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(Cephalopoda)

by K.N. Nesis

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SISTEMA, FILOGENIYA I EVOLYUTSIYA KAL'MAROV SEMISTVA
GONATIDAE (CEPHALOPODA)

TAXONOMY, PHYLOGENY AND EVOLUTION OF SQUIDS OF THE FAMILY
GONATIDAE (CEPHALOPODA)

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After the revision carried out by the author, the family Gonatidae comprises three genera, four subgenera and sixteen species. The genera and subgenera are characterized. Primitive structural features of Gonatidae: radula 7-rowed; tentacles present in adult squid; hooks on tentacles lacking; fixing apparatus non-specialized; hooks on arms weakly developed and appear late in ontogenesis; muscular tissue dense; fin rhombic or oval. Specialized features: radula 5-rowed; tentacles lost in adulthood or strong hooks

* Figures in the right-hand margin indicate the corresponding pages in the original. (Translator)

developing on tentacles of adult squid; fixing apparatus with transverse ridges and grooves; hooks on arms appear early; tissue soft and watery; fin cordiform. Phylogenetic relations between the genera and species of the family are represented schematically. The genus *Berryteuthis* is the least specialized, the subgenus *Gonatus* s. str. is the most specialized. The subgenus *Eogonatus* occupies an intermediate position between them. The genus *Gonatopsis* is diphyletic. Its subgenera, among which *Gonatopsis* is more specialized than *Boreoteuthis*, followed a parallel development. The whole family emerged and evolved in the Pacific boreal realm; the species of *Gonatus* s. str. alone succeeded in penetrating beyond the boundaries of this realm. Their dispersal occurred during the Pleistocene. At present the family has a bipolar distribution. Modern primitive species inhabit the epipelagic zone, demersal waters on the slope, or are eurybathic and rise to the surface at night. Specialized species inhabit the mesopelagic and/or the bathypelagic zone; as a rule, they do not come up to the surface. The family evolved along the line of specialization and development of the life pattern "squid--a predator of the deeps".

COMPOSITION AND TAXONOMY OF THE FAMILY

The family Gonatidae (order Teuthida, suborder Oegopsida) includes common and fairly abundant squids that are widely distributed in the subarctic waters of the North Pacific and North Atlantic, as well as in the Notalian waters of the Southern Ocean^{*}, and are encountered throughout the abyssal region of the Arctic Ocean. They are devoured by sperm whale,

* Translator's note: I.e. the Antarctic Ocean.

bottlenose whale, fur seal, hooded seal, harbour porpoise, salmon and halibut; herring, grenadier, sea perch, albatross, dunce, skua and many others feed on their young. In 1965, the USSR landings of *Berryteuthis magister* (in the Far East) exceeded 28 thousand metric centners,¹ and the squid-jigging industry can be expanded further, although in terms of their food value Gonatidae are inferior to both Loliginidae and Ommastrephidae.

It was believed that the systematics of Gonatidae had been thoroughly studied and that the family comprised 2 genera and 5 species (Akimushkin, 1963; Percy, Voss, 1963). It has been recently proven, however, that the genus *Gonatopsis* includes at least five species and that the most common and abundant species *Gonatus fabricii*, believed to be a cosmopolitan form, is in reality a conglomerate consisting of at least eight or nine affinitive forms (Okutani, 1968a; Okiyama, 1969; Young, 1972; Nesis, 1971). Apart from the two new species already described (Nesis, 1972), we discovered two other species, which had been regarded as invalid (see farther on). The total number of Gonatidae species thus rose to sixteen. Moreover, Young (1972) reports the occurrence of *Gonatus* s. str., a species that has not been described so far, in Antarctic waters. Our materials from the Bering Sea and from the North Pacific include larvae of three *Gonatopsis* species, which we so far failed to correlate with the known adult forms. This family may prove to be made up of no less than eighteen species (Nesis, 1971).

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The abundance of new forms compels us to revise the taxonomy of Gonatidae genera and subgenera. Our data corroborate the view that

¹ I have no data at my disposal that are more recent.

Berryteuthis ought to be classified as an independent genus (Naef, 1923; Ishikawa, 1924; Roper *et al.*, 1969). Phylogenetic analysis of the family leads us to conclude that within each of the genera *Gonatus* and *Gonatopsis* there should be established two subgenera (Nesis, 1971, 1972). The family Gonatidae thus comprises three genera, two of which are composed of two subgenera each.

Diagnosis of the family Gonatidae has been provided in two works (Roper *et al.*, 1969; Young, 1972). Diagnoses of the genera and subgenera are presented below.

Genus *Gonatus* Gray, 1849

Gonatidae with well-developed tentacles at the adult stage; apart from the suckers and rounded knobs, their fixing apparatus includes in the distal area several transverse ridges interspaced by grooves; radula consisting of 5 longitudinal rows of teeth; cordiform fin extending beyond the posterior end of the mantle; hooks on the arms develop at the larval or early postlarval stage.

Subgenus *Gonatus* Gray, 1847 s: str. (= *Lestoteuthis* Verrill, 1880 = *chelotteuthis* Verrill, 1881). Apart from the suckers, the tentacular club bears one or several hooks along its median line. Type species: *Onychoteuthis* ? *amoena* Möller, 1842 = *Onychoteuthis fabricii* Lichtenstein, 1818. Other species: *G. (G.) antarcticus* Lönnberg, 1898; *G. (G.) berryi* Naef, 1923; *G. (G.) onyx* Young, 1972; *G. (G.) californiensis* Young, 1972; *G. (G.) pyros* Young, 1972; ?*G. (G.) camtschaticus* (Middendorff, 1849)²; *G. (G.)* sp. A =

² *G. (G.) camtschaticus* (Midd., 1849) = *Onychoteuthis camtschatica*: Middendorff, 1849: 515-516, Plate 12, Figs. 1-6; ?*Gonatus fabricii*: Okutani, Nemoto, 1964: 112-113, Plate 2, Fig. 2.

Gonatidae type γ Okutani, 1966³.

Subgenus *Eogonatus* Nesis, 1972. The tentacular club bears only sucker. Type species: *G. (E.) tinro* Nesis, 1972.

Genus *Gonatopsis* Sasaki, 1920

Tentacles present only in larvae and in juveniles, are completely reduced in adult squids.

Subgenus *Gonatopsis* Sasaki, 1920, s. str. Radula consisting of five longitudinal rows of teeth. Type species: *G. octopedatus* Sasaki, 1920. Other species: *G. (G.) japonicus* Okiyama, 1969; *G. (G.) okutanii* Nesis, 1972.

Subgenus *Boreoteuthis* Nesis, 1971. Radula consisting of seven longitudinal rows of teeth. Type species: *Gonatopsis borealis* Sasaki, 1923. In all probability it also includes *G. (B?) makko* Okutani et Nemoto, 1964.

Genus *Berryteuthis* Naef, 1921

(= *Pfefferiopsis* C. Ishikawa in M. Ishikawa, 1924, nom. nud. = *Berryiteuthis* Thiele, 1934).

Gonatidae with well-developed tentacles at the adult stage; tentacular club furnished only with suckers; fixing apparatus comprising suckers and rounded knobs; radula of seven longitudinal rows of teeth; fin rhomboid or ovate, does not extend beyond the posterior end of the mantle; hooks on the

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³ *G. (G.)* sp. A = *Gonatus fabricii* adolescent stage: Sasaki, 1929: 268-269, Plate 22, Figs. 10-13; Gonatidae type γ "n. sp.": Okutani, 1966: 66, Plate 3, Fig. 2; 1968a: 34.

arms lacking or develop quite some time after the completion of the larval stage.

Type species: *Gonatus magister* Berry, 1913 (= *G. septemdentatus* Sasaki, 1915). *B. anonychus* (Pearcy et Voss, 1963) also belongs here.

PHYLOGENY AND TAXONOMIC CRITERIA

Before proceeding to the phylogenetic analysis of the taxa composing the family, we must establish which taxonomic features of Gonatidae are primary and primitive, and which ones are more highly specialized.

The radula of *Gonatus* and *Gonatopsis* s. str. consists of five longitudinal rows of teeth; *Berryteuthis* and *Gonatopsis* (*Boreoteuthis*) have a seven-rowed radula characteristic of all the *Coleoidea* (= *Angusteradulata*), including ammonites (Lehmann, 1967), but excepting the octopuses of the suborder Cirrata, where radula is lacking altogether. The five-rowed radula of *Gonatus* and *Gonatopsis* s. str. is the common seven-rowed radula, in which the first marginal tooth disappeared completely (Grimpe, 1927). No other Cephalopoda have a radula of this type. It is beyond doubt that the five-rowed variety developed from the seven-rowed radula. The five-rowed radula is identical in all the species of *Gonatus* s. l. and *Gonatopsis* s. str., a circumstance suggesting that the radula formed as if "spontaneously" as a result of a singular mutation subsequently fixed in the progeny. Squids bite large lumps off their food and do not grind it; the teeth of their radula are poorly specialized and the loss of a row of teeth may have been of no consequence in terms of evolution.

In *Gonatus* and *Berryteuthis* tentacles are well developed; in *Gonatopsis* tentacles are lacking at the adult stage. Larvae of all the

species of *Gonatopsis* are provided with tentacles (Okutani, 1966; Young, 1972; our data). According to our materials, tentacles disappear in *Gonatopsis* after the squids reach a definite size: it occurs at an early age in *G. (B.) borealis*, considerably later in *G. (G.) octopedatus*. In *G. (G.) okutani* rudimentary stalks of the tentacles persist even in adult squids. The structure of the tentacular club in the larvae and juveniles of *Gonatopsis* is species specific and constant. Tentacles do not disappear as a result of their weakening and gradual reduction. They appear to vanish quickly, perhaps at once by breaking off at the base. Tentacles of *Gonatopsis* larvae and juveniles are a normally functioning organ; in evolutionary terms their subsequent disappearance is therefore a secondary phenomenon.

Armature of the tentacles. In the species of *Gonatus* s. str. the central portion of the club bears one or several hooks; in the latter instance the central hook is very large, the distal one is somewhat smaller, the remaining hooks (proximal to the largest one) are quite small. Suckers are arranged on the club in several distinctly outlined groups and vary in size. In *Gonatus (Eogonatus)* and *Berryteuthis* the club bears only suckers. Furthermore, in *B. magister*, the suckers vary in size, whereas in *B. anomychus* and *G. (E.) tinro* they are equidimensional; no distinctly defined groups of suckers. Larvae of all gonatid squids have tentacles furnished with suckers only. In *Gonatus* s. str. the suckers eventually change to hooks. This also occurs after the squid has attained a definite size strictly specified for each individual species.

Fixing apparatus of *Berryteuthis* and *Gonatus* s. l. comprises a row of alternating suckers and knobs extending along the dorsal margin on the club face and on the oral surface of the tentacle stalk. The species of

Gonatus s. str. bear two such rows: one extending along the dorsal, the other along the ventral margin of the stalk. The club face in *Gonatus* s. l. bears a series of transverse ridges interspaced by deep indentations with a sucker at the end of each ridge and a large knob at the rim of each indentation. In the subgenus *Eogonatus* these transverse ridges are weak and short; they number only two or three. *Gonatus* s. str. is furnished with five or six thick, well developed ridges and may have several other short and weak ridges. The ridges on the fixing apparatus develop fairly late, around the time when the hooks appear and the suckers on the clubs become differentiated.

When the tentacular club is furnished with homotypic rather than differentiated suckers and the fixing apparatus comprises only a short row of suckers and knobs extending along the dorsal margin of the tentacle stalk, its structure must be regarded as primary. The development of the hooks, the differentiation of the suckers and the resultant complexity of the fixing apparatus are secondary phenomena.

Armature of the arms. In all the Gonatidae species the middle rows of the suckers on the first three pairs of arms have metamorphosed into hooks, while the fourth pair is furnished only with suckers. In larvae all the arms bear only suckers. The size of the squid at which the hooks appear on the arms is strictly definite. In the species of *Gonatus* s. l. they appear at the larval or early postlarval stage, after the mantle has attained a length of 20-30 mm; they commonly develop (except in *G. berryi*) after the hooks appear on the club. According to our data, they appear latest in *G. (G.) fabricii*, at the mantle length of about 35 mm. In the species of the genus *Gonatopsis* s. l. the hooks develop even later: in *G. (B.). borealis* the first rudiments of the hooks become observable when the mantle reaches

a length of about 35 mm, and the hooks attain full development at the mantle length equal to 45 mm; in the larvae of *G. (G.) octopedatus* and *Boreoteuthis* sp. there is no trace of the hooks when the mantle length is 28 and 33 mm, respectively. Lastly, in *Berryteuthis magister* the hooks appear only after the mantle reaches a length of about 75 mm, and in *G. anonychus* they are present only in adult females and even then number but a few (Pearcy, Voss, 1963). The lack or delayed development of the hooks on the arms is thus a primitive characteristic.

Tissue structure. Tissues, particularly mantle tissues, are fairly dense in *Berryteuthis* and *Gonatopsis (Boreoteuthis)*; the mantle and appendages of these squids are muscular, as in all the free-swimming squids. In *Gonatopsis* s. str., *Eogonatus* and in many *Gonatus* s. str. the tissues are watery, the mantle and appendages are weak and flabby. Since the general body shape and appearance of Gonatidae are those of typical nektonic squids (Naef, 1923), it may be concluded that the flabby tissues saturated with water are a secondary phenomenon, an adaptation to a mode of life where the speed of motions is unimportant, whereas reduction of specific weight is essential.

Fin shape. In *Berryteuthis* and *Gonatopsis (Boreoteuthis)* the fin is rhombic or transversely oval and does not extend beyond the posterior edge of the mantle. In *Gonatus* s. l. and *Gonatopsis* s. str. it is cordiform or (in *G. octopedatus*) reniform with the posterior tip stretched to form a small tail extending beyond the posterior rim of the mantle. The surface area of the fin is therefore smaller in *Gonatus* and *Gonatopsis* s. str. than in *Berryteuthis* and *Boreoteuthis* squids of the same size. It is difficult to determine a priori which shape of the fin is primary, since among the purely nektonic squids there are affinitive species with both rhombic and cordiform

fins. When extended, a rhombic fin is capable of imparting great thrust at high speed and can generate a great lifting power (Spencer, 1969); on the other hand, a cordiform fin ensures a greater manoeuvrability (Zuev, 1966). The fact that rhombic fins are found in the Gonatidae squids provided with a thick muscular mantle, while many species characterized by a poorly muscled watery mantle have cordiform fins, suggests that in Gonatidae (though probably not in the other squid families) the primary shape of the fin was rhombic. p. 1630

Summing up the above, we can draw a table showing the distribution of primitive and specialized features in different genera and subgenera of Gonatidae.

Analysis of the table shows that the species of *Berryteuthis* are the most primitive forms and those of *Gonatus* s. str. and *Gonatopsis* s. str. are the most specialized one with *Boreoteuthis* and *Eogonatus* occupying an intermediate position.

B. anonymus is more primitive than the other species of *Berryteuthis*; it may be the most primitive form among the known Gonatidae. As concerns the species of *Gonatopsis* s. str., *G. okutani* is undoubtedly more primitive than *G. octopedatus*; the latter species, furnished with 6-12 instead of 4 rows of suckers, as is commonly the case, appears to be more highly specialized than *G. japonicus*, which strikingly resembles *Gonatus* s. str. in all but the absence of tentacles.

G. onyx should probably be classified as the least specialized species of *Gonatus* s. str.; it has one single hook on the tentacular club, whereas all the others bear a minimum of two, commonly five or more such hooks. *G. (G.)* sp. A, which retains a semi-larval external appearance well into adulthood, appears to be the most specialized species. *G. berryi*, in which hooks on the

PRIMITIVE AND SPECIALIZED FORMS OF GONATIDAE

Features	Condition of the features		
	Primitive	Intermediate	Specialized
Radula	<i>Berryteuthis</i> , <i>Boreoteuthis</i>	-	<i>Gonatus</i> s. l., <i>Gonatopsis</i>
Tentacles	<i>Gonatus</i> s. l., <i>Berryteuthis</i>	<i>Gonatopsis</i> (<i>G.</i>) <i>okutani</i>	<i>Gonatopsis</i> s. l.
Armature of the tentacular club	<i>Berryteuthis</i> <i>Eogonatus</i>	-	<i>Gonatus</i> s. str.
Fixing apparatus of the tentacles	<i>Berryteuthis</i>	<i>Eogonatus</i>	<i>Gonatus</i> s. str.
Armature of the arms	<i>Berryteuthis</i> <i>anonychus</i>	<i>Berryteuthis</i> <i>magister</i>	<i>Gonatopsis</i> s. l., <i>Gonatus</i> s. l.
Tissue structure	<i>Berryteuthis</i> <i>Boreoteuthis</i>	<i>Gonatus</i> s. str. (in part)	Certain <i>Gonatus</i> s. str., <i>Eogonatus</i> , <i>Gonatopsis</i> s. str.
Shape of the fin	<i>Berryteuthis</i> <i>Boreoteuthis</i>	-	<i>Gonatus</i> s. l., <i>Gonatopsis</i> s. str.

arms develop earlier than in the other species, and *G. pyros*, the only species of this family provided with luminescent organs on its eyes, are more highly specialized than *G. fabricii*, *G. antarcticus*, *G. californiensis* and ?*G. camtschaticus*. The two last pairs of species resemble one another so closely that they might be referred to as genuine twins.

Summarizing the above, we obtain the following evolutionary scheme of the family (Fig. 1). It illustrates the taxonomic isolation of *Gonatus* (*Eogonatus*) *tinro*. With respect to the structure of the tentacular club, this species could be classified with *Berryteuthis*, but it differs from representatives of the latter in five out of seven essential phylogenetic characteristics. The species discussed is closer to *Gonatus* s. str., which it resembles in five characters. It is therefore both logical and reasonable to include *G. (E.) tinro* into the genus *Gonatus* as an independent subgenus. The subgenus *Eogonatus* is an evolutionary stage between the non-specialized Gonatidae of the type *Berryteuthis* and the most highly specialized forms of *Gonatus* s. str.

The scheme also emphasizes that the genus *Gonatopsis* is, strictly speaking, diphyletic: the subgenera *Boreoteuthis* and *Gonatopsis* s. str. evolved in different phyletic branches, stemming from a common root. The tentacles were lost in both the non-specialized phyletic branch characterized p. 1631 by a 7-rowed radula, and the specialized branch provided with a 5-rowed radula. Keeping in mind that the appearance of a 5-rowed radula may have been (as was mentioned earlier) an "instantaneous" ("spontaneous") phenomenon, it may be assumed that the tentacles were cast off by the two phyletic branches before they diverged too far apart and while their genotype and mode of life were still largely identical. We therefore feel that *Boreoteuthis* and *Gonatopsis* s. str. ought to be classified as subgenera rather than as independent genera. The genus *Gonatopsis* is thus an example of parallel development from a common ancestor.

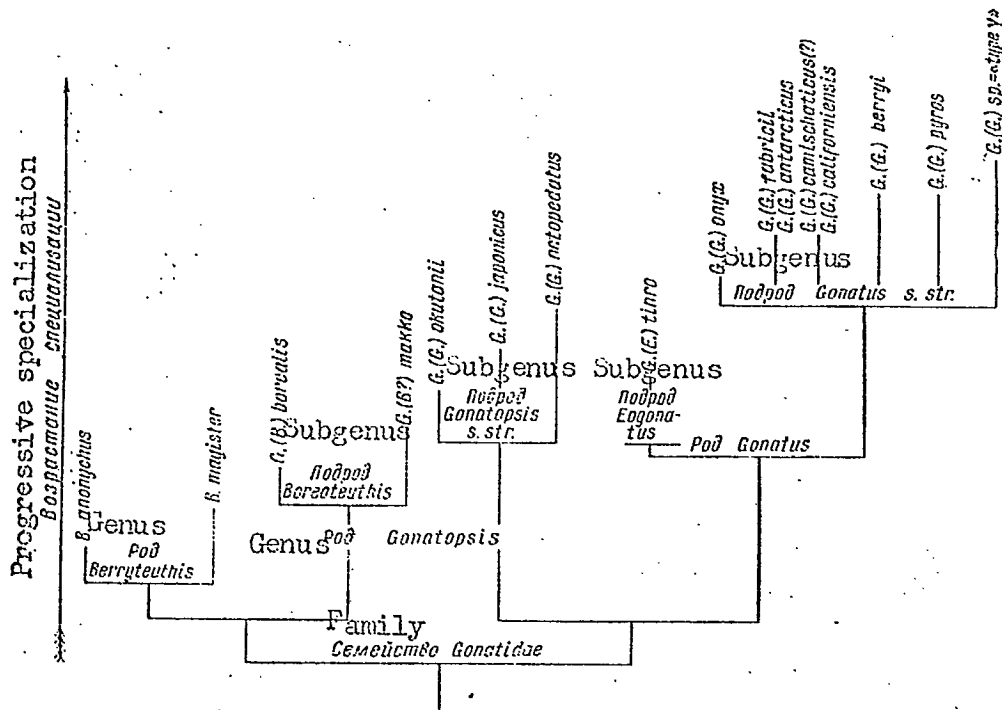


Рис. 1. Схема филогенетических отношений родов и видов Gonatidae

Fig. 1. Scheme of phylogenetic relations between the genera and species of Gonatidae.

DISTRIBUTION AND MODE OF LIFE OF GONATIDAE SQUIDS

Gonatidae are a purely bipolar family occurring in the arctic and temperate waters. They penetrate into the tropical zone only in the "cold tropical regions" off the western coast of America. The centre of the taxonomic diversity of Gonatidae is located in boreal waters of the Pacific Ocean, where all the genera and subgenera, as well as the absolute majority of their species are encountered.

Berryteuthis anonychus, the most primitive species of the family, is found only in the northeastern part of the ocean, from the Gulf of Alaska to central California. *B. magister*, a boreal species, occurs from the Cape Navarin region (Bering Sea) to the Korean Strait and as far as Oregon (Fig. 2A). Of the five *Gonatopsis* 1 species *G. (B.) borealis* is boreal, three others (*G. (B.?) makko*⁴, *G. (G.) octopedatus* and *G. (G.) okutani*) are northern boreal, while *G. (G.) japonicus* has so far been encountered only in the cold waters of the Sea of Japan and is probably also a northern boreal species (Figs. 2B, C).

The genus *Gonatus* is represented in the North Pacific by seven species (Fig. 2D, Fig. 3), two of which (*G. (G.) onyx* and *G. (G.) berryi*) are boreal, while three others (*G. (E.) tinro*, *G. (G.)* sp. A and *G. (G.) camtschaticus?*) are northern boreal. *G. (G.) pyros* was found in the northern Bering Sea ("Ekvator", cruise 3, station B-33, 60°15' N, 179°23' W, squid jigging at

⁴ *G. makko* was recently found (T. Odata *et al.*, Bull. Japan Sea Reg. Fish. Res. Labor., 24 : 21-51, 1973) in the Sea of Japan on the Yamato Bank and on the slope near Oki island, close to the bottom, at the depths of 665-1125 m. *G. octopedatus* was taken on the Yamato Bank at the depth of 635 m.

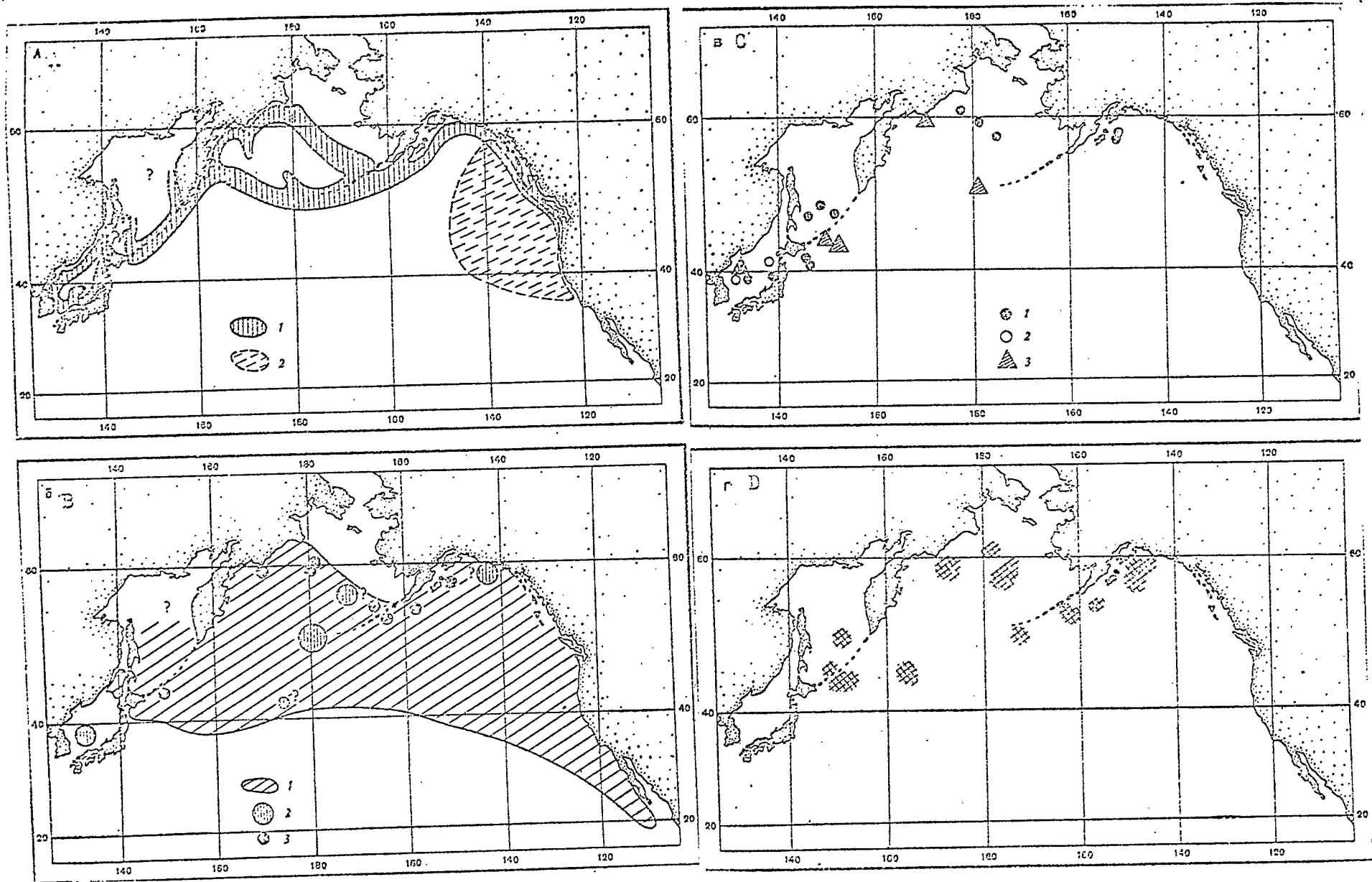


Fig. 2.

Distribution of Gonatidae

A--*Berryteuthis*: 1--*B. magister*, 2--*B. anonychus*; B--*Gonatopsis* (*Boreoteuthis*): 1--*G. (B.) borealis*, 2--*G. (B?) makko*, 3--*G. (B.) spp. larvae*; C--*Gonatopsis* (*Gonatopsis*): 1--*G. (G.) octopedatus*, 2--*G. (G.) japonicus*, 3--*G. (G.) okutani*; D--*Gonatus* (*Eogonatus*): *G. (E.) tinro* (hatched).

the depth of 500 m; 2 specimens with mantle length of 67 mm and 158 mm, respectively; the latter is the largest known specimens) and in the waters off California at 32-34° N; it also appears to be a boreal species. Lastly, *G. (G.) californiensis* was found off California at 28-34° N and is probably a southern boreal-subtropical species (Young, 1972).

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Beyond the North Pacific boundaries we know only two species of *Gonatus* s. str. (Fig. 3). *G. (G.) fabricii* inhabits the arctic regions and the North Atlantic from the pole to the area south of Cape Cod, the Bay of Biscay and Point Barrow (Nesis, 1971a); *G. (G.) antarcticus* (or, according to Young, the two species confused under that name) is found in Notalian waters north as far as Cape Town, Cook Strait and Punta Pariñas (Nesis, 1973). A larva of *G. californiensis*? was caught in the Panama Canal (Young, 1972).

It is evident that the family Gonatidae originated as a whole in the boreal waters of the North Pacific. Its primary evolution also took place in these regions. Gonatidae have successfully adapted to the cold waters of northern boreal regions, but adjusted considerably less well to the warm waters of the southern boreal regions. Eleven of the fourteen North Pacific species have been recorded in the Bering Sea and the Gulf of Alaska, eight species near the southern Kuril Islands, seven species in the northern Sea of Japan, five species near California. Only larvae of two species have been encountered off the southern coast of California, larvae of one species--off the southeastern coast of Honshu. Gonatidae larvae may penetrate into these zones with the sub-surface waters of northern origin (Okutani, 1959; Okutani, McGowan, 1969; Young, 1972), but adult squids cannot exist in these regions.

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Only the species of the most highly specialized group *Gonatus* s. str. dispersed beyond the waters in which the family originated, and even they

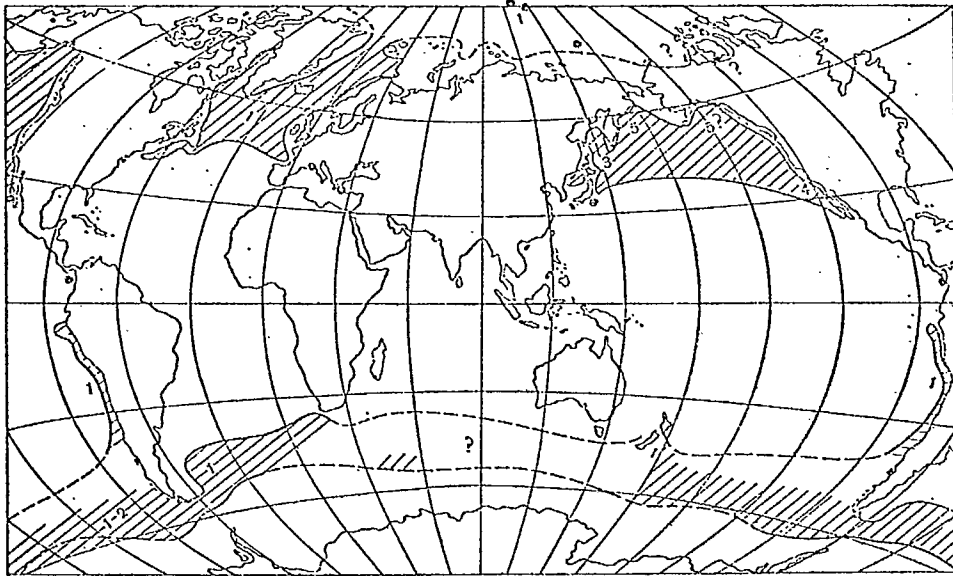


Fig. 3.

Distribution of *Gonatus* s. str.

Figures--number of species in the region; dots--isolated findings outside the main range; dotted line--presumed boundary of the range of the subgenus.

proved unable to overcome the primary adaptation of Gonatidae to cold waters. *G. fabricii* penetrates southward, and *G. antarcticus* migrates northwards only with cold waters, i.e. with cold advection currents, with waters cooled down during the winter or with abyssal waters of upwellings. It suffices to glance at Fig. 3 to perceive that the ancestor of *G. fabricii* migrated to the Atlantic by way of the Bering Sea-Arctic basin-Scandian depression, while the ancestor

of *G. antarcticus* penetrated into the Notalian waters through the California current-cold waters of the upwelling-coastal branch of the Humboldt current (Mercer, 1968; Nesis, 1971, 1971a). This may have occurred at the time, when the water depth over the Bering shelf was considerably greater than it is now, while the depth of equatorial waters in the Panama Canal region was perceptibly smaller. The former may have occurred in the Eopleistocene and during the great interglacial periods, the latter--during the periods of glaciation. The modern range of the family thus formed in the Quaternary period.

Berryteuthis anonychus is an epipelagic species; adolescent and adult squids can be caught at night near the surface (Pearcy, 1965; Pearcy, Voss, 1963; our data). *B. magister* inhabits demersal water layers at the depth of 30 to 1200 m, but mainly between 100 and 600 m; only its juveniles have been caught in pelagic regions (Kondakov, 1941; Berry, 1912; Sasaki, 1929; our data).

Young and adult *Gonatopsis borealis* have been repeatedly caught near the sea surface when attracted by light at night, but have also been taken near the bottom, at depths ranging from 240 to 870 m, as well as in pelagic regions, as by-catches from great depths (Kondakov, 1941; Sasaki, 1929; Young, 1972; our data). Larvae of this species have been encountered at a variety of depths ranging from the surface to 1000 m; we have not succeeded in establishing any relationship between the size of the larvae and the depth at which they were caught. Frequent findings of *G. borealis* in the visceral contents of sperm whales and fur seals suggest that this species is eurybathic, but that it commonly inhabits the epipelagic zone. *G. makko* have been found in the viscera of sperm whales and near the seafloor at the depth of 665 to 1125 m; juveniles of this (?) species have been encountered near the surface

(Okutani, Nemoto, 1964; Okutani, 1966).

Gonatopsis octopedatus have been caught near the bottom at the depths of 635 to 810 m, as well as in pelagic waters, at the depth of 800 to 1000 m (Sasaki, 1920; Okiyama, 1970; our data). This appears to be the form of Gonatidae inhabiting the deepest water layers. *G. okutanii* has been taken both at the surface and at the depths of 500 to 1500 m (Okiyama, 1969; Nesis, 1972). *G. japonicus* have been caught near the surface (Okiyama, 1969).

Gonatus tinro are distributed from epipelagic to bathypelagic layers, but are found mainly in mesopelagic layers (Nesis, 1972).

Larvae of the species of *Gonatus* s. str. (those of *G. fabricii* and *G. onyx* in particular), are found near the surface, as well as down to the depth of 1000 m. As the larvae grow, they abandon the surface waters. During our collections young *G. onyx* and *G. sp.* A specimens were encountered occasionally in the 50-200 m depth range; for the most part, however, both juvenile and adult *Gonatus* were caught at depths over 200 m, in mesopelagic and bathypelagic layers. Adult *Gonatus* appear to be found in epipelagic water layers only in exceptional cases. For example, in Okutani's collections (Okutani, 1966, 1968, 1969, Okutani, McGowan, 1969) there is not one single specimen exceeding 36 mm in length among the squids caught near the surface or at the depths of 140 m or less. Migration to deeper layers with growth has been recorded for the larvae and juveniles of *G. fabricii* in the North Atlantic (Nesis, 1965). Young (i.e. with the mantle length averaging 40 mm) *G. onyx* are found off the coast of Oregon at night mainly in the 200-0 m layer, during the day--in the 500-200 m layer (Pearcy, 1965). Adult *G. fabricii* are found in the North Atlantic mainly at the depth of several hundred meters (Murray, Hjort, 1912; Clarke, 1966). In Antarctic waters there have been recorded two abundance peaks for *G.*

antarcticus: in the 0-250 and 750-1000m layers; the two peaks may correspond to adolescent and adult squids, respectively (Roper, 1969). A specimen of *gonatus* measuring about 18 cm in length, was photographed from the underwater research device "Deepstar" off La Jolla at the depth of 900 m (Church, 1971).

It would thus appear that *B. anonychus*, the most primitive species of the family, inhabits only surface waters, while the other species of the primitive branch (i.e. *B. magister* and *Boreoteuthis*) are either confined to the continental slope, or feel perfectly comfortable in the surface water layers of the open sea. Specialized species of *Gonatus* and *Gonatopsis* (with the exception of *G. japonicus*) are, however, essentially deep-water animals found in the epipelagic regions only in adolescence; their principal biotope comprises the mesopelagic and bathypelagic layers of the open sea and the waters above the continental slope.

EVOLUTION OF GONATIDAE

Analyzing the facts presented above it may be concluded that the ancestor of Gonatidae was a free-swimming (nektonic) squid, which did not dwell at great depths; it was furnished with a powerful muscular mantle, a rhombic fin and a 7-rowed radula; its arms and tentacles were equipped only with suckers; the fixing apparatus of its tentacles were poorly developed.

The appearance of hooks on the arms was an important stage in the evolution of the family. At first they developed only in adult squids, but gradually began to appear earlier and earlier in the ontogenesis. The tentacles with suckers on the clubs appeared then to be functionally redundant and either disappeared (moreover, they disappeared twice, in both evolutionary branches) or the club of the tentacles developed a hook (considerably thicker than that

found on the arms). A tentacle furnished with such a hook was able to operate like a grapple, i.e. in a totally different manner than an arm equipped with hooks. It is therefore natural that tentacles of this kind not only persisted, but grew stronger than the arms. Once that happened, however, it was no longer possible to press together the tentacular clubs furnished with such enormous hooks by using a short and primitive fixing apparatus. But should the long thick tentacles have been allowed to dangle posteriorly while the animal attempted to quickly leap upon its prey, they would seriously impede its mobility. There therefore developed special powerful fixing apparatus operating similarly to a zipper and fastening securely the clubs of the tentacles, as well as a supplementary device for joining the stalks of the tentacles along their entire length. p. 1636

This evolution occurred synchronously with the migration of the squids into the oceanic deeps. In subarctic waters the major bulk of the zooplankton consists of upper-interzonal animals. In the surface layers of water zooplankton abounds only during the short biological summer period, whereas in abyssal layers plankton is available throughout the year (Vinogradov, 1968; Geinrikh (Heinrich), 1961). Having migrated into the deep-water layers, *Gonatus* representatives would have secured an adequate food supply at any time of the year and could have carved out an extensive range for themselves. Here, however, a contrasting factor comes into play, i.e. the paucity of food in the oceanic deeps. At these depths a predator cannot count on catching sufficient amounts of food daily. A bathypelagic predator cannot afford to chase every victim. It is equally inexpedient for the predator to waste energy on maintaining its body in the state of hydrodynamic equilibrium, a factor imperative for all the nektonic squids, because they are heavier than water (Zuev, 1966).

Muscular epipelagic Gonatidae were unable to survive at the great depths. Meso-bathypelagic squids with a flabby watery mantle felt, however, perfectly at ease in these regions. First of all, saturation of the tissues with water reduced the specific weight of the squid body, i.e. increased its floatability; secondly, it decreased its content of metabolically active substances, hence reduced the basal metabolism (Voss, 1967). The large adipose liver allowed the squids to accumulate large reserves of nutrients and increased their floatability (the fat being lighter than water). Once the squids lost their aptitude for moving in quick spurts, it became essential for them to develop a high manoeuvrability and the ability to stretch and reach the prey escaping their grasp. As a result of this there developed a cordiform fin and tentacles in the form of a grapple. Tentacles of the type found in *G. tinro* are transitional between the initial "*Berryteuthis*" type and two evolutionary lines: the loss of tentacles (the path leading to *Gonatopsis*) and their rearmament (the course which resulted in the development of *Gonatus* s. str.).

The abundance of species in the genera *Gonatopsis* and (particularly) *Gonatus*, including sympatric and morphologically close species, which may even be (judging from our so far very limited knowledge on the mode of life of Gonatidae) identical from the ecological viewpoint, demonstrates that the path of specialization followed by Gonatidae and the development of the form "squid--a predator of the deeps" were successful in biological terms. Gonatidae were unable to disperse beyond the boundaries of the regions where they originated, i.e. outside the temperate and cold oceanic waters, but they did attain a high degree of biological progress in these waters.

The biological advance of Gonatidae was not, however, simultaneously a morphophysiological progress in A.N. Severtsov's interpretation (1934). The

main trend of the morphophysiological progress in Cephalopoda was directed towards increasing the activity, developing a free-swimming (nektonic) mode of life. The greatest achievement along this line are nektonic squids, the fast-swimming shoal hunting predators of the type Ommastrephidae or Onychoteuthidae. Octopuses developed via a different course. These are solitary ambushing predators lying in wait for their prey, or foraging predators with strongly developed domestic and nest-building instincts. At the moment we are not concerned with this path. If we examine the evolution of Gonatidae in relation to the main course of the historical development of Cephalopoda from primitive Pholbortellidae and Elsmiroceratidae p. 1637 and up to the modern nektonic squids, we shall encounter only primitive Gonatidae with 7-rowed radula. The Gonatidae which have adapted to abyssal waters, evolved as a result of specialization. The biological progress of Gonatidae occurred as a result of their changing from the path of aromorphosis (arogenesis) to the path of allomorphosis (allogenesis, idioadaptation; Shmal'gauzen, 1939). Allomorphosis appears to be the common road followed by the organisms conquering the oceanic deeps. Once bathypelagic animals become adapted to the abyssal habitat, they switch over to telogenesis, i.e. to narrow specialization. Telogenesis is a characteristic feature of the evolution of many deep-water squids, such as Chiroteuthidae. Gonatidae have not yet reached this stage of development.

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