

Taxonomic status of squids of the genus *Berryteuthis* Naef, 1921 (Gonatidae, Oegopsida) inhabiting the Sea of Japan

D.O. ALEXEYEV¹, O.N. KATUGIN², V.A. BIZIKOV¹

¹ Russian Federal Research Institute of Fisheries and Oceanography (VNIRO), 107140, Moscow, 17 V. Krasnoselskaya Street

² Pacific branch of VNIRO (TINRO), 690091, Vladivostok, 4 Shevchenko Alley

E-mails: ¹ alexeyev@vniro.ru; ² oleg.katugin@tinro-center.ru; ¹ bizikov@vniro.ru

ABSTRACT. Two subspecies of the schoolmaster gonate squid *Berryteuthis magister* (Berry, 1913) have been described to date: *B. magister nipponensis* Okutani et Kubodera, 1987 from the Pacific Ocean off the coast of Japan and Sea of Japan, and *B. magister shevtsovi* Katugin, 2000 from the Sea of Japan. The gonatid species *Gonatus septemdentatus* Sasaki, 1915, which was later recognized as a junior synonym of *B. magister*, was also described from the Sea of Japan. Comparisons among these three taxa and with the nominative subspecies using morphological and ecological features suggest that individuals of the genus *Berryteuthis* inhabiting the Sea of Japan belong to the species *B. septemdentatus* (Sasaki, 1915), which should be considered the valid name for this taxon.

[https://doi.org/10.35885/ruthenica.2022.32\(2\).1](https://doi.org/10.35885/ruthenica.2022.32(2).1)

Таксономическое положение кальмаров рода *Berryteuthis* Naef, 1921 (Gonatidae, Oegopsida) из Японского моря

Д.О. АЛЕКСЕЕВ¹, О.Н. КАТУГИН²,
В.А. БИЗИКОВ¹

¹ Всероссийский научно-исследовательский институт рыбного хозяйства и океанографии (ФГБНУ «ВНИРО»), 107140, г. Москва, в. Красносельская ул., 17

² Тихоокеанский филиал ФГБНУ «ВНИРО» («ТИНРО»), 690091, г. Владивосток, пер. Шевченко, 4

E-mails: ¹ alexeyev@vniro.ru; ² oleg.katugin@tinro-center.ru; ¹ bizikov@vniro.ru

РЕЗЮМЕ. На сегодняшний день описаны два подвида командорского кальмара *Berryteuthis magister* (Berry, 1913): *B. magister nipponensis* Okutani et Kubodera, 1987 из Тихого океана у берегов Японии и Японского моря и *B. magister shevtsovi* Katugin, 2000 из Японского моря. Вид гонатид *Gonatus septemdentatus* Sasaki, 1915, который позднее был признан младшим синонимом *B. magister*, также был описан из Японского моря. Сравнение этих трех таксонов между собой и с номинативным подвидам по морфологическим и экологическим признакам показывает, что кальмары рода *Berryteuthis* из Японского моря представляют собой самостоятельный таксон видового ранга. Валидное название этого вида – *Berryteuthis septemdentatus* (Sasaki, 1915).

Introduction

Until recently, the genus *Berryteuthis* (Gonatidae, Oegopsida) was believed to consist of two nominal species: *Berryteuthis magister* (Berry, 1913) and *Berryteuthis anonychus* (Pearcy et Voss, 1963) [e.g., Jereb, Roper, 2010]. Both species inhabit the boreal Pacific Ocean and its marginal seas [Nesis, 1997]. The former lives mostly near the bottom on the continental slope, and the latter is mainly an offshore pelagic dweller. It has been suggested that *B. anonychus* should be excluded from genus *Berryteuthis* and placed in a new monotypic genus *Okutania* Katugin, 2004, which has been accepted by some researchers [e.g., Okutani, 2015] but not others [e.g., Jereb, Roper 2010]. In our opinion, *Okutania anonycha* (Pearcy et Voss, 1963), described formally by Katugin [2004], is a valid species in a monotypic genus based on both comparative morphology and genetics (allozyme loci).

Berryteuthis magister was first mentioned as an immature stage of the gonatid squid “*Gonatus fabricii*” from the northeastern Pacific Ocean and later received the name *Gonatus magister* [Berry, 1912, 1913]. A new monotypic genus, *Berryteuthis*, was suggested for this species some time later [Naef, 1921]. *Gonatus septemdentatus* Sasaki, 1915, was described, including detailed measurements, based on individuals collected in the Sea of Japan [Sasaki,

1915: 185–188]. In the description of *G. septemdentatus*, Madoka Sasaki [1915: 188] mentioned that this species was very similar to squids found by S. Stillman Berry off the North American coast [Berry, 1912], and described as *Gonatus magister* Berry, 1913. Later Sasaki placed *G. septemdentatus* in the synonymy of *G. magister* [Sasaki, 1929: 270–272]. In subsequent publications, the name *Gonatus septemdentatus* was listed as a junior synonym of *Berryteuthis magister* [e.g., Okutani, 1968; Nesis, 1973, 1982; Jereb, Roper, 2010].

No subspecies of *B. magister* were described until the 1980s, and the population structure of this widely distributed squid species was suggested to be associated with general subdivision of the North Pacific into large geographical regions [Nesis, 1973, 1982, 1997; Katugin, 1998; Fedorets, 2006]. The first formal description of a subspecies of *B. magister* was provided by T. Okutani and T. Kubodera, based on a single male from the Sanriku area (Pacific Ocean off northeastern Honshu), Japan, which received the name *Berryteuthis magister nipponensis* [Okutani *et al.*, 1987]. Another individual in the type series was collected in Toyama Bay (Japan), the Sea of Japan, and measured, but not described. Later it was shown that individuals of the *B. magister*, inhabiting the Sea of Japan differ from conspecific populations in other areas in a number of morphological, reproductive and genetic features, and should be treated as a separate geographic subspecies [Katugin, 1998], which later was formally described as *Berryteuthis magister shevtsovi* [Katugin, 2000].

Therefore, there are now several names associated with the taxon *Berryteuthis magister* for individuals of schoolmaster gonate squid that inhabit the Sea of Japan. The validity and priority of the names remain unresolved, and further consideration is needed to decide on the number, synonymy and priority of the given names, as well as on the taxonomic rank of “*B. magister*” populations in the Sea of Japan.

Results and discussion

The original description of *Gonatus septemdentatus* was based on six female specimens collected by local fishermen “with drag-net at 100 fathoms” in Etchu Province (now Toyama Prefecture), Japan, in the Sea of Japan [Sasaki, 1915]. The author did not give the exact locality for the captured individuals; nor did he provide any information on the date of capture. The description, though very thorough, lacked illustrations showing the general appearance of the new species and its diagnostic characters, and the six specimens used by Sasaki are no longer extant [e.g., Gleadall, 2003; Gleadall, Salcedo-Vargas, 2004; Taki, Igarashi, 1967].

Sasaki [1915] did not discuss the relationships of *Gonatus septemdentatus* from the Sea of Japan,

with *Gonatus magister* Berry [1913] presumably because the latter, at that time, was known only from the northeastern Pacific Ocean. However, Sasaki mentioned the similarity between these two taxa in the original description, and only later considered his taxon to be a synonym of *Gonatus magister* [Sasaki, 1929]. *Gonatus septemdentatus* therefore became a junior synonym of *Berryteuthis magister* [e.g., Okutani, 1968; Nesis, 1973; Jereb, Roper, 2010].

Two subspecies of *Berryteuthis magister* have been formally described by the end of the 20th century: *B. magister nipponensis* Okutani, Kubodera in Okutani, Tagawa, Horikawa, 1987, and *B. magister shevtsovi* Katugin, 2000. The former subspecies was described based on a single specimen (male of mantle length 182 mm) caught in a set net off northeastern Honshu, Sanriku area, and designated as the holotype [Okutani *et al.*, 1987]. One specimen (an unsexed squid of mantle length 120 mm) from the Toyama Bay, the Sea of Japan, was also mentioned in the “Materials” of the subspecies description. However, no morphological traits, standard measurements, except for the mantle length, and comments or designation on its status were provided. Later, the second individual of the new subspecies in the type series was mentioned as the paratype [Kubodera, 2006]. One more individual identified as *B. magister nipponensis* has been reported from the northwestern Pacific Ocean off Cape Erimo, southern Hokkaido, Japan [Kubodera, 1993]. Since individuals assigned by the authors to the subspecies *B. magister nipponensis* occurred along with the “typical” individuals, and therefore, were not separated from the latter neither geographically nor vertically, it was suggested that there must be an ecological isolation between these two forms, with the new subspecies having “stronger swimming ability than the typical population which is quasibenthic” [Okutani *et al.*, 1987]. Certain morphological features were suggested to be characteristic of *B. magister nipponensis*: a mantle narrower than that of the nominative subspecies; fins relatively smaller; head somewhat broader than the mantle width; and size differences of the club suckers less pronounced.

Comparison of the above mentioned character states of *B. magister nipponensis* with those of the type specimens of the nominative subspecies [Berry, 1912: 309–312 pl. LII, 1,2; pl. LIV, 1–4; pl. LV, 1, 3–7; Berry, 1913: 76–77] suggests that there are no clear differences between these two forms. It is worth noting that the type specimen of *G. magister* is also an immature male, and it was shown that, in *B. magister*, some external morphological traits may change with growth. For example, the growth of fin size with an increase in mantle length in the schoolmaster gonate squid can be expressed by a logarithmic curve [Katugin, 1998, fig. 6]. Therefore, relatively shorter fins in small immature individuals

can hardly be considered as a diagnostic feature. Noteworthy, in the description of *B. magister nipponensis*, the fin length index (FLI, fin length divided by mantle length, %) is given as 53.8% in the holotype specimen and slightly larger fins with FLI of 55.7% and 55.8% are mentioned for conspecific specimens captured off Hokkaido and in Yamatotai area, which were identified as *B. magister magister* [Okutani *et al.*, 1987]. However, later, T. Okutani [2015] reported that the FLI of the latter is only 50%, which is in fact smaller than the FLI in the *B. magister nipponensis* holotype. Moreover, in the latter publication, the geographic range for *B. magister nipponensis* does not include the Sea of Japan, leaving only the area off Sanriku as the subspecies locality [Okutani, 2015].

The arrangement and size of suckers on the tentacle club (somewhat smaller number of suckers in a transverse row, of “about 15 rows”, and their almost uniform size across the club manus, with central suckers being “slightly larger” (both citations on p. 134 in Okutani *et al.* [1987]), might serve to distinguish *B. magister nipponensis* from the nominative subspecies [Okutani *et al.*, 1987; Okutani, 2015]. However, these characters are hardly diagnostic, since suckers on the manus are generally uniform in size in immature individuals, and according to our observations, size differences between central and marginal club suckers in *B. magister* appear only with growth and maturation.

Since, judging from the mantle cavity drawings of the type specimen [Berry, 1912, pl. LII, 2], the species was described based on immature individuals, in which central and marginal club suckers do not show clear differences in size, those features do not distinguish *B. magister nipponensis* from the nominative subspecies, suggesting that the former possesses the characters of an immature *B. magister magister*. Assuming that *B. magister* individuals inhabiting the Bering and Okhotsk Seas, as well as the northeast and northwest Pacific Ocean, belong to the nominative subspecies, their only apparent difference from *B. magister nipponensis* is a larger size-at-maturity. However, no mature individuals of *B. magister nipponensis* have been reported so far.

The other subspecies of schoolmaster gonate squid, *Berryteuthis magister shevtsovi* Katugin, 2000, was described thoroughly based on comparative morphology, anatomy, ecology, life cycle, distribution patterns, and genetics [Katugin, 1998, 2000]. The type material was collected in the northwest Sea of Japan, on the continental slope off the coast of the Russian Primorye Region. It was shown that *B. magister shevtsovi* also occurs in large quantities in the central Sea of Japan, near the bottom at the deep-sea Kita-Yamato Bank. This subspecies occurs only in the Sea of Japan, exhibiting clear allopatry (to *B. magister* from the other North Pacific geographic regions); it is clearly distinguishable from the nomi-

native subspecies by a number of diagnostic features in morphology and anatomy, as well as by its notably smaller size-at-maturity, lower individual fecundity and much larger ripe eggs [Katugin, 1998, 2000].

Comparison of the diagnostic features of *B. magister shevtsovi* and *G. septemdentatus* suggests that there are no significant differences between these two taxa in external morphology or radula structure. Lateral teeth on the radula were reported to be bicuspid in *B. magister shevtsovi* and *G. septemdentatus*, and tricuspid in the nominal subspecies [Katugin, 1998: fig. 32, table 25; Sasaki, 2015: 188]. The radula of *B. magister nipponensis* has not been described [Okutani *et al.*, 1987].

Body measurements for the formally described *B. magister* subspecies (the nominative subspecies and *G. septemdentatus*) are difficult to compare because the soft parts of the squid body are difficult to measure accurately, and therefore body indices (proportion of body parts relative to the standard-length measurement for squid, the dorsal mantle length) are open to measurement errors and uncertainty. External body features (in particular mantle width and the length of arms and tentacles) may depend on factors such as muscle tone, storage conditions, length of time between capture and fixation, method of fixation, accidental deformation of the body during measurements, etc. [Katugin, 1998]. Features such as mantle length, as well as head and fin proportions, are less susceptible to measurement error and are more reliable for comparison among squid individuals. It is worth noting that fin-measurement methods in squid may also differ among the researchers [e.g., Okutani *et al.*, 1987; Katugin, 2000; Jereb, Roper, 2010]. Indices from standard measurements of body parts for the type specimens of *G. septemdentatus*, *B. magister shevtsovi* and *B. magister nipponensis* are presented in Table 1.

In view of the above-noted variation inherent in soft structures and their measurement, features claimed to be diagnostic for *B. magister nipponensis*, such as the relatively narrow mantle width, are of doubtful reliability and, in fact, the mantle width index of some of Sasaki's specimens is almost the same as that of *B. magister nipponensis*. A smaller fin length in *B. magister nipponensis* is also considered as diagnostic for this taxon; however, the FLI for this subspecies is within the range for all three subspecies names associated with Japanese waters. Moreover, the somewhat shorter fin of the *B. magister nipponensis* holotype places that individual closer to the typical form, *B. magister magister*. Individuals of *B. magister nipponensis* and *B. magister magister* are common in that their first and fourth arm pairs are somewhat shorter than the second and third arm pairs.

Descriptions of the two taxa from the Sea of Japan suggest that, contrary to *B. magister* individuals from outside the Sea of Japan, they have much in

Table 1. Comparison of morphometric indices for the type specimens of the taxa *Gonatus septemdentatus*, *Berryteuthis magister shevtsovi* and *Berryteuthis magister nipponensis*.

Abbreviations: DML – dorsal mantle length; MWI – mantle width index; FLI – fin length index; AL1I–AL4I – arms 1 to 4 length indices; TLI – tentacle length index; CLI – club length index. S – specimens used in the *G. septemdentatus* description [Sasaki, 1915]; K – specimens used in the *B. magister shevtsovi* description [Katugin, 2000]; OK – data from the *B. magister nipponensis* description [Okutani *et al.*, 1987].

Табл. 1. Сравнение морфометрических индексов особей, использованных при описании таксонов: *Gonatus septemdentatus*, *Berryteuthis magister shevtsovi* и *Berryteuthis magister nipponensis*.

Обозначения: DML – длина мантии по дорсальной стороне; MWI – индекс ширины мантии; FLI – индекс длины плавников; AL1I–AL4I – индексы длины рук 1–4 пары; TLI – индекс длины щупалец; CLI – индекс длины булавки. S – экземпляры из описания *G. septemdentatus* [Sasaki, 1915]; K – экземпляры из описания *B. magister shevtsovi* [Katugin, 2000]; OK – данные из описания *B. magister nipponensis* [Okutani *et al.*, 1987].

	DML	MWI	FLI	AL1I	AL2I	AL3I	AL4I	TLI	CLI
S1♀	138	0.290	0.580	0.507	0.565	0.507	0.471	1.377	0.580
S2♀	164	0.305	0.573	0.497	0.570	0.546	0.500	0.747	0.427
S3♀	169	0.237	0.550	0.459	0.541	0.544	0.462	0.680	0.385
S4♀	185	0.259	0.568	0.476	0.530	0.519	0.462	0.865	0.432
S5♀	220	0.250	0.609						
S6♀	190	0.253	0.579	0.542	0.568	0.566	0.537	1.053	0.526
K1♂	162	0.364	0.543	0.611	0.660	0.704	0.648	1.574	0.438
K2♀	172	0.331	0.552	0.547	0.640	0.628	0.576	1.343	
OK♂	182	0.220	0.538	0.440	0.467	0.478	0.429	1.030	0.478

common. The Sea of Japan taxa are represented by squids of relatively small size in comparison with *B. magister* from other parts of the its range. Dorsal mantle length of the squids described by Sasaki [1915] did not exceed 220 mm. The type specimens described by Katugin [2000] have dorsal mantle lengths of 162 and 172 mm, and, though many individuals collected across the Sea of Japan have been measured, their dorsal mantle lengths rarely exceed 220 mm [Katugin, 1998: 39]. On the contrary, *B. magister* mantle length in the Bering Sea may reach 380 mm and even larger (up to 430 mm, according to our personal observations), with the average mantle length in mature females ranging from 250 to 260 mm [Arkhipkin *et al.*, 1996].

In addition to such features as smaller size and some differences in body proportions (e.g., in somewhat longer fins), individuals of *B. magister shevtsovi* also differed greatly from *B. magister* individuals from the areas outside the Sea of Japan in a several biological, ecological, and genetic features [Katugin, 2000]. The level of genetic differentiation between *B. magister* from the Sea of Japan and *B. magister* from other areas of the North Pacific suggested that, most likely, the geographically isolated *B. magister* population from the Sea of Japan constitutes an allopatric taxon [Katugin, 2000: tables 2–5, pp. 88–90].

The squids described as *B. magister shevtsovi* are also characterized by a lower individual fecundity than in the nominative subspecies: 1,790 to 3,755 oocytes were counted in the adult females of *B. magi-*

ster shevtsovi [Nazumi *et al.*, 1979]. Potential fecundity of conspecific individuals from the Bering Sea was estimated to be in the range of 20,000–96,000 oocytes, depending on the size of females; and their realized fecundity was estimated at about 30% of the potential fecundity, or about 7,000–30,000 oocytes [Nigmatullin *et al.*, 1996], which is several times higher than in *B. magister shevtsovi*. Oocytes of the squids from the Sea of Japan are rather large, ranging in diameter from 3.14 to 5.94 mm, with an average size of about 4–5 mm. Ripe oocytes in the nominative subspecies are notably smaller: 3.3–4.2×2.5–3.3 mm, usually 3.6–4.0×2.7–3.0 mm, with a mean maximum diameter of 2.86–2.97 mm [Nigmatullin *et al.*, 1996: table 23].

Given the above considerations, there appears to be a differentiation in reproductive strategy modes of squids in the Sea of Japan, versus those in the North Pacific Ocean and its northern marginal seas. Squid living in the Sea of Japan with larger eggs and lower fecundity tend to exhibit a more K-selected reproductive strategy, while those from other geographic areas are closer to r-strategists. Such a difference in reproductive strategy of the Sea of Japan squids, compared to that of the nominative subspecies, is in good agreement with the general trend towards the choice of K-strategy among colder-water cephalopod species [Laptikhovskiy, 2005]

In the adult stage (near-bottom nectonic life form), individuals of the nominative subspecies inhabit the warm intermediate layer in the Bering

Sea and Pacific Ocean, which corresponds mainly to depths of 200 to 600 m and occasional occurrence at depths below 1000 m or even more [Arkhipkin *et al.*, 1996]. These squid apparently prefer a water temperature of 3.5°–3.9°C. The main habitat of the adult schoolmaster gonate squid in the Sea of Okhotsk is also associated with the warm deep-water layer, which occurs from approximately 200–600 m (depending on the sea area) and down to 1200 m with temperatures mainly about +2,5°C [Alexeyev, 2020]. In the Sea of Japan, in contrast, the squid inhabit quasi-homogeneous cold water layer that occupies almost the entire deep-sea basin below the surface seasonally warmed layer, with water temperature of ~1.7°C at depths of about 200 m and 0.2°–0.7°C near the bottom on the continental slope [Rostov *et al.*, 2001].

We suggest that the array of morphological, genetic and ecological differences between the schoolmaster gonate squid inhabiting the Sea of Japan, conventionally considered as the species *B. magister*, and conspecific populations from another geographic regions, are sufficient to consider the squids population from the Sea of Japan to constitute an independent species of the genus *Berryteuthis*. The allopatric mode of origin of this species from a common ancestor with *B. magister* due to the isolation of the Sea of Japan is discussed in details by Katugin [1998].

As for the species name for such a taxon, the earliest name was proposed by Sasaki [1915]. He also pointed out that the original placement of the species into the genus *Gonatus* was incorrect and this species must be placed into the genus *Berryteuthis* [Sasaki, 1929]. Therefore, the valid name for the species is *Berryteuthis septemdentatus* (Sasaki, 1915). Unfortunately, the syntypes are not extant but the original description enables unambiguous identification. *Berryteuthis magister shevtsovi* Katugin, 2000, is a junior synonym. Information on the type material for this taxon is given in the original description [Katugin, 2000]. The specimens used in the original description of *Berryteuthis magister nipponensis* were apparently a mixed assemblage, since they included specimens from localities attributable to both *B. magister* (the holotype) and *B. septemdentatus* (the paratype).

The suggested systematic position and synonymy of the *Berryteuthis* squids inhabiting the Sea of Japan is as follows:

Berryteuthis septemdentatus (Sasaki, 1915)
comb. nov.
(Fig. 1)

Gonatus septemdentatus Sasaki, 1915: 185; 1929: 270, Pl. XXII, figs 19–22, textfigs 129, 130.

Gonatus magister Berry, 1913 – Kondakov, 1941: 224, fig. 12, 13 [in part]; Akimushkin, 1963: 185, fig. 51(1) [in part].

Berryteuthis magister – Nesis, 1982: 190, fig. 50 a,b [in part]; Roper *et al.*, 1984: 143 [in part].

Berryteuthis magister nipponensis Okutani, Kubodera in Okutani *et al.*, 1987: 132 [in part]; Jereb, Roper, 2010: 211 [in part].

Berryteuthis magister shevtsovi Katugin, 2000: 91, figs 7–11.

Type material: holotype specimen of *Berryteuthis magister shevtsovi* is designated as **neotype** for *Berryteuthis septemdentatus*: mature male, 162 mm dorsal mantle length (Fig. 1); Research Vessel “Professor Kaganovsky”, Sea of Japan, 42°30'N, 133°42'E, bottom trawl at a approx. 600 m deep, May 23, 1996. Coll. by P.V. Kalchugin, deposited in the Museum of A.V. Zhirmunsky National Scientific Center of Marine Biology (Vladivostok), Far Eastern Branch of the Russian Academy of Sciences, No MIMB 32372.

Paratype: immature female, 172 mm dorsal mantle length, the same locality and date; deposited in the same collection with the holotype, No MIMB 32373.

The transfer of *Berryteuthis anonychus* (Pearcy and Voss, 1963) to new genus *Okutania* [Katugin, 2004] rendered *Berryteuthis* a monotypic genus, but we suggest that there are, indeed, two species, which are now recognized as *Berryteuthis septemdentatus* and *B. magister*. The latter one as presently understood is likely be composed of several geographical populations for which there is preliminary evidence [Katugin, 1998, 1999, 2000; Katugin *et al.*, 2013; Alekseev, 2020].

Acknowledgements

The authors would like to express their sincere thanks to Dr. I.G. Gleadall for his comments on the MS, valuable information on the type specimens from M. Sasaki's collections, and editing English language of the manuscript. We also express our deep gratitude for Dr. Vladimir Laptikhovsky, Dr. John Bower and Chingiz Nigmatullin for valuable recommendations in the work on the manuscript.

References

- Akimushkin I.I. 1963. *Cephalopod molluscs of the seas of the USSR*. Izdatelstvo Akademii Nauk SSSR. Moscow, 235 p. [In Russian].
- Alexeyev D.O. 2020. Spatial biology of Commander schoolmaster squid. *Dissertation for the degree of Doctor of Science*. Moscow, VNIRO, 378 p. [In Russian]. MS
- Arkhipkin A.I., Bizikov V.A., Krylov V.V., Nesis K.N. 1996. Distribution, stock structure, and growth of the squid *Berryteuthis magister* (Berry, 1913) (Cephalopoda, Gonatidae) during summer and fall in the western Bering Sea. *Fishery Bulletin*, 94(1): 1–30.
- Berry S.S. 1912. A review of the cephalopods of western North America. *Bulletin of the Bureau of Fisheries*, 30: 269–336.
- Berry S.S. 1913. Notes on some west American cepha-

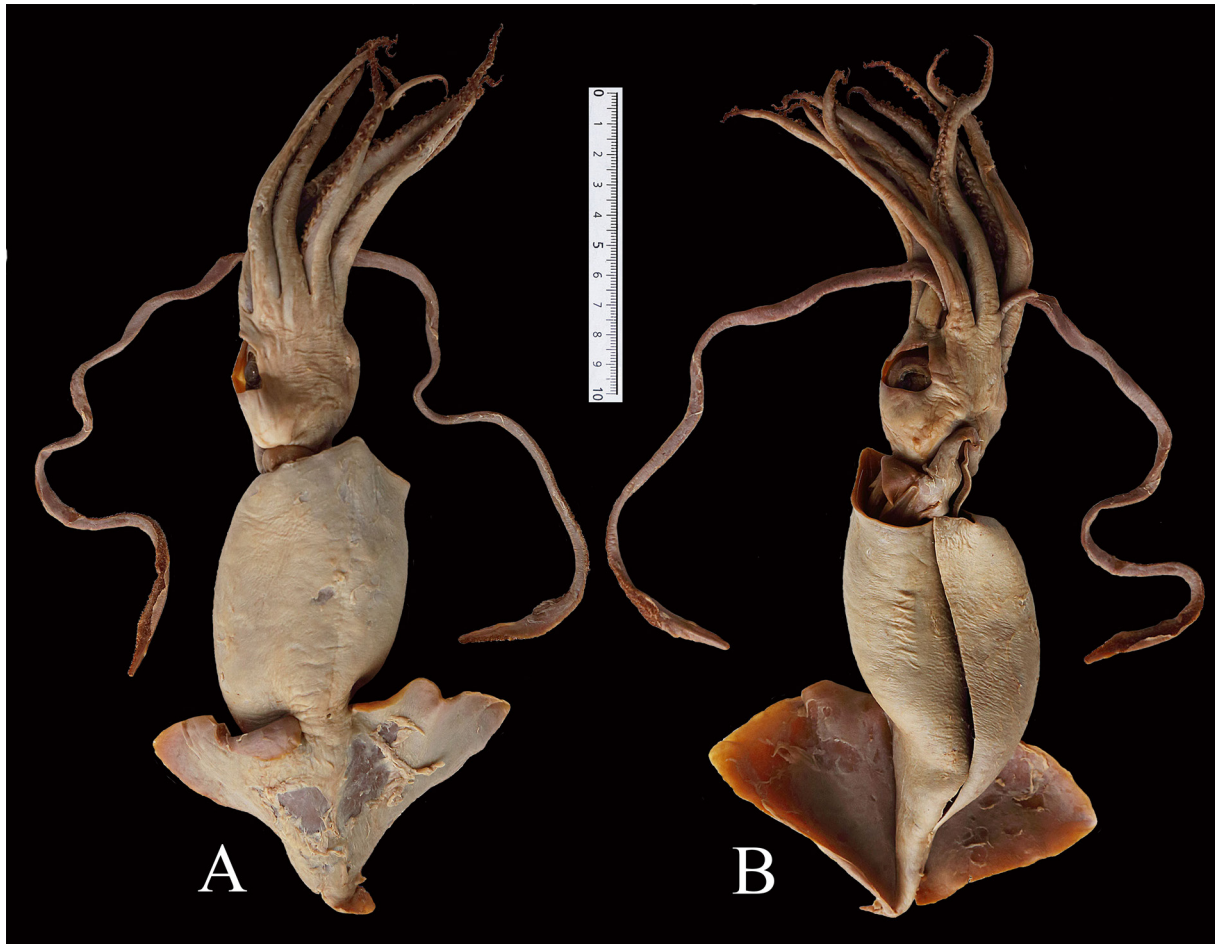


FIG. 1. *Berryteuthis septemdentatus*, neotype. **A.** dorsal view. **B.** ventral view. Scale – 10 cm.

РИС. 1. Неотип *Berryteuthis septemdentatus*. **A.** вид с дорсальной стороны. **B.** вид с вентральной стороны. Шкала – 10 см.

- lopods. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 65: 72–77.
- Fedorets Yu.A. 2006. Commander squid *Berryteuthis magister* (Berry, 1913) from the Bering and Okhotsk Seas (distribution, biology, fishery). *Dissertation for the degree of Doctor of Philosophy*. Vladivostok, 283 p. [In Russian]. MS.
- Gleadall I.G. 2003. A note on the Cephalopoda type specimens in the Zoology Department of Tokyo University Museum. *Journal of Molluscan Studies*, 69: 375–380.
- Gleadall I.G., Salcedo-Vargas M.A. 2004. Catalogue of the Cephalopoda specimens in the Zoology Department of Tokyo University Museum. *Interdisciplinary Information Sciences*, 10: 113–142.
- Jereb P., Roper C.F.E. (Eds.). 2010. *Cephalopods of the World. An Annotated and Illustrated Catalogue of Cephalopod Species Known to Date. Vol. 2. Myopsid and Oegopsid Squids*. FAO Species Catalogue for Fishery Purposes. No 4, Vol. 2. FAO of the UN. Rome, 605 p.
- Katugin O.N. 1998. Commander squid *Berryteuthis magister* (Berry, 1913): intraspecific variability, spatial and taxonomic differentiation. *Dissertation for the degree of Doctor of Philosophy*. Vladivostok, 215 p. [In Russian]. MS.
- Katugin O.N. 1999. Intraspecific genetic variation and population differentiation of the squid *Berryteuthis magister* in the North Pacific Ocean. *Russian Journal of Marine Biology*, 25(1): 34–45.
- Katugin O.N. 2000. A new subspecies of the schoolmaster gonate squid, *Berryteuthis magister* (Cephalopoda: Gonatidae), from the Japan Sea. *Veliger*, 43: 82–97.
- Katugin O.N. 2004. Squids of the family Gonatidae from the North Pacific Ocean and their genetic differentiation: controversial issues in the systematics and phylogeny. *Ruthenica, Russian Malacological Journal*, 14: 73–87 [In Russian].
- Katugin O.N., Shevtsov G.A., Zuev M.A., Didenko V.D., Kulik V.V., Vanin N.S. 2013. *Berryteuthis magister* (Berry, 1913), schoolmaster gonate squid. In: Rosa R., Pierce G., O'Dor R. (Eds.). *Advances in Squid Biology, Ecology and Fisheries. Part II – Oegopsid Squids*. Nova Science Publishers: 1–48.
- Kondakov N.N. 1941. Cephalopod mollusks of the Far Eastern Seas of the USSR. *Isledovania dalnevostochnykh morei SSSR*, 1: 216–255 [In Russian].
- Kubodera T. 1993. Upper bathyal cephalopods off eastern Cape Erimo, Hokkaido, Japan. *National Science Museum, Tokyo*, 26: 83–88.
- Kubodera T. 2006. *Berryteuthis magister nipponensis* Okutani & Kubodera, 1987. Version 06 June 2006 (under construction). <http://tolweb.org/Berryteu->

- this_magister_nipponensis/66578/2006.06.06 in The Tree of Life Web Project, <http://tolweb.org/>
- Laptikhovskiy V.V. 2005. Ecology of the reproduction of coleoid gastropod molluscs. *Dissertation for the degree of Doctor of Science*. Moscow. VNIRO, 321 p. [In Russian]. MS.
- Naef A. 1921. Das System der dibranchiaten Cephalopoden und die Mediterranen Arten derselben. *Mitteilungen aus der Zoologischen Station zu Neapel*, 22: 527–542.
- Nazumi T., Kasahara S., Hamabe M. 1979. Supplements and amendments to the previous paper on reproduction and distribution of *Berryteuthis magister* (Berry). *Bulletin of the Japan Sea Regional Fisheries Research Laboratory*, 30: 1–14.
- Nesis K.N. 1973. Taxonomy, phylogeny and evolution of squids of the family Gonatidae (Cephalopoda). *Zoologicheskii Zhurnal*, 52 (11): 1626–1638 [In Russian, English summary].
- Nesis K.N. 1982. *Concise Key to the World Ocean Cephalopods*. Moscow. Legkaya i Pishevaya Promyshlennost, 360 p. [in Russian].
- Nesis K. N. 1997. Gonatid squids in the Subarctic North Pacific: ecology, biogeography, niche diversity and role in the ecosystem. *Advances in Marine Biology*, 32: 243–324.
- Nigmatullin Ch.M., Laptikhovskiy V.V., Sabirov R.M. 1996. Reproductive biology of *B. magister*: *Commercial aspects of biology of Commander squid Berryteuthis magister and of fishes of slope communities in the western part of the Bering Sea: Scientific results of the Bering Sea expedition of VNIRO by programme of joint Russian–Japanese research of Commander squid Berryteuthis magister and of fishes of slope communities in the western part of the Bering Sea (Bioresources of the seas in Russia)*. Moscow. VNIRO Publishing: 101–124 [In Russian].
- Okutani T. 1968. Review of the Gonatidae (Cephalopoda) from the North Pacific. *Venus*, 27(1): 31–34 [In Japanese].
- Okutani T. 2015. *Cuttlefishes and Squids of the World* [New Edition]. National Cooperative Association of Squid Processors. Tokyo, 247 p.
- Okutani T., Tagawa M., Horikawa H. 1987. *Cephalopods from continental shelf and slope around Japan*. Japan Fisheries Resource Conservation Association. Tokyo, 194 p.
- Roper C.F.E., Sweeney M.J., Nauen C.E. 1984. *FAO species catalogue. Vol. 3. Cephalopoda of the World. An annotated and illustrated catalogue of species of interest to fisheries*. FAO Fisheries Synopsis, 125(3), 277 p.
- Rostov I.D., Yurasov G.I., Rudykh N.I., Moroz V.V., Dmitrieva E.V., Rostov V.I., Nabiullin A.A., Khrapchenkov F.F., Bunin V.M. 2001. *Atlas of oceanography of the Bering and Japan Seas*. Vladivostok: Tikhookeanskii okeanologicheskii institut im. V.I. Il'icheva DVO RAN [In Russian].
- Sasaki M. 1915. On a new species of oegopsids from the Bay of Toyama, *Gonatus septendentatus*. *Transactions of the Sapporo Natural History Society*, 5: 185–189.
- Sasaki M. 1929. A monograph of the dibranchiate cephalopods of the Japanese and adjacent waters. *Journal of the College of Agriculture, Hokkaido Imperial University. Sapporo*, 20, 357 p.
- Taki I., Igarashi T. 1967. A list of cephalopod specimens in the Fisheries Museum, Faculty of Fisheries, Hokkaido University (Sasaki collection and specimens collected by the Marine Zoological Laboratory). *Hokkaido Daigaku Suisangakubu (Hakodate) Suisan Shiryōkan Shiryō* [Hokkaido University Faculty of Fisheries, Hakodate, Hokkaido, Fisheries Museum Contribution] 7: 1–27 [In Japanese].

