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Revision of the Deep-Sea Anglerfish Genus *Bufoceratias* Whitley (Lophiiformes: Ceratioidei: Diceratiidae), with Description of a New Species from the Indo-West Pacific Ocean

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The deep-sea ceratioid anglerfish genus *Bufoceratias* Whitley is revised on the basis of all known material. Three species are recognized: *Bufoceratias wedli* (Pietschmann), now represented by 69 specimens collected from both sides of the Atlantic Ocean; *Bufoceratias thele* (Uwate), 11 specimens from the western Pacific; and a new species, *Bufoceratias shaoi*, described on the basis of four specimens from the Western Indian and Western Pacific oceans. The new species differs from its congeners by having a short illicium and an unusually large and morphologically complex esca. Diagnoses and descriptions are given for all taxa and a revised key to the species of the genus is provided. Diceratiids are found in all three major oceans of the world, but they are conspicuously absent from the eastern Pacific. In contrast to the midwater life style generally assumed for most ceratioids, at least some diceratiids, especially larger individuals, are associated with the bottom.

THE taxonomic history of the deep-sea ceratioid anglerfish genus *Bufoceratias* Whitley (family Diceratiidae) is so complexly intertwined with that of its sister-genus *Diceratias* Günther that a historical review of the family is required for a full understanding. Although appearing superficially like himantolophids or basal oneirodids, especially members of the genus *Oneirodes*, diceratiids are unique among members of the lophiiform suborder Ceratioidei in having a second light-bearing, dorsal-fin spine emerging from the head directly behind the base of the illicium. On that basis alone, they cannot be confused with any other family. The first diceratiid was introduced by Günther (1887), with his description of *Ceratias* (*Diceratias*) *bispinosus* based on a single female specimen collected by the HMS CHALLENGER in the East Indies off Banda Island. Most likely unaware of Günther's (1887) publication, Alcock (1890:206) described a second female, from the Bay of Bengal, under the name *Paroneirodes glomerosus*, recognizing its similarity to *Oneirodes* Lütken, 1871, but, at the same time, realizing the unique presence of "two clavate cephalic tentacles." Alcock (1899) later placed *Paroneirodes* in the synonymy of *Oneirodes*, although maintaining the subgeneric status of *Diceratias*. Emphasizing once again the significance of a "second ray of [the] spinous dorsal [situated] immediately behind the first," Regan (1912: 287) raised *Diceratias* to generic status, although recognizing *Paroneirodes* as a junior synonym.

Somewhat later, Pietschmann (1926, 1930) discovered a very different looking diceratiid in the collections of the Natural History Museum in Vienna. Collected by Steindachner some 60 years earlier off the coast of Madeira, Pietschmann (1926, 1930) described the specimen as a new genus and species naming it *Phrynichthys wedli*. Although sharing with *Diceratias* a second dorsal-fin spine lying just behind the first, *Phrynichthys* was unique in the much greater length of the first dorsal-fin spine (illicium) and in the position of the two spines, emerging on the back at the rear of the skull rather than on the snout (Figs. 1, 2).

Unfortunately, Pietschmann's (1926) important contribution to diceratiid systematics was passed over by several subsequent authors including Norman (1930) who, had he known of Pietschmann's publication, would not have misidentified a small specimen of *P. wedli* from the eastern South Atlantic as *P. glomerosus*, at the same time resurrecting *Paroneirodes* from the synonymy of *Diceratias*. In any case, with two rather distinct genera, differing in similar ways from all other known ceratioids, Regan and Trewavas (1932) established the family Diceratiidae to include *Diceratias* and *Paroneirodes*, with the latter containing *Phrynichthys* as a junior synonym. Contained also in the family Diceratiidae was *Caranactis pumilus*, a new genus and species erected by Regan and Trewavas (1932) to contain a single male specimen from the Indian Ocean subsequently referred to the genus *Oneirodes* by Bertelsen (1951).

Subsequent authors, including Bertelsen (1951) and Maul (1962), followed Regan and Trewavas (1932) in recognizing *Phrynichthys* as a junior synonym of *Paroneirodes*. Karrer (1973) went farther, regarding both *Paroneirodes* and

Phrynichthys as junior synonyms of *Diceratias*. Uwate (1979), however, based on a detailed examination of all known material, was able to show conclusively that *Paroneirodes* is indeed synonymous with *Diceratias* as originally proposed by Regan (1912), the later genus now containing *Diceratias spinosus* and a newly described species, *Diceratias pileatus* Uwate, from the central Atlantic. At the same time, Uwate (1979) provided evidence to resurrect *Phrynichthys* from the synonymy of *Paroneirodes*, to include *P. wedli* and another new species, *Paroneirodes thele* Uwate, based on two specimens from the western central Pacific. However, Uwate (1979) and most other authors before and after (exceptions include Golvan, 1962; Eschmeyer, 1990; and Anderson and Leslie, 2001) failed to recognize Whitley's (1931) *Bufoceratias* as a replacement name for *Phrynichthys* Pietschmann, the latter preoccupied by *Phrynichthys* Agassiz, 1846, which was itself a replacement name for *Bufichthys* Swainson, 1839, a synonym of *Synanceia* Bloch and Schneider, 1801.

In the 25 years since Uwate's (1979) revision, little has been added to our knowledge of diceratiids. One additional species, *Diceratias trilobus*, has been described by Balushkin and Fedorov (1986), bringing the total number to five (three species of *Diceratias* and two of *Bufoceratias*), and a few additional specimens of several species have been collected, including the first known metamorphosed male (Bertelsen, 1983). However, the family is still based almost solely on metamorphosed adolescent females. Only one sexually mature female, one metamorphosed male, and two larvae are known. Differences in the morphology of the illicium and its supporting pterygiophore, various internal osteological features of the cranium, and length of the dermal spinules that cover the skin of the head and body are diagnostic at the generic level, but illicium length and escal morphology are the only diagnostic characters at the specific level. Consequently specimens with a missing or damaged illicium are impossible to identify fully.

The following account was prompted by the discovery of four specimens of *Bufoceratias* that do not conform to the genus as presently diagnosed. One of these specimens was recognized by Uwate (1979) as unique and probably new but set aside and labeled "*Phrynichthys* sp." pending the collection of additional specimens. The other three specimens were recently collected off the east coast of Taiwan.

Materials and Methods

Standard length (SL) was used throughout. Measurements were taken to the nearest 0.5 mm, on the left side whenever possible. The illicium is the first dorsal-fin spine that bears the esca. The esca (or escal bulb, with escal appendages and filaments excluded) is the distal swelling of the illicium that contains the bacteria-mediated light organ (photophore). Illicium length is the distance from the point of emergence of the illicium from the dorsal surface of the body to the distal surface of the escal bulb, excluding escal appendages and filaments. Esca length is the distance from the base of the escal bulb to the tip of the longest escal filament. The distance between the insertion of the illicium and the symphysial cartilage is measured from the ventral surface of the symphysial cartilage of the upper jaw to the point of emergence of the illicium. Tooth fragments, and sockets indicating missing teeth, were included in jaw- and vomerine-tooth counts. All tooth counts are the sum of both left and right sides. To ensure accurate fin-ray counts, skin was removed from the pectoral fins, and incisions made to reveal the rays of the dorsal and anal fins. Caudal-fin rays are numbered from dorsalmost to ventralmost. Terminology used to describe the various parts of the angling apparatus follows Bradbury (1967); that used in describing developmental stages follows Bertelsen (1951). Symbolic codes for institutions are those provided by Leviton et al. (1985) except for the following: ARIK, Atlantic Research Institute for Sea Fisheries and Oceanography, Kaliningrad, Russia; ASIZP, Institute of Zoology, Academia Sinica, Taipei, Taiwan; CAFS, East China Sea Fisheries Research Institute, Chinese Academy of Fisheries Science, Shanghai; IIPB, Instituto de Investigaciones Pesquéras de Barcelona, Spain; SAIAB, South African Institute of Aquatic Biodiversity, Grahamstown (formerly the J. L. B. Smith Institute of Ichthyology); ZIN, Zoological Institute, Russian Academy of Sciences, St. Petersburg.

Systematics

Genus *Bufoceratias* Whitley, 1931

Females:

Phrynichthys Pietschmann, 1926:88 (type species *Phrynichthys wedli* Pietschmann, 1926, by monotypy). Golvan, 1962:173 (name replaced by *Bufoceratias* following Whitley, 1931). Eschmeyer, 1990:313 (*Phrynichthys* "incorrectly treated as valid," following Whitley, 1931, and Golvan, 1962).

Paroneirodes Norman, 1930:356, fig. 46 (in part; based on misidentification; type species *Paroneirodes glomerosus* Alcock, 1890, by monotypy).

Bufoceratias Whitley, 1931:334 (replacement name for *Phrynichthys* Pietschmann, 1926, preoccupied by *Phrynichthys* Agassiz, 1846, a replacement name for *Bufichthys* Swainson, 1839, a junior synonym of *Synanceia* Bloch and Schneider, 1801; therefore taking the same type species *Phrynichthys wedli* Pietschmann, 1926). Golvan, 1962:173 (replacement name for *Phrynichthys* following Whitley, 1931). Eschmeyer, 1990:68 (valid after Whitley, 1931). Anderson and Leslie, 2001:10 (valid after Whitley, 1931; diagnosis).

Males and larvae unknown:

Diagnosis.—Females of the genus *Bufoceratias* are distinguished from those of *Diceratias* (the only other known genus of the family) in having the following character states: length of illicium 25–225% SL (vs 27–47% SL); anterior tip of pterygiophore of illicium concealed beneath skin (vs exposed); illicium emerging from dorsal surface of head at rear of skull, distance from point of emergence to symphysis of upper jaw 29–61% SL (vs emerging from snout, distance from emergence to symphysis 7–15% SL); anterior margin of supraethmoid forming an angle of approximately 65–74 degrees with horizontal plane of cranium (vs 52 degrees; Uwate, 1979: 132, figs. 2–3); illicial trough shallow (vs illicial trough deep; Uwate, 1979:132, figs. 5–6); dermal spinules minute, length 90–110 μm (vs large, length 230–380 μm).

Description.—Metamorphosed females with body short, globular, depth approximately 50% SL; mouth large, cleft extending past eye, opening oblique; oral valve well developed, lining inside of both upper and lower jaws; two nostrils on each side at end of a single short tube; epibranchial I free from wall of pharynx; epibranchials I-IV closely bound together; proximal two-thirds of ceratobranchial I bound to wall of pharynx, distal one-third free; epibranchial IV and ceratobranchial IV bound to wall of pharynx, no opening behind fourth arch; gill filaments present on proximal tips of epibranchials II-IV, on proximal tip of ceratobranchial I, full length of ceratobranchials II and III, and about distal three-quarters of ceratobranchial IV; pseudobranch absent; numerous, small, rounded, darkly pigmented papillae on head and body associated with acoustico-lateralis system, each with an unpigmented distal tip (Regan and Trewavas, 1932; Bertelsen and Pietsch, 1998), pattern of placement as described for other ceratioids (e.g., Pietsch, 1972a, 1974); pyloric caecae absent.

Length of illicium of females highly variable, 25–225% SL; posterior end of pterygiophore of illicium concealed beneath skin of head; second cephalic spine (second dorsal-fin spine) with a distal light organ, emerging from dorsal surface of head just behind base of illicium, tending to sink beneath skin of head with age, but remaining connected to the surface through a small pore; lumen of escal bulb connected to outside by a pore located on posterior margin of base of terminal escal papilla; internal pigment of escal lumen visible in lateral view; basal half of escal bulb usually covered with dark pigment.

Females with dorsal-fin rays 5–6; anal-fin rays 4; pectoral-fin rays 13–14; pelvic fins absent; caudal-fin rays 9 (1 unbranched, 6 branched, 2 unbranched); upper and lower jaws of females with numerous, slender, recurved and depressible teeth, arranged in overlapping sets (as described for other ceratioids; e.g., Pietsch, 1972b); number of teeth in lower jaw 15–48, in upper jaw 12–65; vomerine teeth 4–15; skin everywhere covered with tiny close-set dermal spinules; dark brown to black over entire surface of head, body, fins (except for distal portion of escal bulb), and oral cavity.

Key to Metamorphosed Females of Species of the Genus *Bufoceratias*

1A. Illicium short, 25–40% SL; esca large, with numerous, long slender filaments (Figs. 1, 3A) ..... *Bufoceratias shaoi* n. sp. Four known specimens, 55–101 mm, Western Indian and Western Pacific oceans

1B. Illicium long, 83–225% SL; esca small, with or without short filaments (Figs. 2, 3B, 4) 2

2A. Esca with a low terminal papilla, becoming elongate by 60 mm SL; anterior, posterior, and lateral escal appendages present (Figs. 2, 3B) ... *Bufoceratias wedli* (Pietschmann, 1926) Sixty-nine known specimens, 19–178 mm, Atlantic Ocean

2B. Esca with a small rounded, sometimes pointed terminal papilla; anterior, posterior, and lateral escal appendages absent (Fig. 4) ..... *Bufoceratias thele* (Uwate, 1979) Eleven known specimens, 22–162 mm, Western Pacific Ocean

Bufoceratias shaoi n. sp.
Figures 1, 3A, 5; Table 1

Females:

Phrynichthys sp.: Uwate, 1979:143, fig. 21 (unidentified specimen, MNHN 1977–304, unique among known material of the genus). Machida and Yamakawa, 1990:63 (after Uwa-

Fig. 1. *Bufoceratias shaoi* n. sp., holotype, ASIZP 61796, 101 mm. Digital photograph by Ho Hsuan-ching.

te, 1979; thought to be *B. wedli* with regenerated illicial apparatus).

Males and larvae unknown:

Material.—Four metamorphosed females, 55–101 mm: Holotype: ASIZP 61796, 101 mm, off northeast coast of Taiwan, 24°25–50′N, 122°00–10′E, bottom trawl, 0–800 m, 1999. Paratypes: ASIZP 59952, 2 (56–75 mm), off northeast coast of Taiwan, 24°55′N, 122°04′E, bottom trawl, 0–650 m, 20 March 1998; MNHN 1977–304, 55 mm, Mozambique Channel, 17°36′–22°25′S, 42°59′–43°56.5′E, 0–1200 m.

Diagnosis.—Metamorphosed females of *B. shaoi* differ from those of *B. wedli* and *B. thele* in having a considerably shorter illicium (25–40% SL vs 83–225% SL) and a much larger and more complex esca (Figs. 1, 3A; Table 1).

Description.—Esca with an elongate, unpigmented terminal papilla, cylindrical and truncated in 55-mm paratype (MNHN 1977–304), gradually tapering to a point in remaining specimens; escal pore situated at postero-basal margin of terminal papilla; anterior escal appendage divided into several secondary branches, each branch bearing numerous slender filaments; a pair of slender filaments emerging from escal bulb adjacent to origin of anterior escal appendage (perhaps a basal bifurcation of the anterolateral appendages); a pair of short unbranched anterolateral appendages; a pair of lateral escal appendages, each divided into four or five secondary branches, each bearing numerous long, slender filaments; increased branching and elongation of appendages and filaments with increasing size of specimens; length from base of escal bulb to tip of longest filaments 23–48% SL; proximal parts of all appendages and filaments lightly pigmented, distal ends unpigmented; number of teeth in lower jaw 25–30, in upper jaw 34–42; vomerine teeth 8–11; dorsal-fin rays 5–6; anal-fin rays 4; pectoral-fin rays 13–14 (Table 1).

Etymology.—*Bufoceratias shaoi* is named in honor of Dr. Shao Kwang-Tsao, Research Fellow of the Institute of Zoology, Academic Sinica, Taiwan, Republic of China, in recognition of his many contributions to fishery science and ichthyology of Taiwan.

Distribution.—The holotype and two paratypes of *B. shaoi* were collected near Guei-san Island off the northeast coast of Taiwan in bottom trawls fished at depths of 800 m (ASIZP 61796) and 500–650 m (ASIZP 59952), respectively. The fourth known specimen (MNHN 1977–304) was captured in the Mozambique Channel,

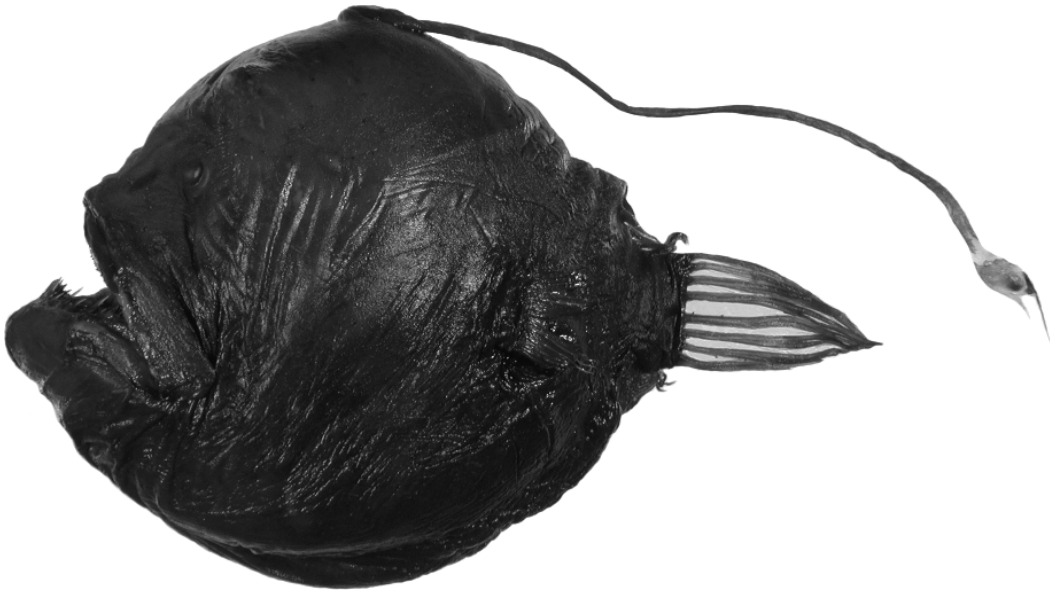

Fig. 2. *Bufoceratias wedli* (Pietschmann), MNHN 1987–993, 89 mm. Digital photograph by Ho Hsuan-ching.

Western Indian Ocean, in an open trawl fished at a maximum depth of 1200 m (Fig. 5).

Comments.—A single specimen of the new species described here was originally recognized as unique but left unnamed some 25 years ago by Uwate (1979) when he brought together all known diceratiids in collections around the world for his revision of the family. The unusual specimen (MNHN 1977–304), the first representative of the family from the Western Indian Ocean, captured in the Mozambique Channel, was easily recognized as a diceratiid by the presence of a distinct second cephalic spine bearing a distal light organ. The posterior insertion of the illicium (emerging from the back at the rear of the skull) clearly indicated that it belonged to the genus *Bufoceratias* (then recognized as *Phrynichthys*). The illicium, however, was considerably shorter than that of all other known specimens of the genus (44% SL vs 83–225% SL), being similar in length to that of *Diceratias* (26–

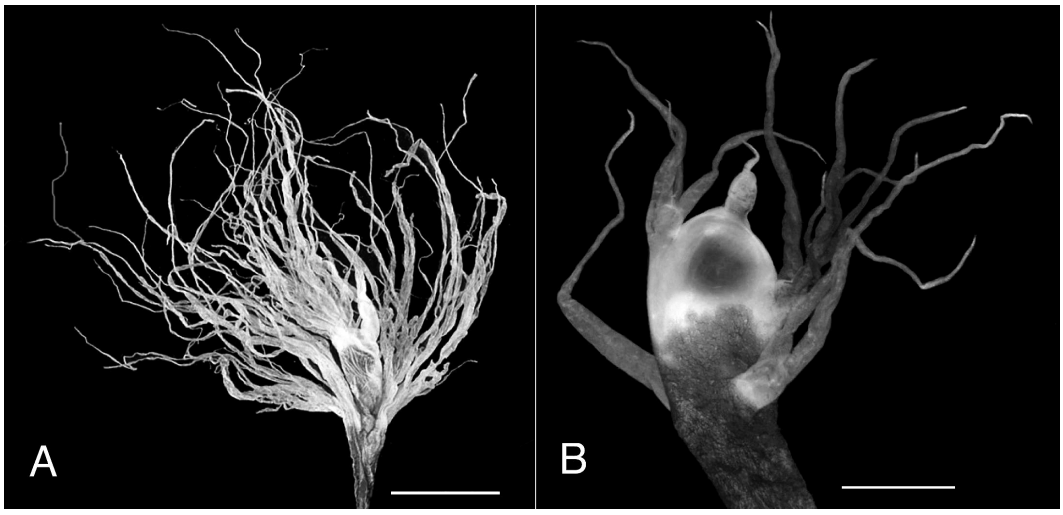

Fig. 3. Escae of species of *Bufoceratias*: (A) *Bufoceratias shaoi* n. sp., holotype, ASIZP 61796, 101 mm (bar = 10 mm); (B) *Bufoceratias wedli* (Pietschmann), MNHN 1987–962, 99 mm (bar = 5 mm). Digital photographs by Ho Hsuan-ching.

TABLE 1. COUNTS, AND MEASUREMENTS EXPRESSED AS PERCENTAGES OF STANDARD LENGTH, OF TYPE MATERIAL OF *Bufoceratias shaoi*.

	MNHN 1977-304 Paratype	ASIZP 59952 Paratype	ASIZP 59952 Paratype	ASIZP 61796 Holotype
Standard length (mm)	55	56	75	101
Head length	48.2	39.6	39.6	37.5
Head depth	60.0	59.1	51.6	49.9
Head width	38.5	38.0	30.8	30.9
Illicium length	36.7	28.6	32.0	25.6
Esca length	22.9	32.1	33.9	48.1
Premaxilla length	44.9	41.1	39.6	33.6
Lower jaw length	51.3	50.0	44.1	42.2
Upper jaw teeth	39	42	34	34
Lower jaw teeth	28	29	25	30
Vomerine teeth	10	11	9+	8
Dorsal-fin rays	6	5	5	5
Anal-fin rays	4	4	4	4
Pectoral-fin rays	14–14	13–13	13–13	13–14

47% SL). The esca differed dramatically from that of all other known diceratiids as well (Uwate, 1979:fig. 21): instead of paired lateral appendages, it had paired anteroventral appendages, each with a distinct trifurcation, each fork branching further to form many secondary filaments; a branched anterior appendage was present, along with an unpigmented elongate cylindrical terminal papilla. Significantly different from all other examined diceratiids but most closely resembling *B. wedli*, Uwate (1979) speculated that the specimen was either a damaged individual of the latter species (with a broken illicium and regenerated esca; Machida and Yamakawa, 1990) or the sole representative of an undescribed species. Unable to decide at the time, Uwate (1979) set it aside to await additional material. The discovery by one of us (HH-c) of three additional specimens collected in bottom trawls by commercial shrimp fishers off the northeast coast of Taiwan has made the present description possible.

Bufoceratias wedli (Pietschmann, 1926)
Figures 2, 3, 5

Females:

Phrynichthys wedli Pietschmann, 1926:88 (original description, single specimen). Pietschmann, 1930:419, fig. (description after Pietschmann, 1926; figured).

Paroneirodes glomerosus: Norman, 1930:356, fig. 46 (in part; misidentification of additional specimen, BMNH 1930.1.12.1101, South Atlantic, specimen referred to *Phrynichthys wedli* by Uwate, 1979).

Paroneirodes wedli: Regan and Trewavas, 1932:58 (new combination; description after Pietschmann, 1926).

Diceratias glomerosus: Fowler, 1936:1344, fig. 563 (new combination; misidentification; figure after Norman, 1930).

Paroneirodes glomerulosus: Maul, 1962:12, figs. 4–6 (in part; misidentification of two specimens referred to *P. wedli* by Uwate, 1979; erroneous spelling of specific name after Regan, 1926; eastern Atlantic).

Paraneirodes wedli: Maurin et al., 1970:21 (additional specimen, eastern Atlantic; erroneous spelling of generic name).

Diceratias wedli: Karrer, 1973:246, figs. 28, 29 (new combination; description of four additional specimens, ZMB 22194, South Atlantic).

Bufoceratias wedli: Anderson and Leslie, 2001:10, figs. 8–9 (new combination, additional material, Namibia).

Males and larvae unknown:

Material.—Sixty-nine metamorphosed females, 19–178 mm: Holotype NMW 3524, 35 mm, off Madeira, Steindachner collection, 1865. Additional material: ARIK, 3 (32–49 mm; Trunov, 1974); BMNH, 1 (19 mm; Norman, 1930); FMNH, 6 (27–38.5 mm; Grey, 1959); HUMZ, 3 (56–142 mm); IFAN, 2 (25–30.5 mm; Maul, 1962); IIPB, 5 (30–134 mm; Lloris, 1981); IOAN, 10 (29–178 mm); LACM, 3 (44–82 mm); MB, 1 (70 mm; Costa, 1980); MNHN, 7 (25–99 mm); NSMT-P, 1 (35 mm; Fujii, 1983); SAIAB, 5 (29–117 mm); SAM, 3 (69–117 mm; Anderson and Leslie, 2001); UF, 9 (26–91 mm); USNM, 1 (140 mm); UW, 1 (70 mm); ZIN, 1 (132 mm); ZMB, 4 (78–117 mm; Karrer, 1973); ZMUC, 2 (94–117 mm).

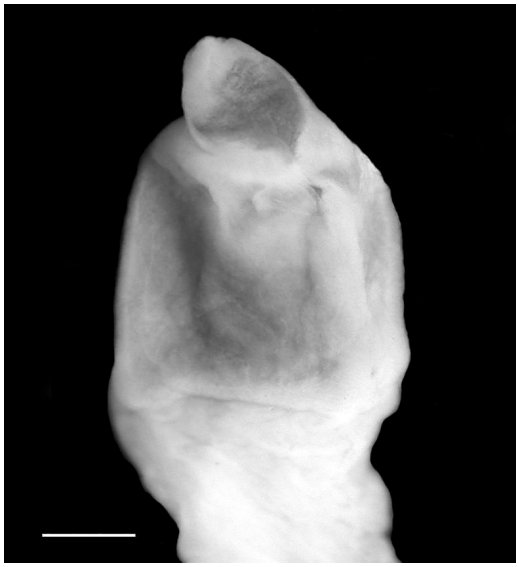

Fig. 4. Esca of *Bufoceratias thele* (Uwate), HUMZ 146798, 41 mm (bar = 1 mm). Digital photograph by Mitsuomi Shimazaki.

Diagnosis.—Metamorphosed females of *B. wedli* differ from those of *B. shaoi* in having a much smaller esca and a longer illicium (83–225% SL vs 26–40% SL) and from those of *B. thele* in having distinct anterior, posterior, and lateral escal appendages (Figs. 2, 3B).

Description.—Esca with a small terminal papilla, rounded in smaller specimens, becoming elongate and cylindrical by 60 mm SL; escal pore at postero-basal margin of terminal papilla; a pair of filamentous anterior escal appendages developing by 40 mm SL, remaining separate at base; a single bifurcated filamentous posterior escal appendage; a pair of lateral escal appendages (usually branched) developing by 40 mm SL; increased branching and elongation evident in all escal appendages by 50 mm SL (Uwate, 1979: fig. 18); number of teeth in lower jaw 16–44, in upper jaw 21–65; vomerine teeth 7–15; dorsal-fin rays 5–6; anal-fin rays 4; pectoral-fin rays 13–14. Additional description as given for the genus.

Distribution.—As concluded by Uwate (1979:fig. 20), *B. wedli* is restricted to the Atlantic Ocean (Machida and Yamakawa's, 1990, report of a specimen from the East China Sea, is a misidentification; see below). In the western Atlantic it is known from the Gulf of Mexico and Caribbean Sea, and southward to coastal waters off Surinam. In the eastern Atlantic it ranges from off Portugal to coastal waters of Namibia, as far south as about 24°S (Fig. 5). All of the known material was collected with open trawls: four individuals (43–178 mm SL) in nets fished at maximum depths of 1200–1750 m, the remaining specimens by nets fished at maximum depths of 400–1000 m. Several specimens were taken in bottom trawls (see Distribution, below).

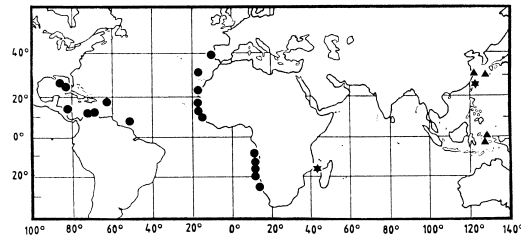

Fig. 5. Distribution of species of *Bufoceratias*: *Bufoceratias shaoi* n. sp., Taiwan and Mozambique Channel; *Bufoceratias wedli* (Pietschmann), Atlantic Ocean; *Bufoceratias thele* (Uwate), Western Pacific. A single symbol may represent more than one capture.

Bufoceratias thele (Uwate, 1979)
Figures 4, 5

Females:

Phrynichthys thele Uwate, 1979:142, figs. 19, 20 (original description, two specimens). Ni, 1988:327, fig. 256 (two additional specimens, East China Sea).

Phrynichthys sp.: Yamakawa, 1984:289, 385, fig. 204 (additional specimen, BSKU 29877, Okinawa Trough).

Phrynichthys wedli: Machida and Yamakawa, 1990:60, figs. 1–3 (misidentification, single specimen, BSKU 29877, Okinawa Trough, East China Sea).

Males and larvae unknown:

Material.—Eleven metamorphosed females, 22–162 mm: Holotype, LACM 36077–1, 32 mm, *Alpha Helix* station 155, Halmahara Sea, 0°38.6′S, 129°05.6′E, 680–850 m, 1210–1400 h, 22 May 1975. Paratype, LACM 36076–1, 22 mm, *Alpha Helix* station 26, Ceram Sea, 2°46.0′S, 127°53.7′E, 0–1500 m, 0150–0800 h, 31 March 1975. Additional material: BSKU, 1 (72 mm; Yamakawa, 1984); CAFS, 2 (115–162 mm; Ni, 1988); HUMZ, 6 (36–103 mm).

Diagnosis.—Metamorphosed females of *B. thele* differ from those of *B. shaoi* in having a much smaller esca and a longer illicium (112–143% SL vs 26–40% SL), and from those of *B. wedli* in lacking escal appendages (Uwate, 1979:fig. 19).

Description.—Esca with a small rounded, sometimes pointed terminal papilla arising from distal surface; escal pore at postero-basal margin of terminal papilla; anterior, posterior, and lateral escal appendages absent (Uwate, 1979:fig. 19); number of teeth in lower jaw 15–48, in upper jaw 12–49; vomerine teeth 4–10; dorsal-fin rays 5–6; anal-fin rays 4; pectoral-fin rays 13–14. Additional description as given for the genus.

Distribution.—*Bufoceratias thele* is known only from the Ceram, Halmahera, and South and East China seas (Fig. 5). The holotype was collected between 680 and 850 m, the paratype somewhere between the surface and 1500 m, the BSKU specimen between 780–810 m (Machida and Yamakawa, 1990), and the two specimens reported by Ni (1988) between the surface and 950 m. The six HUMZ specimens were all taken in bottom trawls at depths of 996–999 m (see below).

Distribution

Like most ceratioid species for which sufficient material is known (e.g., *Oneirodes*; Pietsch, 1974), the distribution of diceratiids follows the contours of high organic productivity. The family is represented in all three major oceans of the world in a narrow belt between 40°N and 25°S (Uwate, 1979:fig. 20; Fig. 5). All known specimens have been collected near land, on the continental slope or shelf. None have been collected in the central gyres of any ocean. Another area conspicuously lacking diceratiids is the eastern Pacific, with no member of the family ever having been taken east of the Hawaiian Islands where a single specimen of *D. pileatus* was reported by Pietsch and Randall (1987). All other Pacific records are from the extreme western margin of this ocean: an individual of *Diceratias bispinosus* from the Philippines and additional records in the nearby equatorial waters of eastern Indonesia and New Guinea (Paxton and Lavenberg, 1973), the holotype of *D. trilobus* from off Japan, and all known material of *B. thele*. Based largely on collections made by the R/V Dana in the 1920s, Regan and Trewavas (1932) and Bertelsen (1951) described the eastern Pacific as especially rich in species and individuals of ceratioids. Although the apparent absence of diceratiids in this region may be explained in part by inadequate sampling, it seems more likely that they are not there, but why this may be so is unknown.

On the basis of an analysis of all known material, Uwate (1979:fig. 20) was able to show that the two diceratiid genera are geographically sympatric in the tropical Atlantic and western Pacific Oceans. He concluded further that the species within each genus are allopatric: *B. wedli* and *D. pileatus* are sympatric in the Atlantic, whereas *B. thele* and *D. bispinosus* are sympatric in the western Pacific. Realizing in the Atlantic that *B. wedli* has a filamentous esca whereas that of *D. pileatus* is relatively unadorned, and in the western Pacific, *D. bispinosus* has a filamentous esca, whereas that of *B. thele* is simple, Uwate (1979: 143) speculated that these character differences may function to reduce interspecific competition, perhaps important in sharing food resources as well as in attracting conspecific mates. Unfortunately, this nice story has been contradicted by Pietsch and Randall's (1987) discovery of a specimen of *D. pileatus* from Hawaii. It was thought also that Machida and Yamakawa's (1990) report of a specimen of *B. wedli* from the Okinawa Trough in the East China Sea was in opposition to Uwate's hypothesis, but recent examination of their specimen shows it to be a good example of *B. thele* (organic debris of some kind wound tightly around the base of the esca had been mistaken for escal appendages; Machida and Yamakawa, 1990:fig. 3).

Most diceratiids have been collected by open midwater trawls, which indicate a broad vertical range for metamorphosed females, between 400 and 2300 m (Uwate, 1979). However, according to Grey (1959), at least three adult specimens of *Diceratias* were caught in gear designed for bottom-fishing. Subsequently, Trunov (1974) reported three specimens of *B. wedli* from bottom trawls, Anderson and Leslie (2001) reported a 117-mm specimen of *B. wedli* (SAM 29918) taken in a crab trap at 800 m, seven specimens of *Bufoceratias* in the HUMZ collections (two *B. wedli* and five *B. thele*) were taken off the bottom, and now three of the four known specimens of *B. shaoi* were collected in bottom trawls. An analysis of 51 diceratiid stomachs (25 empty) reported by Uwate (1979) revealed a variety of partially digested food items including fish and fish scales, coelenterates, various crustaceans, polychaetes, gastropods, and sea urchins (test and spines). Remains of polychaetes, gastropods, and especially sea urchins indicate benthic feeding. Thus, in contrast to the midwater life style generally assumed for most ceratioids (known exceptions include the benthic genus *Thaumatichthys* and the recently discovered upside-down, bottom-swimming individuals of *Gigantactis*; Bertelsen and Struhsaker, 1977; Moore, 2002), it seems evident that at least some diceratiids, especially larger individuals, are at least partly associated with the bottom (Bertelsen, 1990; Anderson and Leslie, 2001).

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