fig. 3). Meristic data of the holotype of *F. capensis* also accord with those reported for *F. heteroclitus*. For example, vertebrae of *F. capensis* number 36; the range for the population of *F. heteroclitus* north of Cape Cod, Massachusetts, is 33 to 36 (Relyea, 1983). Garman (1895) reported 13 anal-fin rays, and Relyea (1983) gave a range of 9–12 anal-fin rays. The anal fin of the holotype is damaged and we cannot confirm the number of anal-fin rays; a difference of one ray would not be sufficient evidence to reject identification of the specimen as *F. heteroclitus,* which is a highly variable species throughout its range (Relyea, 1983).

We conclude that *Fundulus capensis* Garman, 1895 is a subjective junior synonym of *Fundulus heteroclitus* (Linnaeus, 1766). We can but wonder why Garman (1895) described the single specimen as representing a new species. Perhaps he was encouraged by the presumed South African locality to look for possible differences between the specimen and those of North American species of *Fundulus*. The unique holotype (MCZ 6454) was received at the MCZ in August, 1872, based on the ledger and on bottle labels. It was said to be from False Bay, Cape of Good Hope; neither collector nor donor are listed in the ledger or on the label.

Three other MCZ lots have the same collection data as, or were mixed with, the holotype, and catalogued as a flatfish (MCZ 11604, *Paralichthys* sp.), a goby (MCZ 13074, Gobiidae), and a silverside (MCZ 18256, Atherinidae). These cursory identifications were entered in a hand different from the one that entered the locality. MCZ 6454 was not identified in the ledger until the late 1920s when MCZ curator, Nicholas Borodin, wrote: *Fundulus capensis*.

Attempts to identify further the three other MCZ lots said to be from False Bay have only compounded the mystery. The flatfish may be a species of the genus *Paralichthys*, which has species in the Gulf of Maine, but not South Africa, or of the genus *Pseudorhombus,* which has species in South Africa, but not the Gulf of Maine. Fin-ray counts of the MCZ specimen do not match those of any species of *Pseudorhombus* living in South Africa (T. Munroe, pers. comm.). The gobiid is a member of the eastern Pacific, not South African, genus *Quietula* (K. Cole, pers. comm.). The ''atherinid'' has a premaxilla distinctive of New World, not Old World, silversides, following Chernoff (1986), and, therefore, is in the family Atherinopsidae. We identify it as a member of the abundant and well-known New World silverside genus

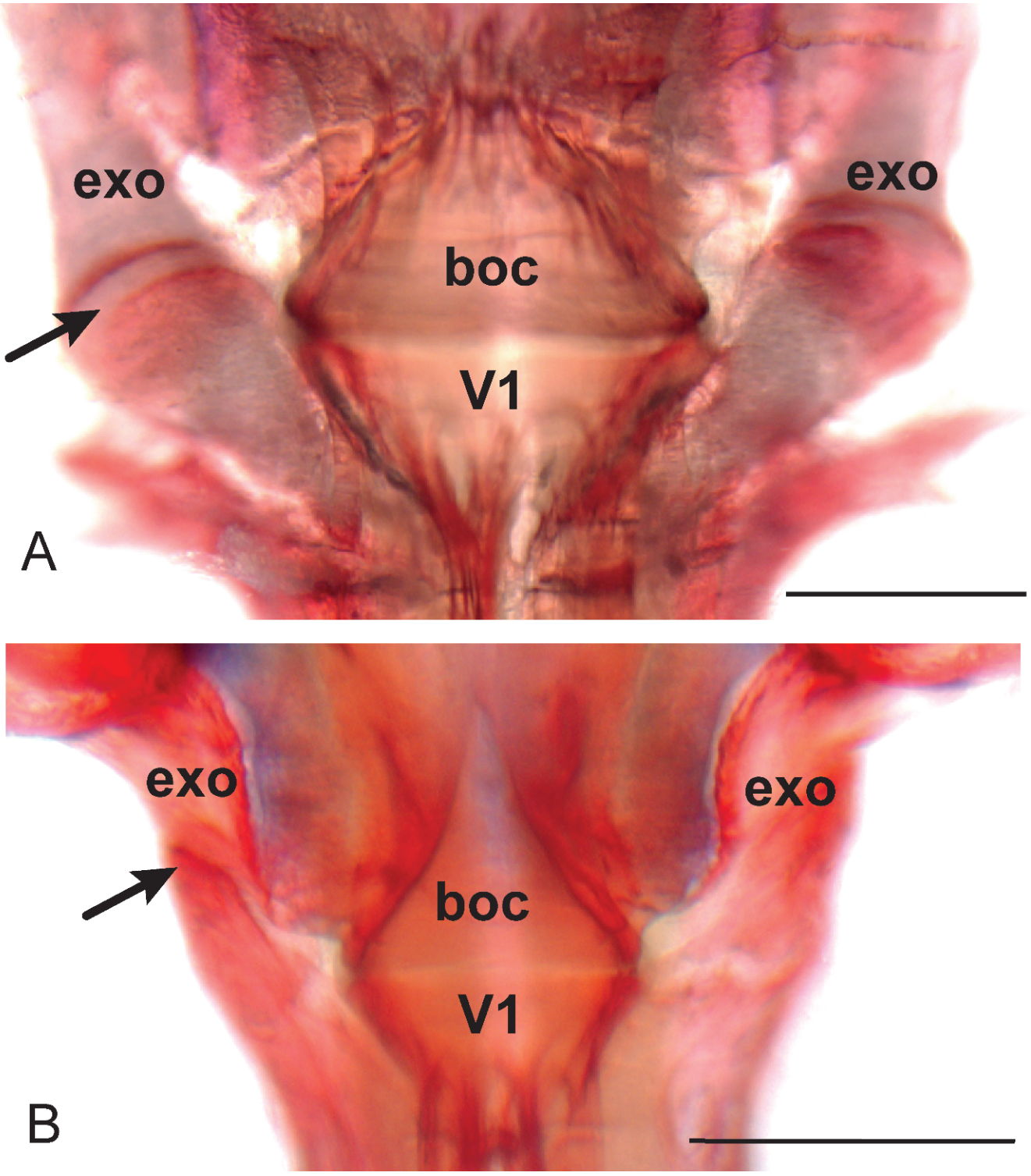

Fig. 9. Cleared-and-counterstained preparations of (A) *Fundulus heteroclitus*, USNM 278883, 39 mm SL, scale bar = 0.5 mm; and (B) *Heterandria formosa,* USNM 227434, 17 mm SL, scale bar = 0.3 mm, to illustrate differences in attachment of the first vertebra to the skull; boc, basioccipital; exo, exoccipital; V1, first vertebra. Arrow points to junction of exoccipital and first vertebra. Anterior is up.

Menidia because origin of the spinous dorsal fin is anterior to the origin of the anal fin (Chernoff, 2002a). We cannot confirm its identity as one of the two species of *Menidia* in the Gulf of Maine, *M. beryllina* and *M. menidia*. It has 47 vertebrae, agreeing with *M. menidia,* but more than the upper range of 42 of *M. beryllina* (Chernoff, 2002b). Unlike *M. menidia*, its head is longer than 25% SL (Chernoff, 2002b). Further study of the specimens in these three MCZ lots may clarify their identification, but they are not part of the South African biota.

Our efforts to identify the collector or donor of the holotype of *F. capensis* have been met with equal frustration. Edgar L. Layard of the South African Museum is said to have sent approximately 400 fish specimens to the MCZ in 1864 (Gon and Skelton, 1997:136). But, strangely, at the MCZ there are only 25 lots totaling 47 specimens received from Layard between 1860 and 1864. There are only 42 lots totaling 86 specimens from South Africa received at the MCZ before 1900. None of Layard's material was received

after 1864. Therefore, it is unlikely that Layard sent the *Fundulus capensis* holotype from South Africa to the MCZ. The simplest explanation is that through curatorial error, the holotype (one of possibly thousands of cyprinodontiform specimens handled by Garman) was put in the wrong bottle to which a ''False Bay'' label was added. This leads us to the mildly humorous conclusion that the False Bay locality may have been attached to all of these specimens as a hoax, something of a curatorial practical joke played on Garman or others at the MCZ. We cannot resolve these 140-plus years of curatorial disharmony, but finally settle over a century of speculation on the identification of a not quite inch-long killifish specimen. It is a Mummichog.

MATERIAL EXAMINED

Cyprinodontiformes: Fundulidae: *Fundulus bermudae,* USNM 112083, 8 cleared and counterstained, Bermuda, St. George's Island. *Fundulus heteroclitus,* USNM 278883, 1 cleared and counterstained, USA, Maryland, Calvert County; USNM 326631, 5 cleared and tripled stained, USA, Delaware, Delaware County; USNM 395762, 1 of 13 radiographed, USA, New Jersey, Ocean County. *Fundulus luciae*, USNM 217385, 2 cleared and counterstained, USA, Virginia, Accomack County. Poeciliidae: Subfamily Procatopodinae: *Procatopus schioetzi,* USNM 323612, 3 cleared and counterstained, Ghana, Kibi. *Procatopus similis,* USNM 303504, 4 cleared and counterstained, Cameroon, Southwest Province. Subfamily Poeciliinae: *Heterandria formosa*, USNM 227434, 3 cleared and counterstained, 1 stained solely with alcian blue, USA, Florida, Indian River County. *Poecilia vivipara,* USNM 279139, 2 cleared and counterstained, Brazil, Santa Catarina. *Tomeurus gracilis*, USNM 225462, 2 cleared and counterstained, Surinam, Corantijn River. *Xiphophorus milleri*, USNM 214150, 2 cleared and counterstained, Mexico, Veracruz.
Atheriniformes: Atherinopsidae: *Menidia beryllina,* USNM 200735, 21 cleared and stained for bone, 1 cleared and stained for cartilage, USA, Maryland, Calvert County. *Menidia menidia,* USNM 200734, 10 cleared and stained for bone, USA, Maryland.

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LITERATURE CITED

Brown, J. L. 1957. A key to the species and subspecies of the cyprinodont genus *Fundulus* in the United States and Canada east of the continental divide. Journal of the Washington Academy of Sciences 47:69–77.

Cashner, R. C., J. S. Rogers, and J. M. Grady. 1993. Phylogenetic studies of the genus *Fundulus*, p. 421–437. *In*: Systematics, Historical Ecology, and North American Freshwater Fishes. R. L. Mayden (ed.). Stanford University Press, Stanford, California.

Chernoff, B. 1986. Phylogenetic relationships and reclassification of menidiine silverside fishes with emphasis on the tribe Membradini. Proceedings of the Academy of Natural Sciences of Philadelphia 138:189–249.

Chernoff, B. 2002a. Atherinopsidae. New World silversides, p. 1090–1106. *In*: The Living Marine Resources of the Western Central Atlantic, FAO Western Central Atlantic Identification Guide for Fishery Purposes. Vol. 2, Bony Fishes part 1 (Acipenseridae to Grammatidae). K. E. Carpenter (ed.). FAO, Rome, Italy.

Chernoff, B. 2002b. New World silversides. Family Atherinopsidae, p. 280–284. *In*: Bigelow and Schroeder's Fishes of the Gulf of Maine. Third edition. B. B. Collette and G. Klein-MacPhee (eds.). Smithsonian Institution Press, Washington, D.C.

Costa, W. J. E. M. 1996. Relationships, monophyly and three new species of the Neotropical miniature poeciliid genus *Fluviphylax* (Cyprinodontiformes: Cyprinodontoidei). Ichthyological Exploration of Freshwaters 7:111–130.

Costa, W. J. E. M. 1998. Phylogeny and classification of the Cyprinodontiformes (Euteleostei: Atherinomorpha) a reappraisal, p. 537–560. *In*: Phylogeny and Classification of Neotropical Fishes. L. R. Malabarba, R. E. Reis, R. P. Vari, Z. M. S. Lucena, and C. A. S. Lucena (eds.). EDIPUCRS, Porto Alegre, Brazil.

Dingerkus, G., and L. D. Uhler. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. Stain Technology 52:229–232.

Eschmeyer, W. N. 2010. Catalog of Fishes. California Academy of Sciences, San Francisco, California, Online database accessed 26 July 2010, at http://research.calacademy.org/ichthyology/catalog/fishcatmain.asp

Farris, J. S. 1968. The evolutionary relationships between the species of the killifish genera *Fundulus* and *Profundulus* (Teleostei: Cyprinodontidae). Unpubl. Ph.D. diss., University of Michigan, Ann Arbor, Michigan.

Garman, S. 1895. The cyprinodonts. Memoirs of the Museum of Comparative Zoology, Harvard University 19:1–179.

Ghedotti, M. J. 2000. Phylogenetic analysis and taxonomy of the poecilioid fishes (Teleostei: Cyprinodontiformes). Zoological Journal of the Linnean Society 130:1–53.

Gon, O., and P. H. Skelton. 1997. A history of the fish collections of South Africa, p. 133–168. *In*: Collection Building in Ichthyology and Herpetology. T. W. Pietsch and W. D. Anderson, Jr. (eds.). American Society of Ichthyologists and Herpetologists Special Publication number 3, Lawrence, Kansas.

Griffith, R. W. 1972. Studies on the physiology and evolution of killifishes of the genus *Fundulus*. Unpubl. Ph.D. diss., Yale University, New Haven, Connecticut.

Hubbs, C. L. 1924. Studies of the fishes of the order Cyprinodontes. University of Michigan Museum of Zoology Miscellaneous Publications 13:1–31.

Hubbs, C. L. 1926. Studies of the fishes of the order Cyprinodontes VI. Material for a revision of the American genera and species. University of Michigan Museum of Zoology Miscellaneous Publications 16:1–87.

Jordan, D. S., and B. W. Evermann. 1896. The fishes of North and Middle America. Bulletin of the United States National Museum 47:1–1240.

Jordan, D. S., B. W. Evermann, and H. W. Clark. 1930. Checklist of the fishes and fish-like vertebrates of North and Middle America north of the northern boundary of Venezuela and Colombia. Appendix X to the Report of the United States Commissioner of Fisheries for 1928: 1–670.

Lazara, K. J. 1979. Killifish Master Index. Second edition. American Killifish Association, Cincinnnati, Ohio.

Lucinda, P. H. F. 2003. Family Poeciliidae (Livebearers), p. 555–581. *In*: Check List of the Freshwater Fishes of South and Central America, , R. E. Reis, S. O. Kullander, and C. J. Ferraris, Jr. (orgs.). EDIPUCRS, Porto Alegre, Brazil.

Lucinda, P. H. F., and R. Reis. 2005. Systematics of the subfamily Poeciliinae Bonaparte (Cyprinodontiformes: Poeciliidae), with an emphasis on the tribe Cnesterodontini Hubbs. Neotropical Ichthyology 3:1–60.

Miller, R. R. 1955. An annotated list of the American cyprinodontid fishes of the genus *Fundulus*, with the description of *Fundulus persimilis* from Yucatan. Occasional Papers of the Museum of Zoology, University of Michigan 568:1–25.

Page, L. M., and B. M. Burr. 1991. A Field Guide to Freshwater Fishes, North America North of Mexico. Houghton Mifflin Company, Boston.

Parenti, L. R. 1981. A phylogenetic and biogeographic analysis of cyprinodontiform fishes (Teleostei, Atherinomorpha). Bulletin of the American Museum of Natural History 168:335–557.

Parenti, L. R. 2005. The phylogeny of atherinomorphs: evolution of a novel reproductive system, p. 13–30. *In*: Viviparous Fishes. Proceedings of the I and II International Symposia. M. del. C. Uribe and H. J. Grier (eds.). New Life Publications, Homestead, Florida.

Relyea, K. 1983. A systematic study of two species complexes of the genus *Fundulus* (Pisces: Cyprinodontidae). Bulletin of the Florida State Museum, Biological Sciences 29:1–64.

Rosen, D. E. 1973. Suborder Cyprinodontoidei. Fishes of the Western North Atlantic. Sears Foundation for Marine Research 1(6):229–262.

Song, J., and L. R. Parenti. 1995. Clearing and staining whole fish specimens for simultaneous demonstration of bone, cartilage, and nerves. Copeia 1995:114–118.

Taylor, W. R., and G. C. Van Dyke. 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. Cybium 9:107–119.

Walford, L. A. 1970. On the natural history of George Sprague Myers. Festschrift for George Sprague Myers. Proceedings of the California Academy of Sciences, fourth ser 30:1–18.

Wiley, E. O. 1986. A study of the evolutionary relationships of *Fundulus* Topminnows (Teleostei: Fundulidae). American Zoologist 26:121–130.