

Gonatus middendorffi, a New Species of Gonatid Squid from
the Northern North Pacific, with Notes on Morphological
Changes with Growth and Distribution in Immature
Stages (Cephalopoda, Oegopsida)¹⁾

By

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Up to 1970 only four species of the genus *Gonatus* were known, namely, *Gonatus fabricii* (LICHTENSTEIN, 1818), *G. kamtschatica* (MIDDENDORFF, 1849), *G. antarcticus* (LÖNNBERG, 1899) and *G. berryi* NAEF, 1923. However, their systematic characters have not always been clear from the old-fashioned original descriptions.

The new light of the systematics of the genus *Gonatus* was thrown by YOUNG (1972) who described three new species, *G. pyros*, *G. onyx* and *G. californiensis*, and revived long-forgotten name, *G. berryi*, all from off Southern Californian waters. The systematic characters he emphatically used were arrangement of tentacular armatures and relative size of animal corresponding to development of hooks on arms and tentacle. In the same year, NESIS (1972) proposed that the genus *Gonatus* could be divisible into two subgenera, *Gonatus* s. str. with one to several strong hooks on the tentacular club in adult stage, and *Eogonatus* n. subg., based on the unique new species, *G. (E.) tinro*, with only suckers on clubs. Further, he (1973) proposed a new hierarchy of the family Gonatidae discussing evolution of the family. KUBODERA and OKUTANI (1977) added a new species, *G. madokai*, describing not only adult type specimen but also immature stages from the western sector of the northern North Pacific including the Sea of Okhotsk. They suggested from the studies on immature specimens taken therefrom that there is a possibility of existence of more sympatric species of the genus.

In 1976, a peculiar specimen of the genus *Gonatus*, 225 mm in dorsal mantle length, with mature taxonomic characters was collected by Mr. K. MURAKAMI, Kushiro Fisheries Experimental Station, and it was placed at our disposal. In 1979, two more mature males were jigged in the northern North Pacific by Mr. MURAKAMI and Mr. M. MURATA, Hokkaido Regional Fisheries Research Laboratory. On the other hand,

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morphological changes with growth of this squid have been traced from adults backwards to earlier life stages on the basis of larva-net collections made by the research vessels.

This species is characterized by comparatively short and weak tentacles as well as small tentacular clubs. Under the light of the recent systematics of this genus, the structure of tentacular club and other morphological characters were examined to the detail. The results indicate that this species is distinguishable from all of the species of the genus described in the last 10 years. Furthermore, based on careful examinations on the Atlantic *G. fabricii* and Antarctic *G. antarcticus* preserved in the Marine Biological Association of the United Kingdom, Plymouth, and Zoological Museum, Copenhagen, it revealed that both species are clearly different from the present species. Among four species established in the earlier days, only *G. kamtschatica*, of which original description and figures are never enduring for comparison, remained uncertain. *G. kamtschatica* has never been re-discovered since it was established in 1849, except only name was cited by the subsequent workers without any reliable information on taxonomic status of the species. After a long search for the types and subsequent literatures, we finally inclined to consider it as a *species dubia*. A new species here to be described might be identical with the one related by MIDDENDORFF. But, giving a new name to this squid and describing its morphology throughout the life would be not only for the practical purpose to distinguish the species but also lay the ground work for advancing ecological studies of the North Pacific ecosystem in which the gonatids are involved as well as elucidating the hierarchy of the family.

We wish to express our heartfelt thanks to Mr. Kouichi MURAKAMI and Mr. Mamoru MURATA for sending the specimens collected from the northern North Pacific to us. Thanks are also due to Drs. M. R. CLARKE and T. KRISTENSEN, who kindly helped us to examine samples deposited in the Marine Biological Laboratory, Plymouth, and Zoological Museum, Copenhagen. We wish to thank Drs. S. MISHIMA, K. SHIMAZAKI and H. OGI for their valuable suggestions. Our thanks also go to the crews of the research vessels for their cooperation with biologists on board in collecting the material from the sea.

Gonatus middendorffi n. sp.

?*Onychoteuthis Kamtschatica* MIDDENDORFF, 1849, p. 186, Taf. xii, fig. 1–6 (*species dubia*).

Gonatus fabricii: OKUTANI & NEMOTO, 1964, p. 112, pl. 2, fig. 2.

Gonatidae type β : OKUTANI, 1966, p. 65, pl. iii, fig. 1.

Diagnosis. A gonatid squid with long, slender mantle (MW=18% DML), short arms (AIII=50% DML) and muscular body. Tentacles weak with small club (TCL=12% DML). Tentacular manus with a large central hook, an additional one distal to it and 5–6 small suckers among which 2–3 sometimes modified into small hooks proximal to it.

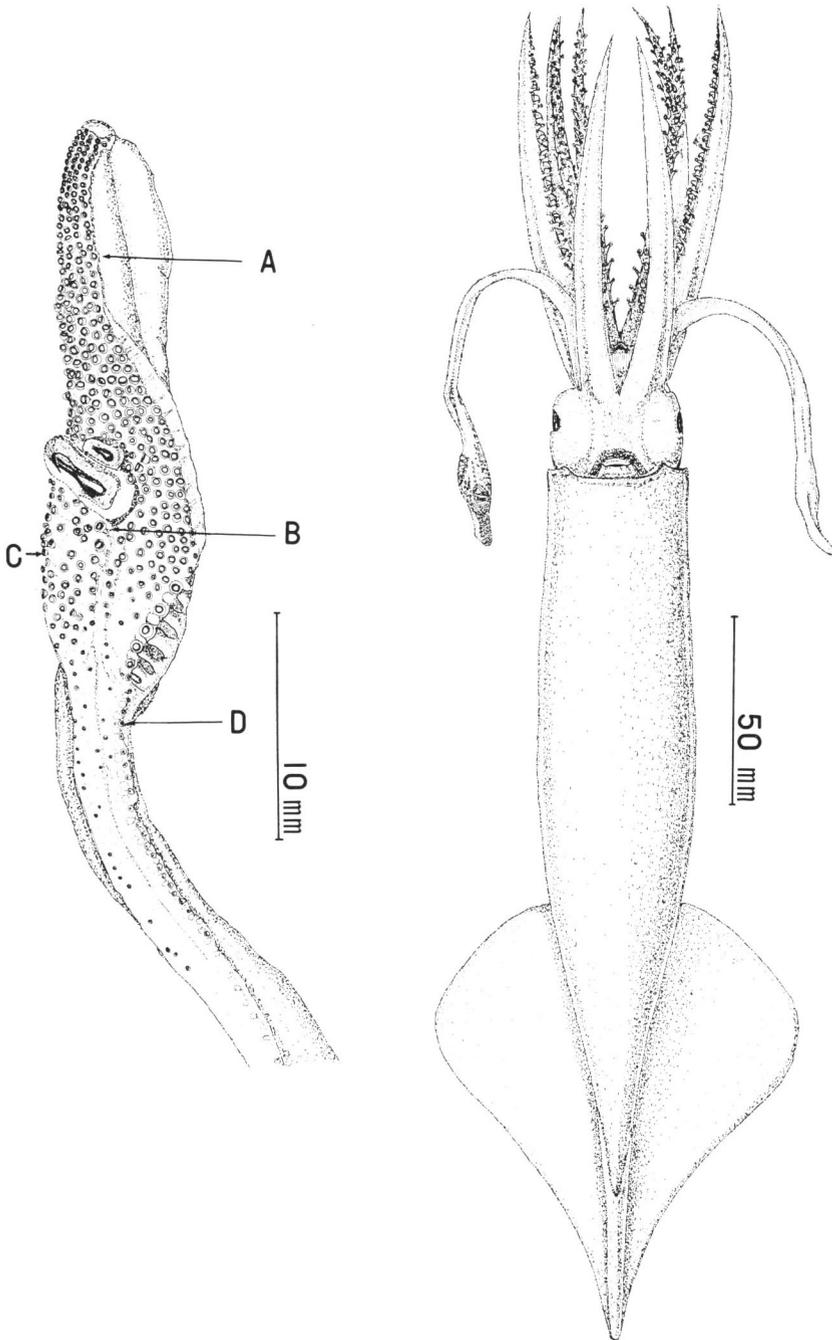


Fig. 1. *Gonatus middendorffi* n. sp. Ventral view of the holotype specimen with tentacular club. A-D correspond to enlarged illustrations of these suckers in Fig. 2A-D.

Description (Figs. 1–3, pl. 1).

Mantle elongate cylindrical, long, slender, moderately thick and muscular, parallel-sided approximately in the anterior half then tapering gently to the pointed posterior end. Ventral excavation shallow, terminating in blunt angles on both sides at the position of funnel cartilages. Antero-dorsal projection small. A long and distinct gelatinous tail continues from the posterior portion of the mantle to the posterior end of the fin.

Body covered with a thin epidermis spotted with purplish chromatophores and easily torn off by handling. Silverly iridescent sheen presents on the lateral surfaces of the mantle.

Fin sagittate in outline with roundish sides and acute extremity. Fin length about half the DML and 1.3 times longer than wide, broadest at about anterior 1/3. The anterior lobe slightly projected anteriorly beyond the base and gently curved to the level of the broadest point then continues to an acute posterior tip.

Head short, almost squarish in shape, slightly narrower than the mantle opening. Eyes large, occupying almost the entire lateral sides of the head. A distinct sinus presents on the anterior edge of each eyelid. Neck moderately constricted and marked off from the head. Two pairs of olfactory crests present on the neck; one lies on just dorsal of the funnel groove and the other on the middle of lateral side.

Funnel small but rather wide with an inverted V-shaped retractor dorsally, free from the head laterally reaching to approximately posterior level of lenses of the eye. Funnel groove smooth.

Funnel cartilages (Fig. 2 J) lanceolate in shape, but both ends rounded and about 11% of DML in length. Median groove very shallow and expanded anteriorly becoming deep and narrow posteriorly.

Mantle locking cartilages linear and ridge-like, almost as same length as the corresponding funnel cartilages.

Nuchal cartilages (Fig. 2 I) rectangular, slightly broader at posterior end with rounded corners, about 10% of DML in length and 3.5% of DML in width. Three straight grooves run along the longitudinal axis of the cartilage, the middle one is the least prominent being about 1/3 in width of lateral grooves.

Funnel organs consist of ventral element which is a pair of large, oval pads, about 15 mm in length and 11 mm in width, and the dorsal element of an inverted V-shaped pad with a short, slender papilla at the anterior apex. From the apex to the posterior end of ramus about 23 mm and each ramus about 8 mm wide. A large semilunar funnel valve presents inside the funnel.

Arms short but thick, muscular, stout proximally and gently tapering to the attenuated distal tips. Arm formula III=II, I, IV. Arms II and III about half of DML. Arm IV about 87% of the Arm III in length. Arm III with pronounced, thick, semi-gelatinous aboral keel along its entire length. Arm IV has thin membranous, large lateral keel along its entire length. Keels of both arms gently taper towards distal tips. Sucker-bearing surfaces of all arms with well-developed margins but less de-

veloped on Arm IV.

Brachial armatures quadriserial throughout. Median two rows of the Arms I, II and III consist of hooks, which are almost entirely covered with fleshy hoods arranged in a zigzag row. Both marginal rows consist of small suckers arranged likewise (Fig. 2 H). Hooks almost same in size at about $2/3$ of arm length then decreasing in size distally. Intervals between adjoining hooks also become smaller distally. Total number of hooks about 45–55 each on Arms I to III. Marginal sucker situated at the distal end of each trabecula and almost similar in structure throughout, decreasing in size towards distal tip. Total number of marginal suckers about 50–55 each on Arms I–III. Arm IV lacks hooks having 4 series of about 150 small suckers. Marginal suckers of the Arm IV slightly larger than those of the Arms I–III. Chitinous rings of marginal suckers of the Arms I–III (Fig. 2 E) all with long and pointed 6–7 teeth on the distal margin, decreasing in size laterally, and smooth proximal border. No difference in size between suckers of marginal and median rows in the Arm IV (Figs. 2 F and G). Chitinous ring of suckers of the Arm IV with long and pointed 7–8 teeth on the distal margin, decreasing in size laterally, and smooth proximal border.

Tentacles weak, slenderer than arms, about half of DML in length with a narrow membranous aboral keel along the stalk. Cross section of tentacular stalk nearly rectangular almost throughout the length.

Tentacular club (Fig. 1 left) extremely small for the size of the animal, approximately $1/10$ of DML, having complicated armatures. Suckers of the dactylus arranged in 4 longitudinal rows, terminating in a circle at the tip, breaking into dorso-marginal and ventro-marginal groups at the border to the manus. Dactylus contains about 100 suckers. Dorso-marginal group consists of 4–5 longitudinal rows of suckers from the distal border of manus to the base of large central hook. Between central hook and carpal group, this group becomes 6–7 irregular rows of suckers diffusing into inner part of carpal group decreasing in number and size. Dorso-marginal group contains about 140 suckers. Ventro-marginal group consists of 3–4 longitudinal rows of suckers from the distal border of manus to the distal portion of large central hook. Proximal to central hook, this group becomes 5–6 irregular rows of suckers, continuing to about half of manus then decreases in number and size proximally extending along the ventral margin of tentacular stalk in a single row. This row of suckers continues to $1/3$ of the tentacular stalk. Ventro-marginal group contains about 95 suckers except for those on the tentacular stalk. Carpal group consists of 5–6 thick, fleshy ridges, each carries a large, smooth-ringed sucker at its proximal end. Alternating with the suckers are large, round fleshy knobs. This area ends to the gap which indicates the proximal limit of club, then a series of alternating small, smooth-ringed suckers and pads continues almost in entire length of dorsal margin of the tentacular stalk. The median zone of manus contains a large central hook with a moderately large hook immediately distal to it. Both hooks covered by fleshy hoods. Proximal to the central hook, 5–6 small suckers continue longitudinally. The distalmost sucker about 1.2

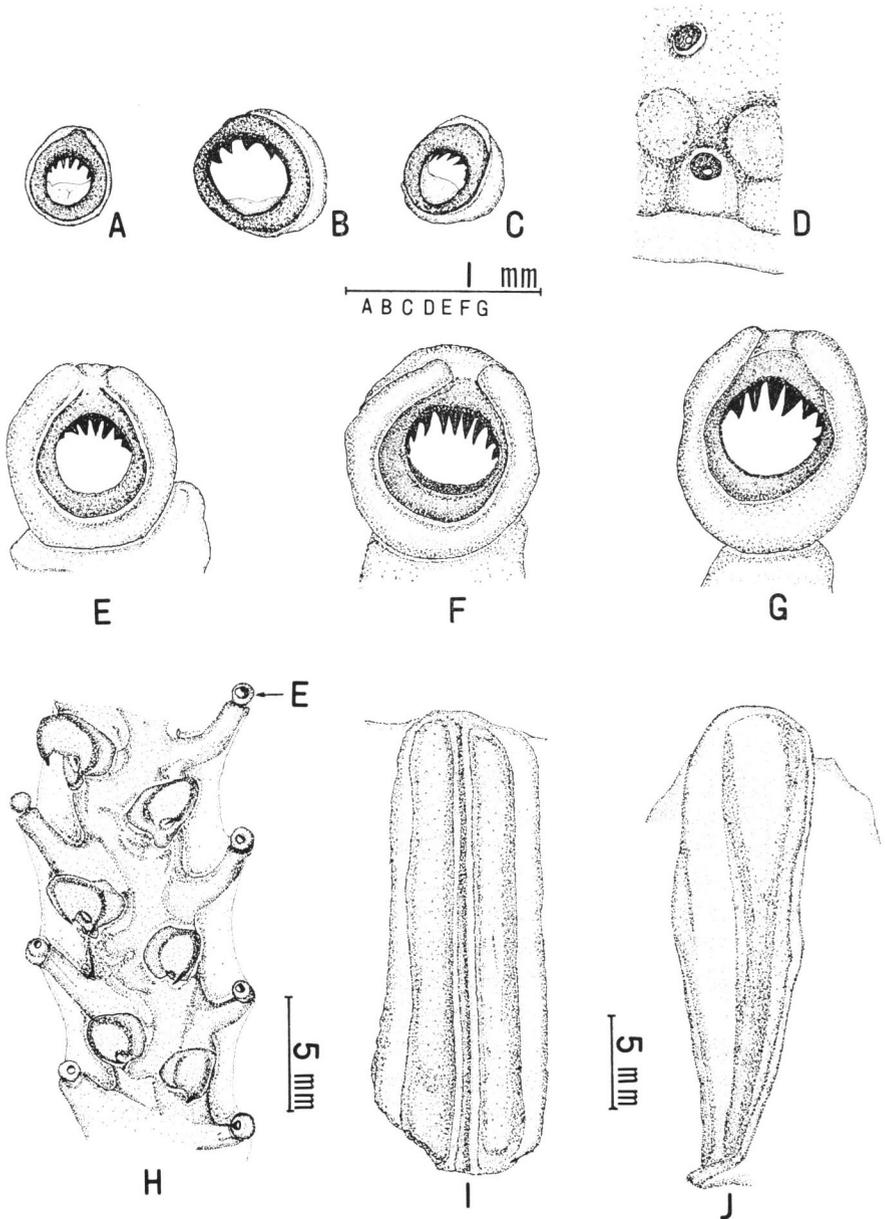
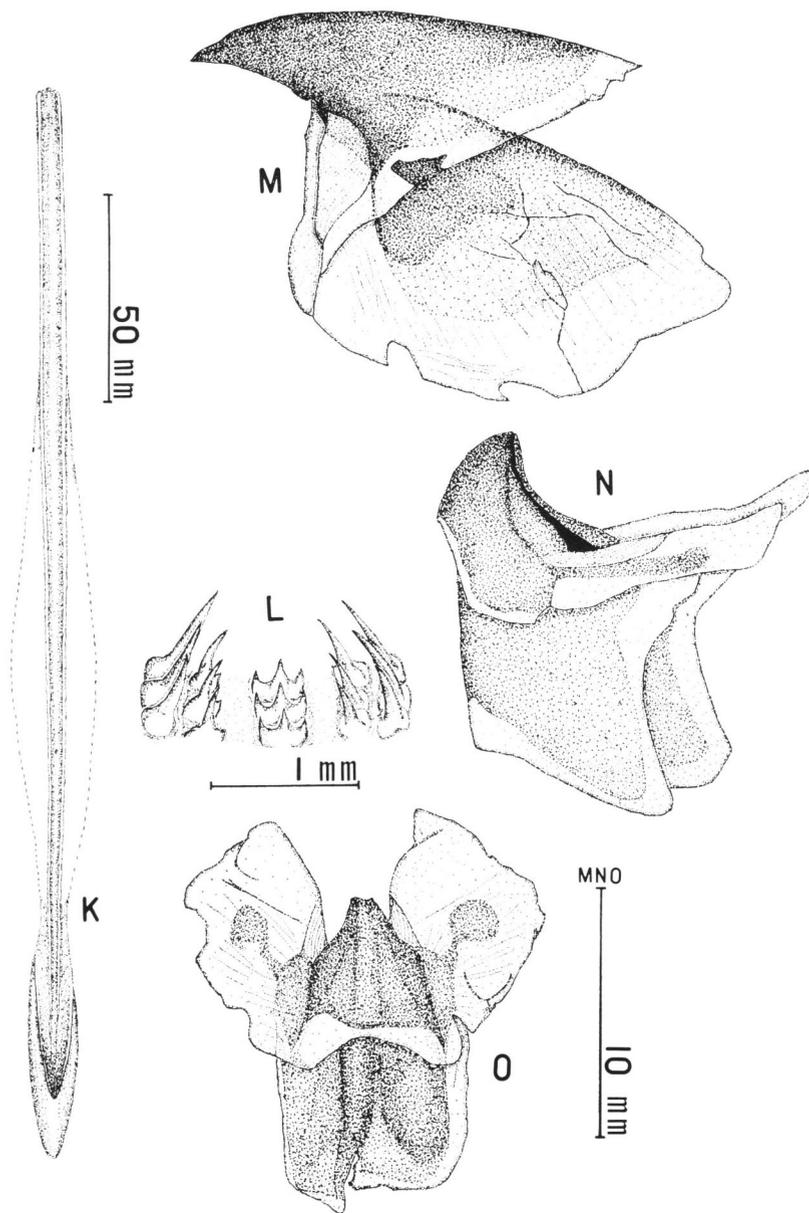


Fig. 2. *Gonatus middendorffi* n. sp. (A-H: Holotype; I-J: Paratype M-1544; K-O: Paratype M-1545) A-C, Suckers of dactylus (A), the manus proximal to the central hook (B), and the ventro-marginal group (C) (cf. Fig. 1); D, Carpal suckers and pads (cf. Fig. 1); E-G, Suckers of the mid-portions of the outer row of the Arm III (E), outer row of the Arm



IV (F), and inner row of the Arm VI (G); H, Mid-portion of the Arm III (E corresponds with Fig. 2E); I, Nuchal cartilage; J, Funnel locking cartilage; K, Gladius; L, Three transverse rows of the radula; M, Upper beak, lateral view; N, Lower beak, slightly obliquely lateral view; O, Lower beak, ventral view.

times larger than the other suckers of club decreasing in size proximally. A few small suckers present on the distal portion of the oral surface of tentacular stalk between marginal rows. Large suckers of dactylus and manus about half in size of suckers of the Arm IV. Suckers of dactylus with 5–6 teeth on the distal margin, decreasing in size laterally and with smooth proximal margin (Fig. 2 A). Suckers of dorso-marginal and ventro-marginal groups with similar dentition, but with slightly fewer teeth (Fig. 2 C). Suckers of median zone of manus with stout, pointed 4–5 teeth on the ventro-distal margin and smooth proximal border (Fig. 2 B). Suckers of oral surface of tentacular stalk with smooth inner ring (Fig. 2 D). Dorso-aboral keel presents on the dactylus. Small trabeculate protective membrane presents on the dorsal margin.

Buccal membrane with 7 distinct lappets and its connectives attach to the dorsal borders of Arms I and II, and to the ventral borders of Arms III and IV, being of DDVV-type.

Upper beak (Fig. 2 M) has acutely pointed rostrum, about 6.1 mm. Jaw angle curved. Outer anterior edge of the wing layer lies behind the anterior edge of lateral wall, forming a distinct semilunar thin plate with a false angle. Semilunar thin plate forms a cutting edge at the shoulder. Wing about 5.9 mm long, slightly extends along the anterior edge of lateral wall, narrowing from front to back. Hood about 16.8 mm, covers about half of the crest. A weak indentation presents on the inner margin of lateral wall. Crest 22.3 mm long. Rostrum, hood and lateral wall darkly pigmented lightening towards transparent marginal zone. About outer 1/3 area of the semilunar thin plate lightly pigmented.

Lower beak (Figs. 2 N, O) has narrow, not so acute rostrum, about 5.7 mm long. Jaw angle obtuse. Cutting edge with crescent-like transparent ridge. Hood narrow, broadest at each side of midline, about 5.2 mm long. Crest about 2.2 times of hood length in central line. Wing narrow, about 9.5 mm in length, about 1.6 times longer than the length of rostrum. The lateral wall nearly parallelogram in shape. Posterior half broadens anteriorly. Lateral wall present neither fold nor thickening. Rostrum and lateral wall darkly pigmented but marginal zone transparent. Wing with lightly pigmented area which is connected to the main dark area of the rostrum by an isthmus in its center.

Radula (Fig. 2 L) with 5 teeth in each transverse row. Central tooth tricuspid with a squarish base. Central cusp slightly longer than the outer ones. Right inner lateral with a single long, pointed cusp slightly curved inwardly, 3 times as long as the central cusp of the central tooth. Left inner lateral tooth has same structure but with a minute cusp on its base. Outer lateral teeth with a single, long, pointed cusp twice as long as the inner lateral teeth and slightly curved inwardly. Both lateral teeth with squarish bases.

Gladius (Fig. 2 K) penniform, with lateral wall along the posterior 73% of the axis, broadened posteriorly at about the middle then decreasing width at the position about 1/5 of the axis and again broadened margining into both walls to form a regular cone at about 5.5% of the posterior portion. Lateral walls badly damaged.

Statolith (Pl. 1, figs. 3–5) with dorsal dome weakly separated from the lateral dome by a groove on dorso-lateral side. Outline of the dorsal dome almost semicircular. Anterior side of the dorsal dome flattened separating from the anterior swell of lateral dome. Lateral dome large, divided into indistinct inferior lobe by a weak groove on lateral side. Outline of the lateral dome, together with the dorsal dome, almost crescent in shape. Rostrum short, about 1/4 of the total length, almost parallelogram in outline. No anterior rostral lobe presents. Dorsal spur weak and the medial fissure shallow. Spur distinct, bluntly triangular in outline, separated from the lateral dome by groove. Indentation roughly triangular in outline and dorsal one deeper than the ventral indentation. Wing broken. Lateral view of the lateral dome, together with the dorsal dome, almost semicircular mound. Shallow grooves present among dorsal dome, lateral dome and superior lobe. Groove in posterior dome weak.

Visceral organs in Paratypes indicate sexual maturity as both carry mature testis and spermatophore sac.

Material examined: Holotype: NSMT-Mo 58621, Lat. 45°30' N, long. 151°40' E, North Pacific Ocean, collected by Mr. K. MURAKAMI, Kushiro Fisheries Experimental Station, Kushiro, on August 29, 1976. Deposited in National Science Museum, Tokyo.

Paratypes: M-1544, Lat. 50°59' N, long. 177°40' E, North Pacific Ocean, collected by Mr. K. MURAKAMI on June 1, 1979. M-1545, Lat. 43°30' N, long. 147°18' E, North Pacific Ocean, collected by Mr. M. MURATA, Hokkaido Regional Fisheries Research Laboratory, Kushiro, on August 30, 1979. Paratypes deposited in the Fisheries Museum, Faculty of Fisheries, Hokkaido University, Hakodate. Measurements are shown in Table 1.

Comparison

At present, 7 valid species are known in the genus *Gonatus*, namely, *Gonatus fabricii*, *G. antarcticus*, *G. berryi*, *G. pyros*, *G. onyx*, *G. californiensis* and *G. madokai*. For comparison of external morphology, some bodily proportions of the present new species *G. middendorffi* and the other known species are summarized in Table 2 except for *G. pyros*, which is clearly distinguishable from the others as it is a sole species having photophore on ventral surface of each eye.

Since bodily proportions are changing with growth, it is necessary to make a comparison among specimens of the same size. In comparisons among types of *G. middendorffi* and *G. madokai*, young *G. fabricii* and *G. antarcticus* under such a consideration, *G. middendorffi* is apparently different from *G. madokai* in having much slenderer mantle, smaller fin and shorter arms. The bodily proportions of *G. middendorffi* are considerably close to those of young *G. fabricii* and *G. antarcticus*. However, *G. middendorffi* has slightly smaller head and longer fin than the other two.

In comparison to the similar size classes of different species, juvenile of *G. middendorffi* has much slenderer mantle, smaller fin and relatively shorter arms than juveniles of *G. madokai*, *G. fabricii* and three sympatric Californian species. Besides such

Table 1. Measurements of *Gonatus middendorffi* n. sp. (in mm)

Characters*	Holotype NSMT-Mo 58621	Paratype M-1544		Paratype M-1545		OS-76727***	OS-76727***	HO-78711***
		male	male	male	male			
Sex		male	male	male	male			
BW	139.0	183.0	245.0	245.0	245.0	4.5	1.6	3.5
DML	225.0	251.0	296.0	296.0	296.0	60.7	40.1	58.8
MW	42.0	44.0	—	—	—	11.3	8.8	11.0
FL	116.5	117.0	—	—	—	23.4	14.6	24.4
FBL	109.5	114.5	—	—	—	20.0	12.6	21.0
FW	90.0	102.0	—	—	—	30.4	19.8	32.8
HW	32.0	38.0	39.0	39.0	39.0	10.0	6.6	9.8
ED	21.5	23.0	22.0	22.0	22.0	6.4	4.2	7.0
NCL	—	25.0	26.4	26.4	26.4	7.0	4.4	7.0
NCW	—	9.5	9.5	9.5	9.5	2.2	1.5	2.4
FCL	—	27.3	26.4	26.4	26.4	7.7	5.3	7.3
FCW	—	7.0	7.2	7.2	7.2	2.1	1.4	2.1
AL	right	I	101.0	141.0	141.0	21.9	13.0	26.5
		II	108.0	104.0	154.0	24.8	15.3	30.5
		III	84.0**	98.0	154.0	24.8	15.4	30.0
		IV	93.0	96.0	139.0	14.5**	8.9**	22.4
left	I	99.0	92.0	140.0	19.0	12.8	25.7	
	II	106.0	103.0	151.0	24.2	14.6	30.1	
	III	109.0	104.0	155.0	24.1	16.0	30.0	
	IV	94.0	96.0	141.0	19.4	9.5	22.8	

AAC	right	I	47/42	50/43	49/43	49/9+22+14	44/13+12+16	52/8+23+14
		II	52/1+48	52/1+46	52/45	52/8+28+10	45/11+16+18	53/8+30+9
		III	35/31**	56/55	57/49	51/9+26+10	46/12+16+16	54/6+29+6
		IV	150/	160/	—	114**/	114**/	130/
AAC	left	I	52/47	—	51/42	50/9+22+12	—	53/9+24+13
		II	50/46+1	56/52	56/48	52/8+25+12	—	54/8+31+6
		III	55/54	56/53	55/47	54/9+28+8	—	53/7+30+6
		IV	145/	150/	—	120/	—	135/
TL	right		114.0	195.0	310.0	30.0	12.0	33.4
	left		111.0	149.0	290.0	31.0	12.3	29.5
TCL	right		23.5	27.0	38.3	6.8	—	—
	left		21.8	25.5	38.1	7.8	—	—

* BW body weight, DML dorsal mantle length, MW mantle width, FL fin length, FBL fin base length, FW fin width, HW head width, ED eye diameter, NCL nuchal cartilage length, NCW nuchal cartilage width, FCL funnel cartilage length, FCW funnel cartilage width, AL arm length, AAC arm armatures count, expressed in suckers/hooks, except counts of minute suckers on tips, TL tentacle length, TCL tentacular club length.

** Whole counts were not taken as the part was mutilated.

*** Conventional specimen number indicating vessel, year, month and day.

Table 2. Percentage of some bodily proportions against dorsal mantle length in *Gonatus middendorffi* n. sp. and 6 *Gonatus* species with schematic formula of the median zone of tentacular armatures.

	<i>G. middendorffi</i> n. sp.		<i>G. madokai</i>		<i>G. fabricii</i> *		<i>G. anti-arcticus</i> *		<i>G. onyx</i> **		<i>G. berryi</i> **		<i>G. californiensis</i> **	
	Types	Juve.	Type	Juve.	Young	Juve.	DML	DML	PL	PL	PL	PL	PL	PL
Range of DML or PL in mm	225-296	40-60	329	40-72	148-186	36-86	235	34-98	23-119	34-98	23-119	29-112	29-112	
mean	18.1	19.7	23.4	28.3	18.2	28.7	—	24.1	32.0	24.1	32.0	27.3	27.3	
range	17.5-18.7	18.6-21.9	—	27.3-29.7	16.9-19.4	24.3-33.0	—	21.4-27.3	25.0-39.4	21.4-27.3	25.0-39.4	18.8-32.6	18.8-32.6	
number	2	3	1	5	2	2	—	10	10	10	10	10	10	
mean	14.1	16.6	17.8	25.6	18.6	27.2	16.2	—	—	—	—	—	—	
range	13.1-15.1	16.5-16.7	—	22.6-27.8	19.3-17.9	20.5-33.9	—	—	—	—	—	—	—	
number	3	3	1	5	2	2	1	—	—	—	—	—	—	
mean	49.2	38.8	56.2	63.2	44.3	41.8	43.8	42.7	44.7	42.7	44.7	42.0	42.0	
range	46.6-51.8	36.4-41.5	—	41.6-70.9	44.2-44.3	39.9-43.6	—	37.3-47.7	39.1-54.6	37.3-47.7	39.1-54.6	34.2-48.6	34.2-48.6	
number	2	3	1	5	2	2	1	7	9	7	9	9	9	
mean	40.3	51.8	48.6	89.9	44.8	61.6	35.7	66.3	70.8	66.3	70.8	62.8	62.8	
range	40.0-40.6	49.4-55.8	—	77.4-94.8	41.2-46.0	51.9-71.2	—	51.4-76.5	60.5-78.8	51.4-76.5	60.5-78.8	53.6-69.6	53.6-69.6	
number	2	3	1	5	2	2	1	10	10	10	10	10	10	
mean	47.4	43.5	90.9	95.9	46.9	48.4	48.1	53.2	63.3	53.2	63.3	48.4	48.4	
range	41.4-52.4	39.7-51.0	—	89.6-102.7	43.9-49.8	47.5-49.3	—	50.0-59.4	60.0-71.7	50.0-59.4	60.0-71.7	46.0-50.0	46.0-50.0	
number	3	3	1	5	2	2	1	10	10	10	10	10	10	
mean	11.2	12.0	20.1	19.8	15.1	21.7	15.0	20.4	31.9	20.4	31.9	20.3	20.3	
range	10.2-12.9	—	—	18.7-20.5	14.8-15.4	21.4-22.0	—	16.3-22.4	21.7-37.0	16.3-22.4	21.7-37.0	16.8-23.7	16.8-23.7	
number	3	1	1	5	2	2	1	10	10	10	10	10	10	
TCAF	HHsssss or HHshss	HHshss	HHhhhh	HHsssss or HHshss	HHhhhh or HHhhhhhh	HHhhhhhhhh	HHhhhh	Hsssss	HHhhhhhh	HHhhhhhh	HHhhhhhh	HHhhhh	HHhhhs	

* The specimen deposited in the Marine Biological Laboratory, Plymouth, and Zoological Museum, Copenhagen. ** After YOUNG (1972). TCAF: Tentacular club armatures formula expressed in the number of hooks or suckers from distal to proximal with symbols H indicating the distal large hook, H, the central large hook, h, the proximal small hook and s, the proximal small sucker. See Table 1 for abbreviations of characters.

differences, distinct characters of *G. middendorffi* by which one can easily distinguish it from the others are extraordinarily smaller tentacular club and weaker stalk. Tentacular club length of *G. middendorffi* is less than 13% of DML throughout the life while exceeding 15% in the other species. The differences of these values are not so pronounced, but the meagerness of tentacular club will be apparent visually.

As proposed by YOUNG (1972), the structure of tentacular club and stalk is one of important systematic characters, especially arrangement of armatures on the median zone of the manus and oral surface of the stalk. Typically, the median zone of the manus contains one large central hook with a relatively smaller hook immediately distal to it and some of much smaller hooks or suckers proximal to the large central hook. The schemes of the arrangements of armatures in each species are summarized in Table 2. The sequence of the symbols indicates the numbers of hooks and/or suckers from distal to proximal, such as H indicating the distal large hook, **H**, the central large hook, h, the proximal small hook and s, the proximal small sucker.

G. middendorffi has the distal and central large hooks and 5 small proximal suckers among which 2–3 are sometimes modified into immature hooks on the median zone of the manus even in mature animal. On the other hand, all of the other species, except *G. onyx*, have already developed two large hooks and 3–6 small proximal hooks in young stages. *G. onyx* is a sole species having only central large hook with very small proximal suckers on the manus.

The size at which the armatures of tentacular club and arms develop is not only useful for classification but also implied in life form of the species. In *G. middendorffi*, the large central hook of manus is still immature and distal hook still remains as suckers even in the largest specimen, about 60 mm DML, collected with a larva net. The distal and central hooks of *G. madokai* are also still in process of development at about 70 mm DML. While, in all four Californian species, armatures of median zone of the manus are metamorphosed into mature hooks at smaller than 30 mm PL, as they

Table 3. The known largest size of species and the size at which arm and tentacular club hooks develop for eight *Gonatus* species.

Species	Known largest size (in mm)	Arm hook (in mm)	Club central hook (in mm)	Club distal hook (in mm)	Club proximal hook (in mm)
<i>G. middendorffi</i> n.sp.	296 (DML)	20–30(DML)	>60(DML)	>60(DML)	>250 (DML)
<i>G. madokai</i>	329 (DML)	20–50(DML)	>72(DML)	>72(DML)	>72 (DML)
<i>G. fabricii</i> *,**	249 (DML)	20–40(DML)	30–40(DML)	40–50(DML)	40–50 (DML)
<i>G. antarcticus</i> **	340 (DML)	—	—	—	—
<i>G. pyros</i> ***	42 (PL)	16–21(PL)	14–19(PL)	17–22(PL)	21–27 (PL)
<i>G. californiensis</i> ***	122 (PL)	25–29(PL)	16–24(PL)	24–31(PL)	35–41 (PL)
<i>G. onyx</i> ***	98 (PL)	24–27(PL)	16–24(PL)	—	—
<i>G. berryi</i> ***	199 (PL)	6–8 (PL)	12–17(PL)	19–28(PL)	26–34 (PL)

* After CLARKE (1966). ** The specimen deposited in the Marine Biological Laboratory, Plymouth. *** After YOUNG (1972). DML: Dorsal mantle length. PL: Pen length.

reach to adult form at comparatively smaller size than two species from the north-western North Pacific. An observation on the specimens deposited in the Marine Biological Association of the United Kingdom, Plymouth, revealed that *G. fabricii* in the Atlantic seems to have a mature tentacular club at larger than 60 mm DML. Comparing among the known largest specimens and the size at which armatures of the tentacular club developed (Table 3), the species of which armatures are not developed completely until comparatively larger size seems to grow bigger than those having mature armatures at smaller size. The size at maturity or full growth of species could be thus estimated by comparing the developmental phase of armatures in the earlier life stages.

In summarizing above comparisons, *G. middendorffi* is characterized by slender muscular mantle, small head, relatively short arms, weak tentacular stalk, small tentacular club, less than 13% of DML, having two hooks and 5–6 small suckers, some of which occasionally modify into incomplete hooks proximally. This species seems to attain about 250 mm DML at maturity.

Morphological Changes of *Gonatus middendorffi* n. sp. with Growth during Immature Stages

Among the specimens collected with a larva net in the northern North Pacific during 1975–1976, five types of immature *Gonatus* squids have been discriminated. However, immaturity of taxonomic characters and lack of adult specimens prevented us to determine some of them into species level. But, one of them was successfully traced to the adult specimen. It was *G. madokai* and descriptions of morphological changes with growth were given together with establishment of a new species (KUBODERA & OKUTANI 1977). The earlier stages in growth of that species were tentatively divided into three, namely, “Adolescent”, “Postlarval” and “Larval” stages according to external morphology with special emphasize to development of tentacular armatures.

The immature stages of the present new species were also identified on the basis of such characters as long, slender, muscular mantle, small tentacular club, structure of tentacular armatures and some bodily proportions. The largest specimen of *G. middendorffi* in the larva net collection is about 60 mm DML. It is classified to “Adolescent” stage based on the same standard applied for *G. madokai*. While, the smallest is about 20 mm DML, which is in “Postlarval” stage. The border of these two adjoining stages may lie at about 34–40 mm DML. Characters of immature *G. middendorffi* throughout examined range are given as follows (Fig. 3, A–F):

Mantle long, slender, muscular, widest at the anterior margin of the mantle and tapering to the posterior pointed end. Ratio of MW/DML about 20% in larger specimen while about 24% in smaller specimens.

Fin sagittate in larger specimens while oval in smaller specimens, attaining only about 30% DML in length and 50% in width in advanced specimens, while 18%

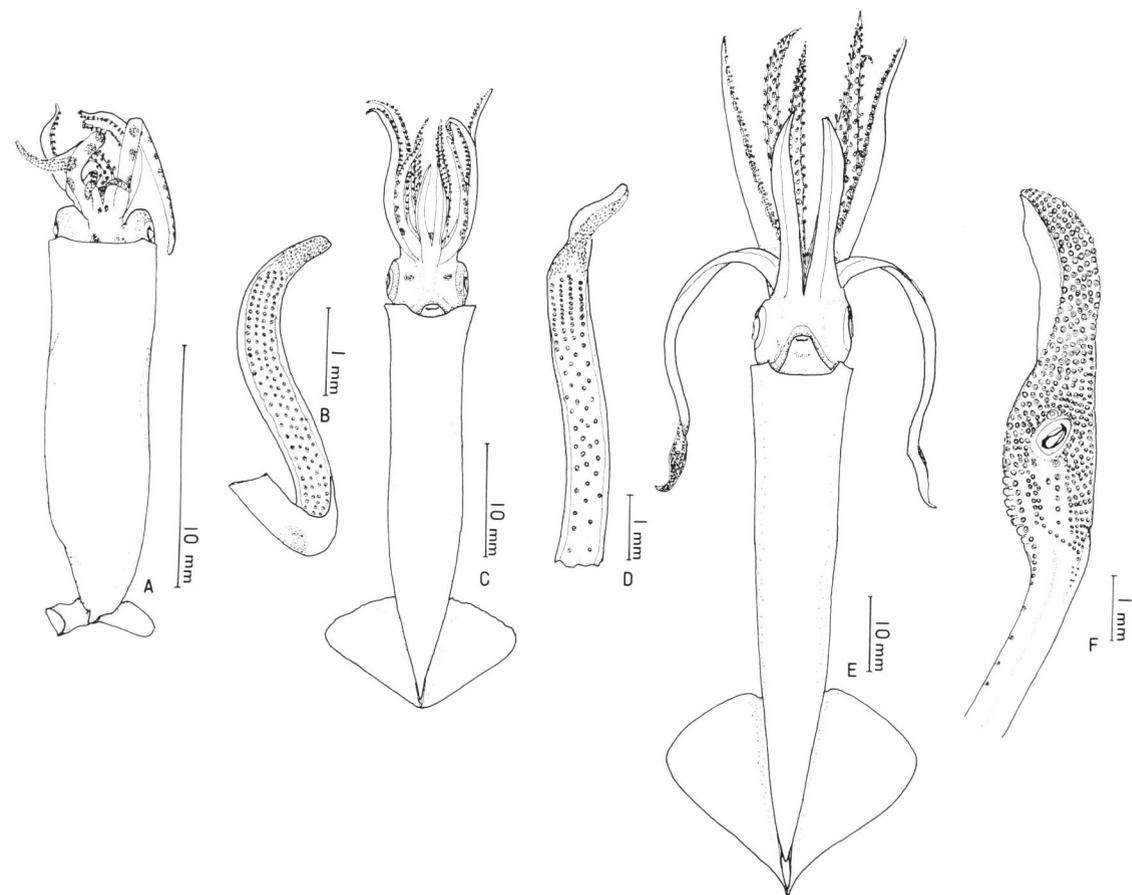


Fig. 3. *Gonatus middendorffi* n. sp. Morphological sequence with growth, ventral views of immature specimens and tentacles. A, 16 mm DML specimen; B, Tentacle of the same; C, 35 mm DML specimen; D, Tentacle of the same; E, 72 mm DML specimen; F, Tentacle of the same.

and 45% in earlier ones, respectively.

Head large as same as the mantle opening and squarish in shape. Eyes large enough to occupy almost entire lateral sides. Distinct sinus presents on the eyelid recognizable in larger specimens.

Funnel large, muscular, reaching to the anterior level of the lenses in advanced specimens, but not so large, sometimes withdrawn into the mantle cavity in smaller specimens.

Arms moderately long and muscular. Arm formula II, III, I, IV throughout the examined range. Arm II longest of all, about 45% DML and Arm IV about 35% in larger specimens, while 30% and 15%, respectively, in smaller specimens. Arm IV

with thin membranous aboral keel. Arm armatures normal for the genus. Median two rows of the Arms I, II and III modified into hooks at about 20–30 mm DML.

Tentacle as same as or slightly longer than the Arm II throughout the examined size spectra with complicated tentacular club in specimens larger than about 35–40 mm DML.

Tentacular club small, not exceeding 15% DML in length in specimens larger than 40 mm DML. Tentacular club not developed at smaller than 35 mm DML and distal portion covered with minute sucker buds followed by methodical four longitudinal rows of small suckers proximally, decreasing in number reducing into two sparse rows at the base. Armatures of club in specimens larger than 40 mm DML consist of compact 4–5 rows of small suckers on the dactylus and 7–10 rows on the distal 1/3 of the manus breaking into dorso-marginal and ventro-marginal groups with development of a large immature hook, slightly large sucker immediately distal to the former, and five small suckers proximal to the same. Ventro-marginal group consists of 4–5 longitudinal rows, decreasing in number proximally and finally terminating at about proximal limit of the club. Dorso-marginal group consists of 4 longitudinal rows continuing to the distal end of the carpa lgroup decreasing into two longitudinal rows at the inner part of the carpal region and merging transversely and obliquely into the ventro-marginal group. Carpal group consists of 6–7 thick ridges, each carries a large sucker at proximal end. Proximal to this group, small suckers extend along the dorsal margin of the stalk in a single row. Large central sucker not yet metamorphosed into a hook in 40 mm DML specimen.

Distribution

Localities at which holotype and paratype specimens were collected are plotted in Fig. 4. The type locality is located in the Pacific off southern Kurile Islands, while localities of paratypes are in the southeast off Kiska Island (M-1544) and in the Pacific off eastern Hokkaido (M-1545). Only other information concerning the distribution of adult specimen was by OKUTANI and NEMOTO (1964) who reported a single specimen from the food of sperm whale caught in the inner part of the Alaskan Gulf. That specimen was about 300 mm DML and provisionally identified to be *G. "fabricii"*, at is has a much elongated mantle. A re-examination of this specimen revealed that it also belongs to *G. middendorffi*. It may be thus concluded that the present new species is distributed in an extensive area extending from the eastern sector to western sector of the northern North Pacific.

In the almost entire areas of the northern North Pacific, Bering Sea and Okhotsk Sea, 315 micronekton samplings were conducted by the R/V *Oyashio-Mar*u, the R/V *Habomai-Mar*u and the T/R *Oshoro-Mar*u during the mid-April to early September in 1975 and 1976. The net used for this sampling was a Maruchi-A type net of NAKAI (1962), a conical net 1.3 m in mouth diameter and 4.5 m in length of which the anterior 3 m is about 2.5 mm in mesh-size and the rest is about 0.3 mm in mesh-size. The net

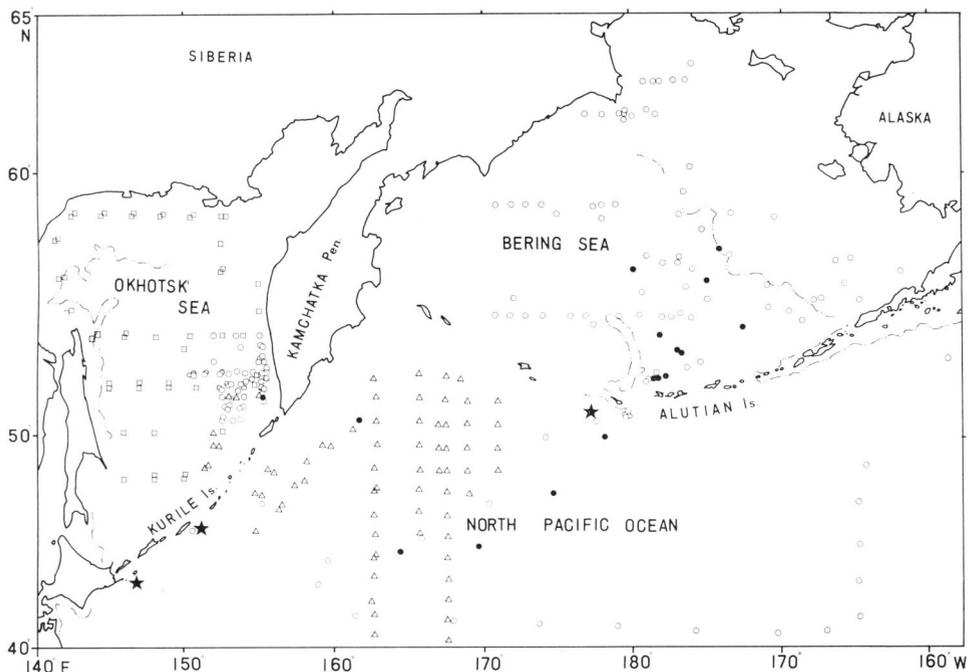


Fig. 4. Localities of the type specimens (stars) and larva-net sampling stations during 1975 and 1976. Each solid symbol indicates the positive station and blank symbol does negative station for immature specimens of *Gonatus middendorffi* n. sp. Triangles are April–May stations, circle (and dots), June–July stations and square, August–September stations.

was towed by all boats immediately below the sea surface for 10 minutes at about 2 knots one hour after sunset.

About twenty thousands larval cephalopods in total were collected with these sampling. Among them 248 specimens were identified to be immature *G. middendorffi*. Detailed examination on them is still in the progress. For the purpose of giving an outlook of distribution pattern of immature stages, sampling and positive stations for *G. middendorffi* are plotted also in Fig. 4.

During the mid-April to late May in both years, investigations were made in the western sector of the northern North Pacific between $165^{\circ}30' E$ and $171^{\circ}00' E$ and between $39^{\circ}30' N$ and $52^{\circ}30' N$ as well as the Pacific and Okhotsk Sea sides along the Kurile Islands. But, there was no positive station during that period. In June and July, the survey extensively covered the Bering Sea and the northern North Pacific. In the Okhotsk Sea, sampling in this period was concentrated in the coast off southern Kamchatka. In the Bering Sea, positive stations were restricted in the southern sector between Bowers Ridge and the continental shelf demarcated off by a 200 m-isobath. There was no occurrence on the shelf, central area and off Cape Navarin. Not many

sampling stations in the North Pacific were present in this period, nevertheless distribution of immature *G. middendorffi* seems to be biased northwesterly. In spite of heavy sampling off the coast of southern Kamchatka in the Okhotsk Sea, there was only a single positive station near the Chishima Pass. During August to early September, the survey covered broad range in the Okhotsk Sea with no positive station.

As larval squids have so little capability of avoiding samplers that their distribution and abundance in netted samples may reflect those in the ocean. The larval distribution of this species indicates that *G. middendorffi* is distributed in the area extending from southern Bering Sea to northwestern North Pacific and occasionally in the part of Okhotsk Sea. The larval specimens mentioned here all came from just below the sea surface at night, so that the above comment may be concerned only limited time-space fraction of the whole larval population.

Discussion

The genus *Gonatus* is one of exceptional genera among the Oegopsida in respect to such a diversity within a single genus. (Another example may be the genus *Histioteuthis* among others.) NESIS (1973) proposed an evolutionary scheme of this genus. He considered that *G. onyx* YOUNG will be the most primitive form among this genus from view point of possession of only a single central hook of the club. He also took a pair, *G. kamtschatica* (*G. camtschaticus* in his paper) and *G. californiensis*, a "genuine twin" because of a very closeness in morphology. It is not clear if he could recognize *G. kamtschatica* based on such an ambiguous original description. If his "*G. camtschaticus*" was conspecific with our new species, we disagree that these two species are a twin. Because *G. californiensis* has 3 additional hooks proximal to the central hook on the club, relatively stronger tentacles and smaller size at which the central club hook develops (smaller than 20 mm in *G. californiensis* vs larger than 40 mm in *G. middendorffi*). If we retain NESIS's view of evolutionary trend, our species should be placed between *G. onyx* and *G. fabricii-antarcticus* complex, which means at the second primitive grade within this genus. The accumulation of biological data of this family from various aspects lead us a different view of the evolution of this family, but it seems to be still premature to put the conclusive comment here.

As has been frequently pointed out that the family Gonatidae plays a very important role as the major diet of the marine lives in the Subarctic Pacific. This species also occupies a significant portion of the food of salmon, particularly *Oncorhynchus nerka* and *O. kisutch*, which feed this species selectively (KUBODERA, MS). Therefore, this species may be a key species in the study on marine food web in the Subarctic Pacific.

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Explanation of Plate 1***Gonatus middendorffi*** n. sp.

Figs. 1–2. Holotype specimen (225 mm DML)

1. Ventral view
2. Dorsal view

Figs. 3–5. Statolith

3. Anterior view
4. Posterior view*
5. Lateral view*

(* A crack on the lateral dome is the trace of mending
as it was broken after Fig. 3 was taken.)

