



ISSN: (Print) (Online) Journal homepage: <https://www.tandfonline.com/loi/ghbi20>

A Neogene bristlemouth of the genus *Cyclothone* (Stomiiformes: Gonostomatidae) from South Korea

Gi-Soo Nam & Mikhail V. Nazarkin

To cite this article: Gi-Soo Nam & Mikhail V. Nazarkin (2021) A Neogene bristlemouth of the genus *Cyclothone* (Stomiiformes: Gonostomatidae) from South Korea, *Historical Biology*, 33:11, 2639-2645, DOI: [10.1080/08912963.2020.1820000](https://doi.org/10.1080/08912963.2020.1820000)

To link to this article: <https://doi.org/10.1080/08912963.2020.1820000>



Published online: 15 Sep 2020.



Submit your article to this journal [↗](#)



Article views: 84



View related articles [↗](#)



View Crossmark data [↗](#)

ARTICLE



A Neogene bristlemouth of the genus *Cyclothone* (Stomiiformes: Gonostomatidae) from South Korea

Gi-Soo Nam^a and Mikhail V. Nazarkin^b

^aDepartment of Science Education, Gongju National University of Education, Gongju-si, Korea; ^bZoological Institute, Russian Academy of Sciences, St. Petersburg, Russia

ABSTRACT

A fossil specimen of bristlemouth fish of the genus *Cyclothone* is reported for the first time from the marine deposits of the middle Miocene Duho Formation, South Korea, and described as new species *Cyclothone duhoensis*, sp. nov. This is the second stomiiform fish discovered there. It represents the oldest nominal species of its genus, and the third and southernmost record of fossil bristlemouth from the ancient Eastern Sea (Sea of Japan) basin after the findings in the Sakhalin (Russia) and Honshu (Japan) islands. The new Miocene bristlemouth is very similar to the Recent congeners. Nevertheless, it can be separated from them by the presence of more than 15 photophores in the AC series, of which at least four photophores are behind the anal-fin base, and by a peculiar upper jaw dentition. The biological features of the Recent bristlemouths along with this unique finding hint at shallow-water conditions during the Duho Formation sedimentation.

ARTICLE HISTORY

Received 23 July 2020
Accepted 2 September 2020

KEYWORDS

Bristlemouth; *Cyclothone*; new species; Stomiiformes; Serravallian; South Korea

Introduction

The bristlemouths of the gonostomatid genus *Cyclothone* are among the most abundant fishes in the modern oceans, and, arguably, the numerically dominant vertebrate genus on the Earth (Parin 1988; Nelson 2006). The standard length of these fishes does not exceed 75 mm. They are comparatively deep-sea inhabitants of the meso- and bathypelagic water masses. The bulk of the populations of *Cyclothone* species live below 300 m, although there are records from shallower waters (Grey 1964; Mukhacheva 1974). They are widely distributed from the tropical to subarctic waters of all oceans (Grey 1964; Mukhacheva 1964, 1974; Badcock 1984; Miya and Nishida 1996). *Cyclothone* species are mass consumers of plankton, and, in turn, serve as prey for many predatory fishes. Bristlemouths are members of the scattering layers community; however, in contrast to the majority of other fishes of this community, they are not involved in vertical daily migrations (Mukhacheva 1967; Badcock 1984; Parin 1988).

In the modern fauna, 13 species of this genus are distinguished (Grey 1964; Mukhacheva 1974; Badcock 1984; Miya and Nishida 1996). In general, their basic morphological pattern is very similar, and comparatively simple due to the reduction of some osteological structures (Miya and Nishida 1996). There are several records of fossil *Cyclothone* species that indicate these fishes acquired their main morphological characters prior to the middle Miocene and were widespread already at this time. The earliest fossil skeletal remains of bristlemouths are known from the Pacific basin and include *Cyclothone* sp. from the middle Miocene of Honshu Island, Japan (Ohe 1993; Yabumoto and Uyeno 1994), *C. mukhachevae* from the middle-late Miocene of Sakhalin Island, Russia (Nazarkin 2015), and *C. solitudinis* and *C. cf. solitudinis* from the late Miocene of California, U.S.A. (Jordan 1907; David 1943; Fierstine et al. 2012). Another centre of the fossil bristlemouths diversity is the Mediterranean basin: *C. gaudanti* is known from the late Miocene deposits of Crete, Greece (Gaudant 2004; Prikryl and

Carnevale 2017), whereas *Cyclothone* sp. was recorded in the Pliocene of Italy (Sorbini 1988; Landini and Sorbini 1993). Several forms of *Cyclothone* were described from the Plio-Pleistocene sediments of Italy, among which were also representatives of two Recent species (Landini and Menesini 1978, 1986).

In this paper, we report a new fossil record of *Cyclothone*, which came from the beds of the middle Miocene Duho Formation of South Korea. This is the second member of the order Stomiiformes to come from the beds of the Duho Formation after the previously described lightfish *Vinciguerria orientalis* (Nam et al. 2019). The morphological characters of this form allow its separation from congeners, and, consequently, we allocate this bristlemouth to a new species. The age of this finding makes it the oldest nominal species of its genus. This is the third, and southern-most fossil bristlemouths from the Neogene Sea of Japan (Eastern Sea) basin. This finding is proof of the distribution of *Cyclothone* spp. throughout this ancient sea and shows some diversity degree of the Miocene representatives of the genus.

The Duho Formation of South Korea is distributed in the south-eastern part of the Korean Peninsula in the vicinity of the Pohang City (Yun 1986). It is well-known due to the rich association of fossils, which include both terrestrial (plants and insects), and marine (echinoderms, crustaceans, molluscs) organisms (Chun 1982; Yun 1985; Seong et al. 2009). In addition, the diverse community of marine fishes, especially of teleosts, discovered from these beds provides important information for understanding the features of the Neogene fish fauna of the southern part of the Eastern Sea. Among the fish fossils collected until now from the layers of the Duho Formation, most belong to the mid-water pelagic inhabitants such as myctophiforms and stomiiforms. The abundance of deep-sea fishes on the one hand conflicts on the other hand with the presence of the more shallow-water fishes and invertebrates in the same layers (Yun 1985; Kim and Lee 2011). The age of these fossiliferous layers is middle Miocene as concluded from

microfossil (Coccolithaceae and Radiolarian) faunal analysis (You et al. 1986; Bak et al. 1996).

Materials and methods

The materials studied include the sole, nearly complete fish skeleton collected by the first author from the middle Miocene Duho Formation, and stored in the collections of the Gongju National University of Education (GNUE). The matrix was removed from the fossil by needles under a stereomicroscope. The measurements were made with dial calipers to the nearest 0.1 mm. The osteology of Recent species was studied by radiographed and cleared and stained specimens from the collections of Zoological Institute (ZIN). The comparative material is the same as in Nazarkin (2015). The nomenclature of photophores follows Morrow (1964).

Institutional abbreviations

GNUE, Gongju National University of Education, Gongju City, South Korea; ZIN, Zoological Institute RAS, St.-Petersburg, Russia.

Other abbreviations

SL, standard length.

Systematic paleontology

Order STOMIIFORMES *sensu* Harold and Weitzman, 1996
Suborder Gonostomatoidei *sensu* Nelson et al., 2016
Infraorder Gonostomata *sensu* Harold, 1998
Family Gonostomatidae Gill, 1893
Genus *Cyclothone* Goode et Bean, 1883

Cyclothone duhoensis, sp. nov. (Figs. 1 and 2).

Etymology

Species name derived from the Duho Formation.

Holotype. GNUE 32080, the complete skeleton with the head region damaged, approximately 40.0 mm SL.

Type locality. The outcrop in the road cut 7 km northeast from the Centre of Pohang City, near the Hwanho-dong, Buk-gu, Pohang City, South Korea.

Type horizon. Duho Formation, middle Miocene (Serravallian).

Diagnosis

A species of *Cyclothone* with a scaled body, gradual transition zone in the maxillary dentition, weakly expressed alternation of the posterior maxillary teeth, not less than 16 photophores of the AC series, and at least four photophores behind the anal fin base.

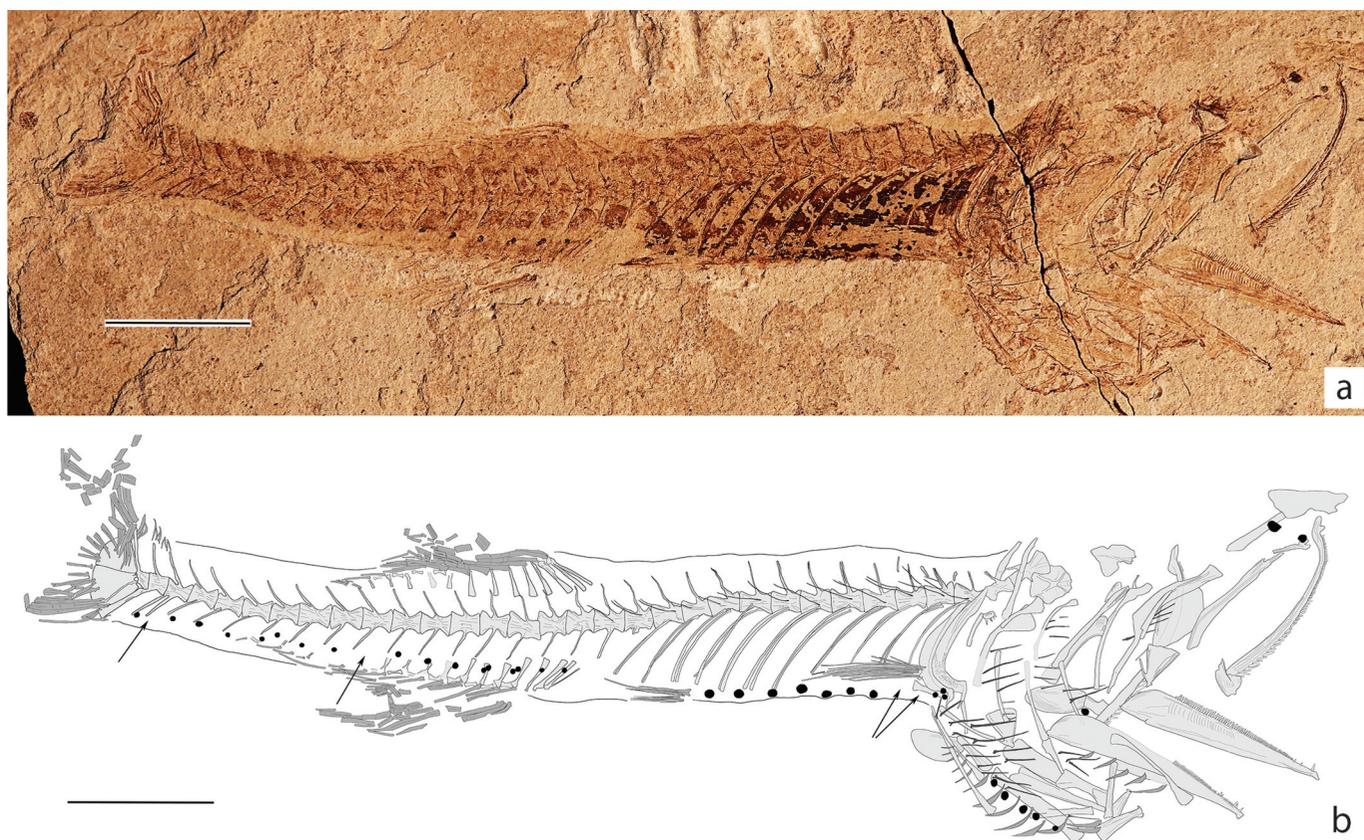


Figure 1. *Cyclothone duhoensis*, sp. nov. from the Duho Formation, holotype GNUE 32080. General view (a) and interpretative reconstruction (b) of the specimen. Arrows indicate the gaps in the photophore rows. Scale bar equals 5 mm.

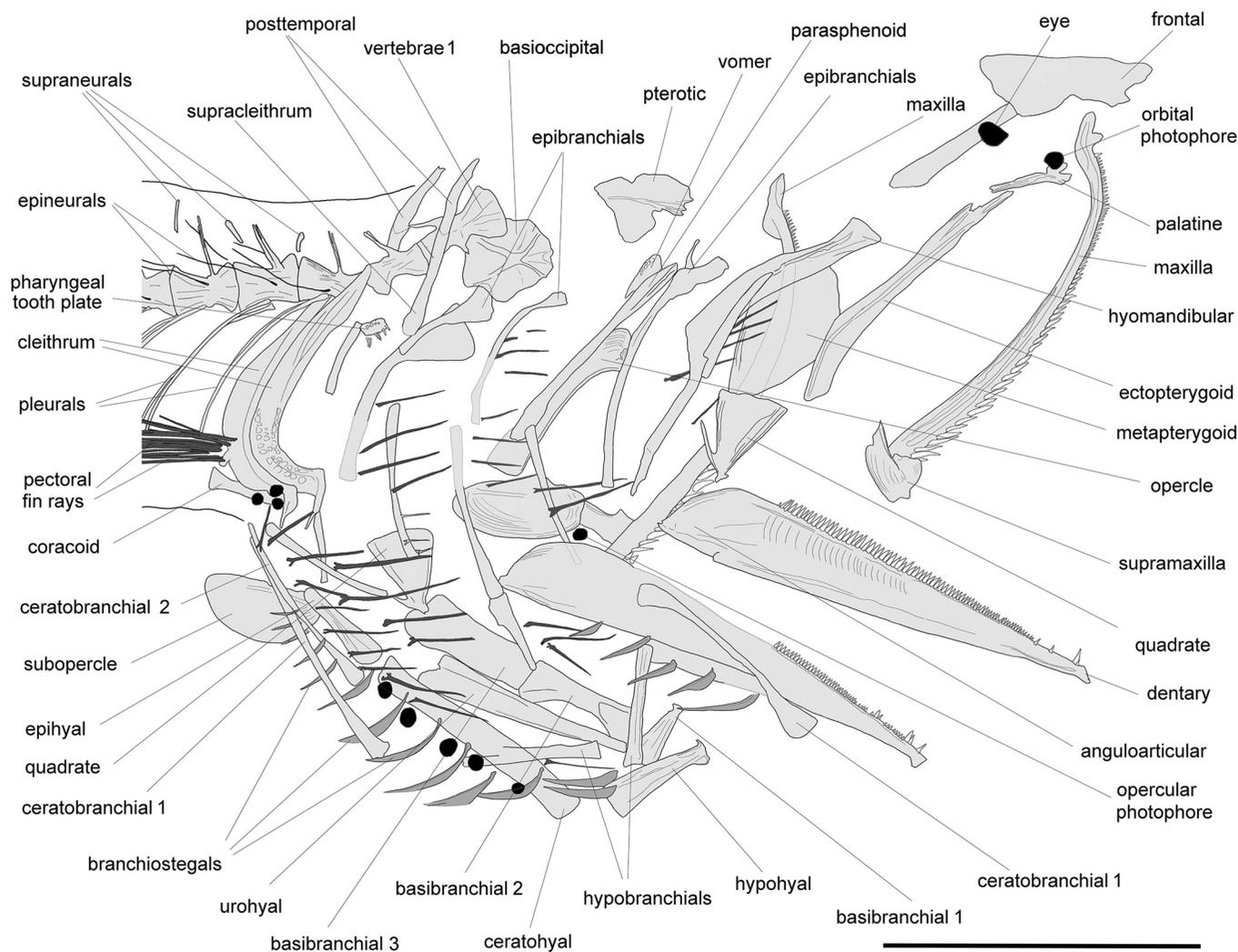


Figure 2. *Cyclothone duhoensis*, sp. nov. from the Duho Formation, holotype GNUE 32080. Outline drawing of the head region. Gill rakers, branchiostegals, and fin rays are darker. Scale bar equals 5 mm.

Description

The body is low and moderately elongated (Figure 1). Its depth at the level of the dorsal fin origin is slightly less than 12.0% SL, whereas the caudal peduncle is one-third less than this depth. The head skeleton is much crushed and shifted; consequently, the head length can be only very approximately estimated as a quarter of the SL. The mouth is wide and oblique. The eye is extremely small, about 0.9% SL, positioned dorsally in the anterior extremity of the head (Figure 2). The dorsal and anal fins are located approximately opposite to each other in the posterior body half. The pelvic fin base is well anterior to the beginning of the dorsal fin base. The pectoral fin base is immediately posterior to the head and close to the ventral body margin.

Most of the neurocranium bones in the specimen did not preserve or are not recognisable. The parasphenoid is thin and stria (Figure 2). The lateral part of the vomerine head bearing the row of 7 tooth alveoli is recognised near to the anterior extremity of the parasphenoid. The complete basioccipital is seen anterior to the first vertebral centrum. This bone has a roundish outline ventrally and an x-shaped crest bounding the otic capsules. The pterotic is almost the same size as the basioccipital and equipped with a longitudinal ridge. The frontal is twice larger, and a roughly

rectangular bone greatly shifted antero-dorsally from its natural position.

The jaws are long and thin, almost equal in length. The premaxilla is not preserved. The maxilla is long, thin, and upwardly curved anteriorly. Its ventral edge is convex and equipped with a row of 60 closely spaced teeth on almost all its length. The maxillary teeth are short and subequal (Harold 1998). The anterior nineteen maxillary teeth are very small, of the same size, and positioned at right angles to the edge of the maxilla. In the posterior 80% of the tooth row, the teeth become higher and gradually enlarged posteriorly so that the posteriormost teeth are more than eight times taller than the teeth in the anterior part of the maxilla. These posterior teeth are noticeably inclined forward, and make an acute angle with the bone's edge. There is no alternation of the short and long teeth in the maxillary row, but the width of some teeth is noticeably less than that of their neighbours (Figure 2). The supramaxilla is a small, oval bone with a sharp and short anterior outgrowth. The lower jaw is wedge-shaped. The coronoid process of the anguloarticular is wide and blunt; the mandible gradually tapers anteriorly from this process. The dentary bears an inner row of 73 small, densely spaced and slightly anteriorly inclined teeth throughout its dorsal edge. The tooth size gradually increases posteriorly. In the anterior extremity of the dentary, there is a short lateral tooth row, which contains at

least four high, caniniform teeth along with a few smaller ones. The lateral surface of the dentary has densely spaced sub-vertical wrinkles beneath the posterior half of the inner tooth row.

The opercle is sub-rectangular, laminar, thin and high, with a roundish antero-dorsal corner and a strong vertical ridge along its anterior edge. The subopercle is comparatively large, oval, and membranous. Other bones of the opercular series are not preserved.

The axis of the suspensorium is strongly inclined ventro-caudally. The hyomandibula is a bulky arched bone, not subdivided dorsally in to two articulation heads, and with a greatly reduced articular process. The quadrate is fan-shaped. The metapterygoid is a low, longitudinally elongated triangle. The ectapterygoid is a wide and very thin laminar bone, whose borders cannot be determined exactly. The mesopterygoid did not preserve. The palatine is short, with a roundish anterior head and a thin posterior part. There are no traces of palatine teeth.

The epiphyal is a flat, elongated bone. The ceratohyal is more than twice longer and comparatively wide. The hypohyal is elongated and trapezoid. At least 13 short, sabre-like branchiostegal rays of the right body side can be recognised. Of these, the anterior two are attached to the hypohyals, with five on both the ceratohyal and epiphyal, whereas one ray was, probably, associated with the cartilage between the latter two.

Several rod-shaped branchial bones are preserved in the head region of the specimen. Of these, comparatively high basibranchials 1–3, along with some thinner hypo-, cerato-, and epibranchials, can be recognised (Figure 2). The pharyngeal tooth plate with a dozen small teeth is seen under the second vertebra. No fewer than 37 long, needle-like gill rakers remain; most of them are in association with some branchial bones, but the number of rakers on specific gill arches cannot be determined.

There are 32 (14 + 18) moderately elongated, symmetrical vertebrae. The first vertebral centrum is slightly longer than subsequent ones and possesses a prominent ventral parapophysis. The neural arches are very short; those of the few anterior vertebrae are shorter than the corresponding vertebral centra. The neural arches become fused, forming short neural spines starting, apparently, from the 13th vertebra. The posterior abdominal centrum possesses a short parapophysis and lacks ribs. There are 11 pairs of pleural ribs attached to the vertebrae from the third to the penultimate. They are strong and long bones almost reaching the ventral body margin. Epineurals are present from the third to the 15th (first caudal) vertebra. They are thin, rod-like bones, slightly longer than the appropriate vertebral centrum. Epipleurals are absent. Three supraneurals are preserved in front of the neural arches of the 4th, 5th and 6th vertebrae (Figure 2).

The dorsal and anal fins are placed in the posterior body half, opposite each other. The bases of the anterior dorsal and anal fin rays are on the level of the third caudal vertebra. The anal fin base is noticeably longer than that of the dorsal fin – the posteriormost rays of these fins are placed on the level of the sixth and the ninth preural centra, respectively. Anterior pterygiophores of both fins are complex elements consisted of two rods fused distally. They are inserted behind the neural and haemal spines of the first caudal centrum. There are 13 proximal pterygiophores and 14 rays discernible in the dorsal fin. The anterior dorsal proximal pterygiophores are expanded proximally. Medial pterygiophores are seen starting from the eighth series; they are short and constricted in the middle. The distal elements of the pterygiophore series are not seen. The anterior dorsal fin ray is very short and supernumerary, as in Recent congeners. Some dorsal rays are definitely branched; the height of the longest of them is less than the length of the dorsal fin base. The structure of the anal fin is similar to that of the dorsal one. Seventeen rays and 14 proximal

pterygiophores are observed, and medial pterygiophores begin from the fourth series. The posterior anal fin pterygiophore inserts behind the haemal spine of the eighth preural centrum. Obviously, the pterygiophores should have been present in some empty interhaemal spaces above the anal fin rays, but they not preserved in the specimen. Taking that into account, the total number of anal fin rays can be estimated as 19–20 at least.

The pectoral fin is narrow. Its base is placed immediately behind the head closer to the ventral body margin than to the vertebral column. There are at least seven long pectoral rays, almost reaching midway between the pectoral and pelvic fin bases. The cleithrum is C-shaped, with a strong and sharp hook ventrally; its upper end reaches lateral to the vertebrae located above. The high, posteriorly expanded coracoid is underlies almost the whole ventral edge of the cleithrum. The supracleithrum and posttemporal are strait narrow bones; the border between them is indistinguishable. A postcleithrum is, apparently, absent. The pectoral radial did not preserve.

The base of the pelvic fin is on the vertical through the 12th vertebra. The pelvic fin consists of at least six comparatively short rays – the length of the longest ray is equal to the length of the three vertebral centra above it. The pelvic skeleton did not preserve.

The caudal fin is, apparently, deeply forked; it consists of 10 + 9 principal rays and, at least, six upper and three lower procurvent rays. The caudal fin skeleton structure is the same as in Recent congeners (Borodulina 1982; Harold 1998). There are two (upper and lower) large hypural plates, tightly attached to the urostylar centrum. A prominent ridge separates the parhypural from the lower hypural plate, but it is not clear whether the parhypural is fused with this plate or is autonomous from it. There is a narrow cleft between the urostyle and the epaxial hypural plate distally. Two roundish openings are observed proximally in the hypaxial plate: between the bases of the parhypural and hypural 1, and between those of hypurals 1 and 2. Epurals are absent. An uroneural is indiscernible. The second preural centrum has a long, fully developed neural spine; its haemal spine is expanded distally. The vertical spines of the second and third preural centra are slightly longer than the preceding spines. The third preural centrum abnormally has two haemal spines.

The body covered by large, roundish, cycloid scales. There are five scales in an oblique vertical row anterior to the beginning of the dorsal fin. A dark pigmentation is preserved throughout the body, but it is especially strong in the abdominal cavity. This apparently means that when alive the fish body was pigmented, but was coloured lighter than its peritoneum. There are small dark dots on the bases of the dorsal and anal fin rays.

The condition of the specimen allows recognising some photophores on its body and head. There is one orbital photophore ahead and slightly beneath the eye, a position that is connected with the palatine head, as in Recent species (Figure 2). One of the opercular photophores is seen beneath the opercle. Five branchial photophores are preserved between the branchiostegals associated with the ceratohyal. There are 10 elements that can be recognised in the IV series. Of them, three are anterior to the pectoral fin base. One of the latter is positioned above the row; probably, it belongs to the IV series of the opposite body side. Under the base of the pectoral fin there is a gap in the IV series, where two or three photophores could fit (Figure 1(b)). Thus, the IV series probably contained 11 to 13 elements. In the AC series, 15 photophores remain but, because there are obvious gaps between the seventh and eighth and between the 11th and 12th elements, the total number of photophores in this series was greater, probably, 16 or 17. At least four AC elements are placed posterior to the anal fin base.

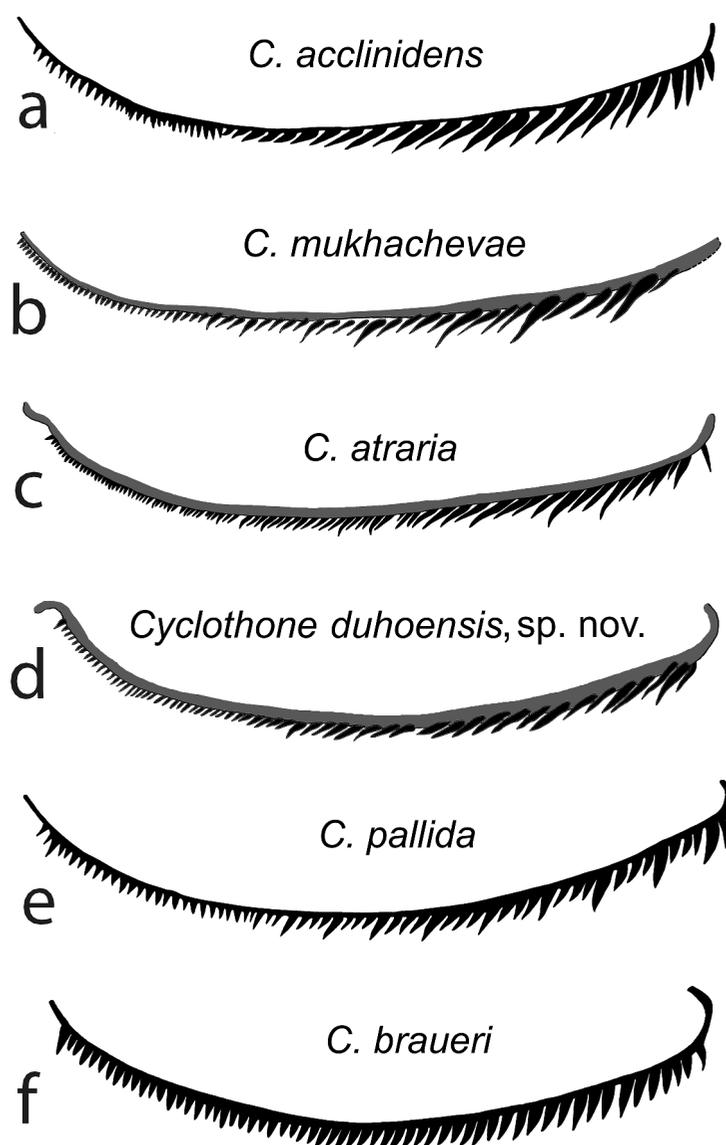


Figure 3. The maxillary dentition in some Recent and fossil bristlemouths. (a, e) redrawn from Kawaguchi (1971, p. 5, fig. 3); (b) specimen ZIN 55629; (c) specimen ZIN 49451; (f) redrawn from Grey (1964, p. 191, fig. 52). Bones are scaled to the same length. Scale bar omitted.

Measurements (in mm). Distance between the pectoral fin base and the posterior edge of hypurals 29.2; length of ten abdominal vertebrae 10.6; dorso-anal distance 4.8; caudal peduncle depth 2.6; pecto-ventral distance 8.6; ventro-anal distance 4.7; dorsal fin base length 7.1; anal fin base length 10.7; pectoral fin length 4.7; pelvic fin length 3.2; mandible length 7.6; maxilla length 6.6; eye diameter 0.5.

Discussion

The fossil specimen described herein is undoubtedly a member of the order Stomiiformes because it possesses such characters as an elongated body, a wide mouth with the position of the lower jaw articulation behind the orbit, a toothed maxilla which contributes to the mouth edge, a hook-like ventral process of the cleithrum, some branchiostegals articulating with the ventral hypohyal, an absence of spiny fin rays, a pectoral fin insertion near the ventral body margin, an abdominal pelvic fin, a forked caudal fin with 19 principal rays, and the presence of photophores (Fink and Weitzman 1982; Prokofiev 2005). Further, the highly elongated

vertebral centra, the placement of the dorsal and anal fin origins opposite each other and close to a vertical passing through the first caudal vertebra, the subequal jaw dentition, the antero-dorsally flexed hyomandibula with a greatly reduced articular process, a caudal skeleton structure with the hypurals fused into the two large plates, a fully developed neural spine of the second preural centrum, an absence of epurals, an absence of the common glands of the serial photophores, and extremely small eyes all indicate that the fossil under consideration is a member of the family Gonostomatidae and of the genus *Cyclothone* (Grey 1960; Harold and Weitzman 1996; Harold 1998).

Both Recent and fossil representatives of this genus are very similar one to another in main body proportions and counts (Nazarkin 2015, p. 172, table 1; Prikryl and Carnevale 2017, p. 276, table 2). *Cyclothone duhoensis*, sp. nov., is not an exception, and, in general, possesses the same morphological features. Traditionally, representatives of the genus were separated into the two groups – of the light-coloured, semitransparent, and the dark-coloured species (Grey 1964; Mukhacheva 1964, 1974). The former

species group is characterised also by the absence of the scales. Subsequent molecular research has shown that these groups are phylogenetically unnatural (Miya and Nishida 1996). The presence of the scales and of the remains of dark body pigmentation allows us to consider the new species described above as a member of the species group with a darkly pigmented body. Among them, it is similar to those species possessed more than 15 photophores in the AC series, namely *C. acclinidens* Garman and *C. atraria* Gilbert with 14–16, and *C. pallida* Brauer with 15–16 elements (Mukhacheva 1964, 1974; Badcock 1984). Moreover, the presence of at least four photophores between the last anal-fin ray and the caudal-fin base separates the bristlemouth from the Duho Formation from all congeners because they have not more than three elements in this area (Mukhacheva 1964, 1974; Badcock 1984).

Another character distinguishing the new Miocene species described herein is the features of the maxillary dentition (Figure 3). In all members of the genus, the maxilla bears short, downwardly directed teeth anteriorly and large, forwardly inclined teeth posteriorly (Grey 1964). Recent *C. acclinidens* differ in having an abrupt transition between the two types of dentition, and also in a gradual enlargement of posterior teeth to the rear (Figure 3(a)). On the contrary, all other species demonstrate the gradual transition between the dentition types and the regular alternation of smaller and large posterior teeth (Grey 1964; Mukhacheva 1964, 1974; Borodulina 1984; Miya 1994). The Duho Formation bristlemouth possesses the gradual transition zone and very weakly expressed alternation of the posterior teeth (Figure 3(d)). Such a condition is not observed in most members of this genus, including fossil *C. mukhachevae* (Figure 3(b)), and partly resembles only the dentition of recent *C. braueri* Jespersen et Tåning from the lightly-coloured species group, in which the alternation of posterior teeth is also weakly expressed (Figure 3(f)). Considered together, the features of the dentition and of the number of AC photophores well separates the new species described above from all congeners.

It is appropriate to note here that the both oldest known nominal species of the genus, middle-Miocene *C. duhoensis* sp. nov. and middle-late-Miocene *C. mukhachevae*, have very small differences from the Recent species, showing almost the same morphological structure. On the contrary, a younger species, *C. gaudanti* from the Mediterranean late-Miocene, has much greater differences from the Recent congeners: it possesses some atavistic characters (the presence of epipleurals and autogenous parhypural) along with the least number of the anal-fin rays (Přikryl and Carnevale 2017). Such a difference in the morphology of the Neogene bristlemouths, apparently, reflects the separate evolutionary history of the Mediterranean representatives of the genus.

The water depth of the Duho Formation sedimentation is a subject of discussion (Yun 1986; Kim and Paik 2013). Its sediments contain the fossils of deep-water organisms along with numerous shallow-water and terrestrial (higher plants and insects) remains (Chun 1982; Jung and Lee 2009). Among the former, the lanternfishes (Myctophidae) and lightfishes (Phosichthyidae) are especially numerous (Nam et al. 2019), and suggest deep-water sedimentation. At the same time, the finding of a bristlemouth in the Duho Formation appears unique. If the sedimentation had occurred in a deep-water area, we could expect a frequency of *Cyclothone* fossils not fewer than those of the lanternfishes or lightfishes. This discrepancy can be explained by distinct fish behavioural patterns. Most modern lanternfish and lightfish undergo extensive diurnal migrations during which they rise to the upper water layers, where they can be carried by surface currents to shallower areas and may end up buried in the coastal sediments (Parin 1988). In contrast, the modern *Cyclothone* species do not perform vertical migrations,

staying in deep waters most of the time (Mukhacheva 1967; Badcock 1984), so that they can occur in the shallow areas only by a rare event. Possibly, the rarity of *Cyclothone* remains in these beds can be explained by the shallow-water origin of the deposits of the Duho Formation.

Acknowledgments

We would like to express our sincere thanks to M.V.H. Wilson (University of Alberta, Canada) and two anonymous reviewers for their valuable comments and corrections which greatly improved the manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

The reported study was funded by RFBR and National Research Foundation of Korea according to the research project № 19-54-51001 and under the framework of international cooperation program managed by the National Research Foundation of Korea [2019K2A9A1A0609922511].

ORCID

Mikhail V. Nazarkin  <http://orcid.org/0000-0001-7634-7957>

References

- Badcock J. 1984. Photichthyidae. In: Whitehead PJP, Bauchot M-L, Hureau J-C, Nielsen J, Tortonese E, editors. Fishes of the North-eastern Atlantic and the Mediterranean. Paris: UNESCO; p. 318–324.
- Bak US, Lee JD, Yun HS. 1996. Middle Miocene radiolarians from the Duho Formation in the Pohang basin, Korea. J Paleontol Soc Korea. 12:225–261.
- Borodulina OD. 1982. Features of the axial skeleton of mass species of the families Gonostomatidae and Photichthyidae. In: Parin NV, editor. Maloizuchennye ryby otkrytogo okeana. Moscow: Institute of Oceanology AN SSSR; p. 32–41. Russian.
- Borodulina OD. 1984. Identification of the remains mesopelagic fishes from predators stomachs: part 3: some structural features of jaws of mass stomioid fish species of the families Gonostomatidae, Sternoptychidae, and Photichthyidae. Voprosi Ikhtiologii. 24:628–635. Russian.
- Chun HY. 1982. Plant fossils from the Tertiary Pohang sedimentary basin, Korea. Korea Inst Energy Resourc. 14:7–23. Korean.
- David LR. 1943. Miocene fishes of southern California. Geol Soc Am Spec Pap. 43:1–193.
- Fierstine HJ, Huddleston RW, Takeuchi GT. 2012. Catalog of the Neogene bony fishes of California. A systematic inventory of all published accounts. Occas Pap California Acad Sci. 159:1–206.
- Fink WL, Weitzman SH. 1982. Relationships of the stomiiform fishes (Teleostei), with a description of *Diplophos*. Bull Mus Comp Zool. 150:31–93.
- Gaudant J. 2004. Additions à l'ichthyofaune tortonienne du bassin de l'erapetra (Crète orientale, Grèce). Ann Naturhist Mus Wien Ser A. 105:257–285.
- Gill TN. 1893. Families and subfamilies of fishes. Mem Natl Acad Sci. 6:125–138. doi:10.5962/bhl.part.6303.
- Goode GB, Bean TH. 1883. Reports on the results of dredging under the supervision of Alexander Agassiz, on the east coast of the United States, during the summer of 1880, by U.S. coast survey steamer “Blake”, Commander J.R. Bartlet, U.S.N., commanding. Bull Mus Comp Zool. 10:183–226.
- Grey M. 1960. A preliminary review of the family Gonostomatidae, with a key to the genera and the description of a new species from the tropical Pacific. Bull Mus Comp Zool. 122:57–125.
- Grey M. 1964. Family Gonostomatidae. Mem Sears Found Mar Res. 4:78–240.
- Harold AS. 1998. Phylogenetic relationships of the Gonostomatidae (Teleostei: Stomiiformes). Bull Mar Sci. 62:715–741.
- Harold AS, Weitzman SH. 1996. Interrelationships of stomiiform fishes. In: Stiassny MLJ, Parenti LR, Johnson GD, editors. The interrelationships of fishes. San Diego (CA): Academic Press; p. 333–353.
- Jordan DS. 1907. The fossil fishes of California with supplementary notes on other species of extinct fishes. Bull Department Geol Univ California. 5:95–145.
- Jung SH, Lee SJ. 2009. Fossil-winged fruits of *Fraxinus* (Oleaceae) and *Liriodendron* (Magnoliaceae) from the Duho Formation, Pohang basin, Korea. Acta Geol Sin. 83:845–852. doi:10.1111/j.1755-6724.2009.00113.x.

- Kawaguchi K. 1971. Gonostomatid fishes of the Western North Pacific. *Jpn J Ichthyol.* 18:1–16.
- Kim DH, Lee SJ. 2011. Fossil scallops from the Hageon Formation and the Duho Formation, Pohang basin, Korea. *J Geol Soc Korea.* 47:235–244. Korean.
- Kim JM, Paik IS. 2013. Chondrites from the Duho Formation (Miocene) in the Yeonil Group, Pohang basin, Korea: occurrences and paleoenvironmental implications. *J Geol Soc Korea.* 49:407–416.
- Landini W, Menesini E. 1978. L'ittiofauna plio-pleistocenica dell'area della Vrica (Crotone, Calabria). *Boll Soc Paleontol Ital.* 17:143–175.
- Landini W, Menesini E. 1986. L'ittiofauna pliocenica della sez. di Stuni e suoi rapporti con l'ittiofauna plio-pleistocenica della Vrica (Crotone, Calabria). *Boll Soc Paleontol Ital.* 25:41–63.
- Landini W, Sorbini L. 1993. Biogeographic and palaeoclimatic relationships of the Middle Pliocene ichthyofauna of the Samoggia Torrent (Bologna, Italy). *Ciências da Terra (UNL), Proceedings of the 1st Regional Committee on Atlantic Neogene Stratigraphy (R.C.A.N.S) Congress; Lisboa.* Vol. 12, p. 83–89.
- Miya M. 1994. *Cyclothone kobayashii*, a new gonostomatid fish (Teleostei: Stomiiformes) from the southern ocean, with notes on its ecology. *Copeia.* 1994:191–204. doi:10.2307/1446685.
- Miya M, Nishida M. 1996. Molecular phylogenetic perspective on the evolution of the deep-sea fish genus *Cyclothone* (Stomiiformes:Gonostomatidae). *Ichthyolog Res.* 43:375–398. doi:10.1007/BF02347637.
- Morrow JE Jr. 1964. General discussion and key to families. In: Bigelow HB, Cohen DM, Dick MM, Gibbs RH Jr, Grey M, Morrow JE Jr, Schultz LP, Walters V, editors. *Fishes of the Western North Atlantic, part 4. Sears foundation for marine research, memoir 1.* New Haven (CT): Yale University; p. 71–76.
- Mukhacheva VA. 1964. Species composition of the genus *Cyclothone* (Pisces, Gonostomatidae) in the Pacific Ocean. *Trudy Instituta Okeanologii AN SSSR.* 73:93–138. Russian.
- Mukhacheva VA. 1967. Bristlemouths (genus *Cyclothone*, Gonostomatidae). In: Rass TS, editor. *Tikhii okean. Biologiya Tikhogo okeana.* 3 Ryby otkrytykh vod. Moscow: Nauka; p. 182–199. Russian.
- Mukhacheva VA. 1974. Bristlemouths (genus *Cyclothone*, family Gonostomatidae) in the World ocean and their distribution. *Trudy Instituta Okeanologii AN SSSR.* 96:189–254. Russian.
- Nam K-S, Ko J-Y, Nazarkin MV. 2019. A new lightfish, † *Vinciguerria orientalis*, sp. Nov. (Teleostei, Stomiiformes, Phosichthyidae), from the middle Miocene of South Korea. *J Vertebr Paleontol.* 39(3):e1625911. doi:10.1080/02724634.2019.1625911.
- Nazarkin MV. 2015. Fossil bristlemouth *Cyclothone mukhachevae* sp. nov. (Stomiiformes: Gonostomatidae) from the Neogene of western Sakhalin, Russia. *Paleontological J.* 49:162–175. doi:10.1134/S0031030115020045.
- Nelson JS. 2006. *Fishes of the World.* 4 ed. New Jersey: Wiley, Hoboken.
- Nelson JS, Grande T, Wilson MVH. 2016. *Fishes of the World.* 5 ed. New Jersey: Wiley, Hoboken.
- Ohe F. 1993. Osteichthyes. Deep fish assemblage from the Middle Miocene Morozaki Group, southern part of Chita Peninsula, Aichi Prefecture, central Japan. In: Ohe F, Nonogaki K, Tanaka T, Hachiya K, Mizuno T, Momoyama T, Yamaoka T, editors. *Fossils from the Miocene Morozaki Group.* Nagoya: The Tokai Fossil Society; p. 169–262.
- Parin NV. 1988. *Fishes of the open ocean.* Moscow: Nauka. Russian.
- Přikryl T, Carnevale G. 2017. Miocene bristlemouths (Teleostei: Stomiiformes: Gonostomatidae) from the Makrilia Formation, Ierapetra, Crete. *C R Palevol.* 16:266–277. doi:10.1016/j.crpv.2016.11.004.
- Prokofiev AM. 2005. Systematics and phylogeny of the stomiiform fishes (Neoteleostei: Stomiiformes) from the Paleogene–Neogene of Russia and adjacent regions. *J Ichthyol.* 45:S89–S162.
- Seong MN, Kong DY, Lee BJ, Lee SJ. 2009. Cenozoic brittle stars (Ophiuroidea) from the Hageon Formation and the Duho Formation, Pohang basin, Korea. *J Econ Envir Geol.* 42:367–376. Korean.
- Sorbini L. 1988. Biogeography and climatology of Pliocene and Messinian fossil fish of Eastern-Central Italy. *Boll Mus Civ Stor Nat Verona.* 14:1–85.
- Yabumoto Y, Uyeno T. 1994. Late Mesozoic and Cenozoic fish faunas of Japan. *Island Arc.* 3:255–269. doi:10.1111/j.1440-1738.1994.tb00115.x.
- You HS, Koh YK, Kim JY. 1986. A study on the Nannoplankton from the Neogene formation, Pohang, Korea. *J Paleontol Soc Korea.* 2:137–154.
- Yun H. 1985. Some fossil squillidae (Stomatopoda) from the Pohang Tertiary basin, Korea. *J Paleontol Soc Korea.* 1:19–31.
- Yun H. 1986. Emended stratigraphy of the Miocene formation in the Pohang basin; part 1. *J Paleontol Soc Korea.* 2:54–69.