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Conchocele bisecta (Conrad, 1849) (Bivalvia: Thyasiridae) from Cold-Water Methane-Rich Areas of the Sea of Okhotsk

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Abstract. Dense aggregations of *Conchocele* sp., containing sulfur- and methane-oxidizing endosymbiotic bacteria, were found in 1986 near cold-water methane-rich seeps off Paramushir Island (Kuril Islands, Sea of Okhotsk, depth 750–804 m). Upon examination of shell morphology and gross anatomy, this species proved to be *Conchocele bisecta* (Conrad, 1849) widely distributed in the northern Pacific Ocean. This is the first record of this species in Russia. In the Sea of Okhotsk it is found only in zones of cold-water methane-rich seeps. We presume that *C. bisecta* also occurs in other parts of its range in organic-rich sediments with high total methane and sulfide concentrations. A description of *C. bisecta*, including some additional data on shell morphology, gross anatomy, geographic distribution, and habitat, is presented.

INTRODUCTION

In the spring of 1982, fishermen and then researchers of the Institute of Volcanology, Russian Academy of Sciences, found sound-scattering anomalies northwest of Paramushir Island, Kuril Islands (50°30.8′N, 155°18.45′E) (Avdeiko et al., 1984; Obzhirov, 1993). The studies of volcanologists have shown that the anomalies were formed by gas plumes of methane-rich fluids from a gas hydrate area on the submarine slope of Paramushir Island (depth 750–800 m). In June–July 1986, a joint expedition of the Institute of Oceanology, Russian Academy of Science (R/V *Akademik Mstislav Keldysh*) and the Institute of Volcanology (R/V *Vulkanolog*) examined these methane-rich vents and the benthic animals (Kuznetsov et al., 1987, 1989). Dense aggregations of the bivalve *Conchocele* sp. and a polychaete of the family Ampharetidae were found immediately near the vents. The polychaete was subsequently assigned to a new genus and described as *Pavelius ushakovi* Kuznetsov & Levenstein, 1988 (Kuznetsov & Levenstein, 1988). The bivalves were large (shell length 12 to 15 cm [Kuznetsov et al., 1991]) and had some anatomical features suggesting that they were a new species (Kuznetsov et al., 1987, 1989). Study revealed the presence of sulfur- and methane-oxidizing symbiotic bacteria in the body of *Conchocele* sp. (Galchenko et al., 1988a, b; Strizhov et al., 1990; Kuznetsov et al., 1991). Bacterial symbiotrophy proved to be the principal mode of feeding by *Conchocele* sp. near methane-rich vents of Paramushir Island, supplemented by sestonophagy. However, despite all these investigations, the morphological study of the shell and the identification of this species have not yet been performed.

Expeditions of 1996–1998 of the Pacific Research Institute of Fisheries and Oceanography (R/V *Professor Kaganovsky*; R/V *TINRO*) in the Seas of Japan and Okhotsk found abundant fresh valves and live individuals of a species of the genus *Conchocele* Gabb, 1866. Moreover, in collections of the Zoological Institute, Russian Academy of Sciences, and the Pacific Research Institute of Fisheries and Oceanography, we found unrecorded material of this species from the Sea of Okhotsk and the Pacific Ocean. We were also given materials on *Conchocele* sp. from Paramushir Island deposited at the Institute of Oceanology, Russian Academy of Sciences. Comparative analysis of the results of research in shell morphology and the gross anatomy of these specimens with descriptions and pictures of all species of the genus *Conchocele* occurring in the northern Pacific showed that we are dealing with one species, the well known *Conchocele bisecta* (Conrad, 1849). This is the first record of this species for the Russian fauna.

Shell morphology and anatomy of the soft parts of Recent *C. bisecta* are described in several works (Oldroyd, 1924; Nakazima, 1958; Bernard, 1972; Kuznetsov et al.,

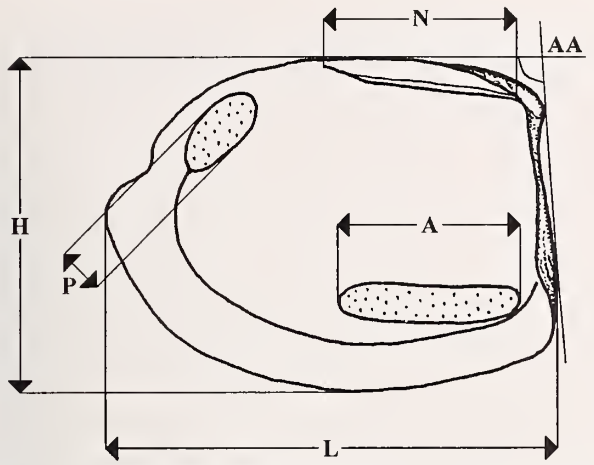

Figure 1. Placement of shell measurements: A—length of anterior adductor scar; AA—apical angle; H—height; L—shell length; N—length of nymph; P—width of posterior adductor scar.

1991). Nevertheless, the discovery of this species in different areas of the Seas of Okhotsk and Japan supplements the description of this species with new data on shell morphology, anatomy, and distribution in the northwestern Pacific.

The following abbreviations are used: IMB, Institute of Marine Biology, Russian Academy of Sciences, Vladivostok; MIMB, Museum of the Institute of Marine Biology, Vladivostok; IORAS, Institute of Oceanology, Russian Academy of Sciences, Moscow; PRIFO, Pacific Research Institute of Fisheries and Oceanography, Vladivostok; ZIN, Zoological Institute, Russian Academy of Sciences, S.-Petersburg; ZMU, Zoological Museum of Far East State University, Vladivostok.

MATERIALS AND METHODS

In this study we have used the material of *C. bisecta* collected by expeditions PRIFO (Kyushu-Palau Ridge, Pacific Ocean, R/V *Mys Tikhiy*, 1982; Sea of Japan, R/V *Professor Kaganovsky*, 1996; west coast of Kamchatka, Sea of Okhotsk, R/V *TINRO*, 1997, 1998), IORAS (Paramushir Island, R/V *Akademik Mstislav Keldysh*, 1986; northeastern coast of Sakhalin Island, R/V *Akademik M.A. Lavrentiev* 1998), ZIN (southeastern coast of Sakhalin Island, R/V *Novoulyanovsk*, 1984; northeastern coast of Sakhalin Island, R/V *Novodrutsk*, 1987).

All live specimens from various collection areas were fixed in 4% formaldehyde solution and then with 70% ethanol.

Figure 1 shows the position of our shell morphology measurements. Shell length (L), height (H), width of each valve (W) (not shown on the picture), length of anterior adductor scar (A), width of posterior adductor scar (P), length of nymph (N) and apical angle (AA-angle between the line parallel to the ventral nymph margin and the line parallel to the anterior shell margin or [if the anterior shell margin is concave] the line running through the beak and shell angle formed at the transition of the anterior into ventral shell margin) of intact and partially damaged specimens were measured, and ratios of some of these parameters to shell length (H/L, W/L, A/L, P/L, and N/L) were determined. Shell measurements were made using calipers with an accuracy of 0.1 mm.

The gross anatomy and internal structure has been described from whole mount specimens.

SYSTEMATICS

Conchocele bisecta (Conrad, 1849)

(Figures 2–22, Table 1)

Venus bisecta Conrad, 1849:724, pl. 17, figs. 10, 10a.
Conchocele disjuncta Gabb, 1866:27, pl. 7, fig. 48a, b.

Type material and locality: *Venus bisecta*, holotype (USNM 3518), two almost complete valves, length 46.5 mm (incomplete), height 53 mm (incomplete), thickness 38.9 mm (incomplete); paratypes (USNM 561518 (originally USNM 3518), 563440 (originally USNM 3500)), five specimens; Astoria, Oregon, Miocene fossil (Moore, 1963).

Conchocele disjuncta, lectotype (Academy of Natural Sciences, Philadelphia); Deadman Island, near San Pedro Bay, California, Pliocene fossil (Bernard, 1972).

Material examined: Three lots from the northeastern Sea of Okhotsk (57°02′N, 152°29′E–57°16.8′N, 152°40.4′E), 482–491 m, silty sand + H_2S, bottom temperature 1.65°C, Coll. V. A. Nadtochy, 14 October 1997 and I. V. Volvenko, 3 November 1998 (R/V *TINRO*) two whole specimens; ZMU (no number), one whole specimen and one right valve); one lot from west coast of Kamchatka, Sea of Okhotsk (55°00′2″N, 154°06′3″E), 522–531 m, mud + H_2S, bottom temperature 2.2°C, Coll. V. A. Nadtochy, 15 September 1997 (R/V *TINRO*) (one whole specimen, six right and four left valves); one lot from Paramushir Island, Kuril Islands, Sea of Okhotsk (50°30.88′N, 155°18.14′E), 792–804 m, mud + H_2S, Coll. A. P. Kuznetsov, 4 July 1986 (R/V *Akademik Mstislav Keldysh*) (IORAS (no number), one whole specimen and one right valve); two lots from northeastern coast of Sakhalin Island, Sea of Okhotsk (52°22′9″N, 144°38′4″E), 502–517 m, mud + H_2S, Coll. V. V. Fedorov, 28 July 1987 (R/V *Novodrutsk*) (ZIN (no number), one whole specimen) and (54°26.751′N, 144°04.940′E), 702 m, sandy silt + shell fragments, Coll. S. V. Galkin, 17 August 1998 (R/V *Akademik M. A. Lavrentyev*) (one whole specimen, one right valve); two lots from southeastern coast of Sakhalin Island, Sea of Okhotsk (45°53′2″N, 143°53′E and 47°14′8″N, 143°42′7″E), 510 m and 300–320 m, correspondingly, silty sand, Coll. S. D. Grebelny, 19 and 20

September 1984 (R/V *Novoulyanovsk*) (ZIN (no number), one left and one right valves); one lot from Sea of Japan (42°19.6′N, 131°10.6′E), 130 m, silty sand, Coll. V. V. Gulbin and Yu. M. Yakovlev, 20 May 1996 (R/V *Professor Kaganovsky*) (MIMB (no number), three right and one left valves; ZMU (XII 14973/Bv-1936), one right valve); one lot from Kyushu-Palau Ridge south of Shikoku Island (Japan), Pacific Ocean (24°46′N, 134°39′E–28°03′N, 135°39′E), 3–18 January 1982 (R/V *Mys Tikhiy*) (PRIFO (no number), two right and two left valves). Total of seven whole specimens, 16 right and eight left valves.

Description: Exterior: Shell very large (to 165.4 mm in length), thick, inequilateral, equivalve (left valve sometimes slightly more inflated), subquadrate, elongated posteriorly, apical angle 90°–125°, high (H/L = 0.69–0.84), convex (W/L = 0.22–0.33), white under periostracum. Periostracum thin, gray-yellow, not adherent, usually peeled off near beaks, in adult specimens preserved only on shell margins. Surface with conspicuous growth lines. Beaks small, prosogyrate, terminal, anteriorly placed. Anterior end abruptly truncated. Posterior end ovate-angulate with distinct radial sulcus extending from beaks to tip, forming deep notch in posterior shell margin and separating distinct posterodorsal depressed area from main part of valve; another very faint radial ridge extending from beaks to ventral shell margin causing hardly noticeable ventral angulation. Anterior shell margin straight (sometimes concave), almost vertically extending ventrally, forming distinct (almost right) angle at transition to ventral shell margin. Ventral shell margin slightly curved. Posterodorsal shell margin straight or slightly convex, extending almost horizontally, parallel to ventral margin, forming rounded angle at transition to posterior shell margin. Posterior shell margin rounded, with deep notch, smoothly transitioning to ventral margin. Lunule just below beaks, smooth, wide, well expressed along entire anterior shell margin, demarcated by the ridges extending along anterior shell margin from beaks to ventral shell margin. Escutcheon absent. Ligament opisthodetic, external, long and elliptical, with calcareous deposition in inner layer, partly sunken, extending from beaks to posterior pedal retractor muscles, attachment to strong and broad nymph, consisting of three layers: periostracum ligament layer, outer ligament layer, and inner ligament layer.

Interior. Hinge plate thin, without teeth. Nymph strong, long (N/L = 0.33–0.63), wide, with a small shelf along ventral nymph margin, extending from beaks to three-quarters of distance to posterior shell margin. Pallial line without pallial sinus. Anterior muscle scar large, long (A/L = 0.40–0.48), ovately elongate, extending almost parallel to ventral shell margin. Posterior muscle scar small (P/L = 0.12–0.21), ovate. Interior of valves white, smooth, with fine radiating striae, more visible near anterior muscle scar; sulci visible as two prominent ridges.

Gross anatomy: Mantle thin, margins thickened. Mantle fusion limited to a small interconnection below the posterior adductor, forming a posterior exhalant aperture. Anterior adductor muscle very large, greatly elongated, curved almost parallel to ventral shell margin. Posterior adductor muscle small, broader than anterior, ovate. Foot long, vermiform, with bulbous distal section. Anterior pair of narrow pedal retractor muscles passing as a single sheet of muscle from base of foot parallel to dorsal margin of posterior adductor toward either side of esophagus and attaching dorsal to anterior adductor muscle. Posterior pedal retractors vertically passing dorsally from base of foot and attaching dorsal to posterior adductor muscle. Ctenidia thick, dark, consisting of two demibranches, equal in width and thickness (sometimes the outer demibranch slightly smaller than the inner). Labial palps forming small triangular extensions of anterior margins of proximal oral groove, lying close to antero-ventral corner of gill. Mouth wide, situated posteriorly on mid-dorsal line of anterior adductor muscle. Esophagus extending along dorsal side of anterior retractor muscle. Stomach divided into two parts: anterior—elongated and narrow; posterior—short and globular. Two ducts of digestive diverticula opening into anterior stomach compartment. Short combined midgut-style sac (though no style detected) extending posteriorly. Hind gut forming an anterior loop dorsal to mid gut, running anteriorly, then turning dorsally and passing through the heart and running posteriorly dorsal to kidney and posterior adductor muscle, opening at ventral side of posterior adductor muscle (food remains present in hind gut and stomach). Digestive diverticula and gonad forming a single large mass penetrated by a complex system of ciliated ducts. Kidneys large, elongate, unlobed sacs, occupying a postero-dorsal position between posterior adductor muscle and heart. Heart triangular, lying between kidney and dorsal margin of digestive diverticula.

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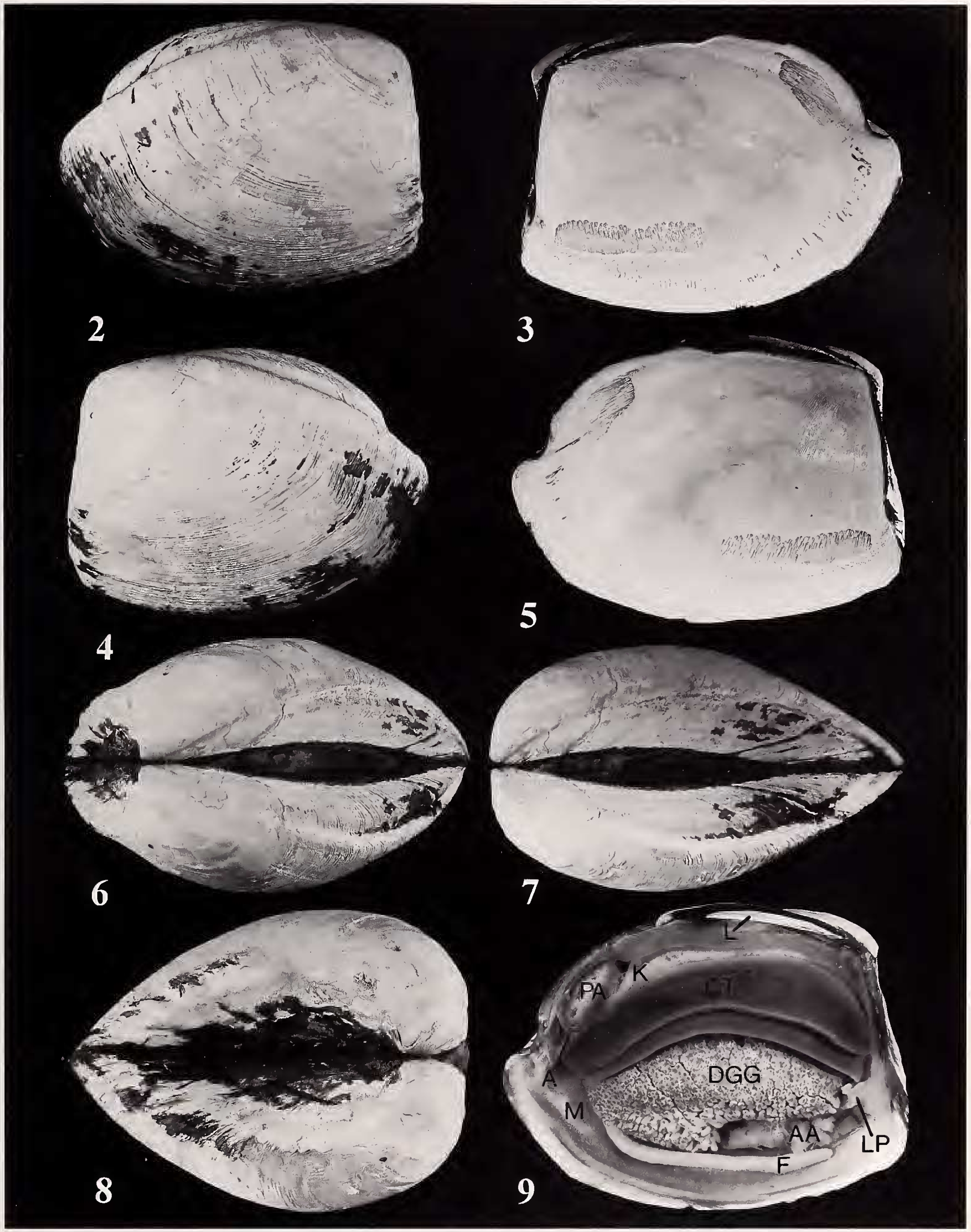
Figures 2–9. *Conchocele bisecta* (Conrad, 1849), west coast of Kamchatka, Sea of Okhotsk (57°02′N, 152°29′E), 482–491 m. Figures 2, 3. Right valve, length 152.5 mm. Figures 4, 5. Left valve, length 152.5 mm. Figure 6. Dorsal view of both valves. Figure 7. Posterodorsal view of both valves. Figure 8. Anterior view of both valves. Figure 9. Organs of the mantle cavity as seen from the right side with shell and mantle removed. Key: A—anus; AA—anterior adductor muscle; CT—ctenidia; DGG—digestive gland and gonad; F—foot; K—kidney; L—ligament; LP—labial palp; M—mantle; PA—posterior adductor muscle.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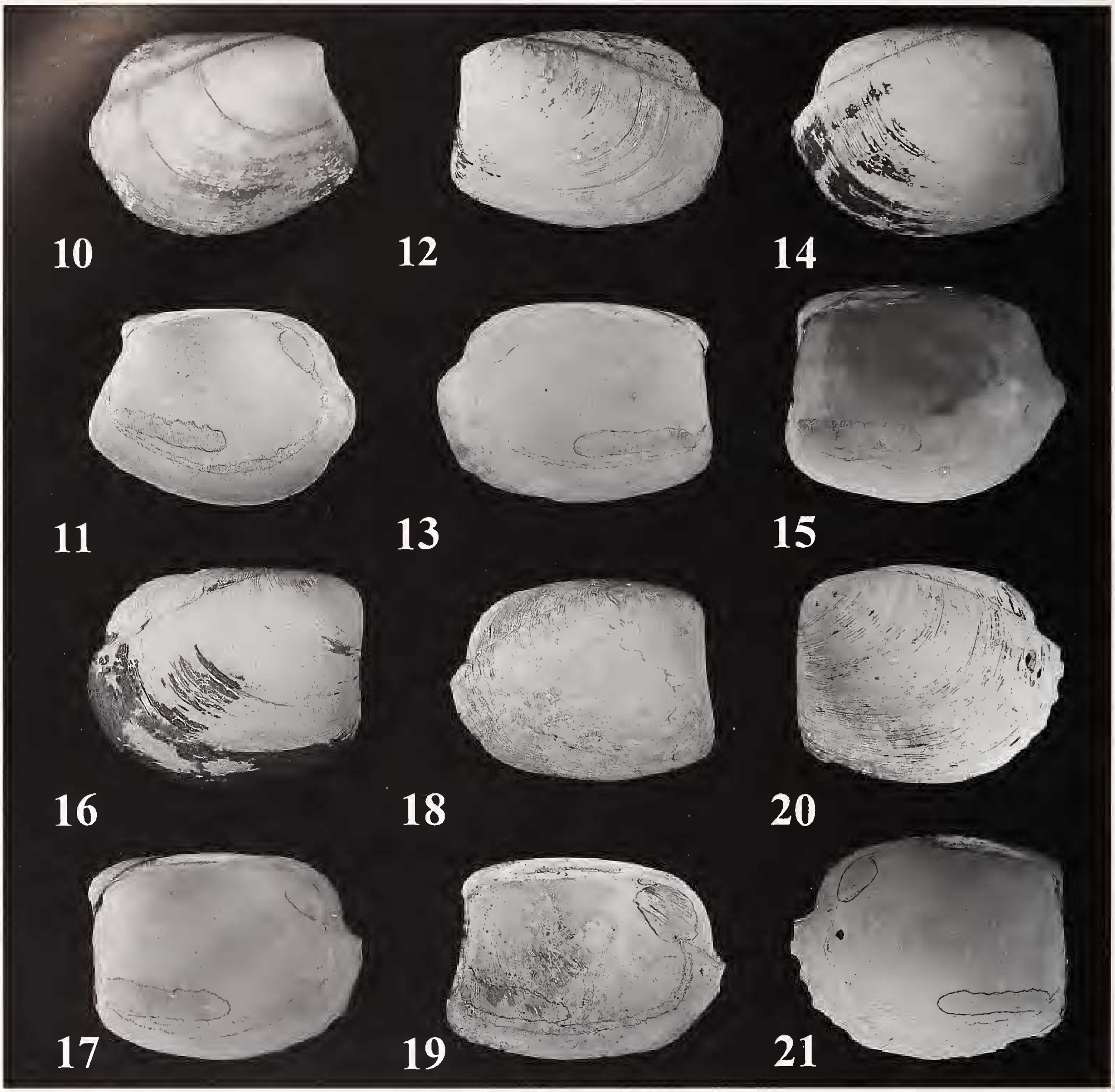

Figures 10–21. *Conchocele bisecta* (Conrad, 1849). Figures 10–15. West coast of Kamchatka, Sea of Okhotsk (55°00′2″N, 154°06′3″E), 522–531 m. Figures 10, 11. Right valve of young specimen, length 46.8 mm. Figures 12, 13. Left valve, length 78.9 mm. Figures 14, 15. Left valve, length 127.9 mm. Figures 16, 17. Paramushir Island, Sea of Okhotsk (50°30.88′N, 155°18.14′E), 792–804 m, right valve, length 77.5 mm. Figures 18, 19. Sea of Japan (42°19.6′N, 131°10.6′E), 130 m, right valve, length 133.3 mm. Figures 20, 21. Kyushu-Palau Ridge, Pacific Ocean, left valve, length 131.3 mm.

Variability: Shell shape and proportions distinctly change with age (Table 1). In young specimens (up to 50–70 mm), in contrast to adults, the shell is much thinner, more rounded, and less convex; the apical angle is larger; the beaks are more prominent; the anterior shell margin is concave; the lunule is less expressed; the nymph is shorter; and the anterior muscle is more vertical (Figures 10, 11). Moreover, in young specimens the mantle is thicker, the posterior part of stomach is not globular, kidneys and digestive diverticula are smaller, the ducts of digestive diverticula are shorter, and the tubules branch off almost immediately. In adult specimens the shell shape and proportions also vary significantly. Shell height, width, and apical angle vary. Some specimens

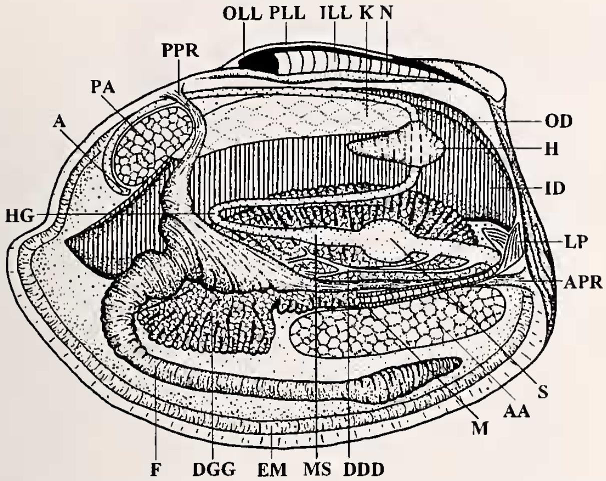

Figure 22. *Conchocele bisecta* (Conrad, 1849) (specimen from west coast of Kamchatka, Figures 2–9): internal morphology as seen from the right side with the right ctenidium and digestive diverticula removed. Key: A—anus; AA—anterior aductor muscle; APR—anterior pedal retractor muscle; DGG—digestive gland and gonad; EM—edge mantle; F—foot; H—heart; HG—hind gut; ID—inner demibranch; ILL—inner layer of ligament; K—kidney; LP—labial palp; M—mouth; MS—mid gut and style sac; N—nymph; OD—outer demibranch; OLL—outer layer of ligament; PA—posterior aductor muscle; PLL—periostracal layer of ligament; PPR—posterior pedal retractor muscle; S—stomach.

have a rather elongated shell. Many exhibit a concave anterior shell margin (Figures 12, 13). This is especially characteristic of specimens from the southern Sea of Okhotsk and the Sea of Japan (Figures 18, 19). All of these specimens have a concave anterior shell margin. In addition, *C. bisecta* from the Sea of Japan is distinguished by a far thicker shell, a wider and longer nymph, and noticeably wider anterior and posterior adductor scars (Table 1). Variable anatomical features are relative length of the foot and bulb form.

Remarks: Live individuals of *C. bisecta* were found in Puget Sound, Washington (Dall, 1892). Dall placed *C. disjuncta* in a synonymy of *C. bisecta* because he did not notice significant distinctive features between these species (Dall, 1895, 1901). However, in succeeding years many investigators regarded Recent *C. disjuncta* and *C. bisecta* as separate species (Tegland, 1928; Habe, 1964; Boss, 1967; Golikov & Scarlato, 1967; Keen, 1969; Bernard, 1972, 1983). Nevertheless, some American and Japanese researchers consider *C. disjuncta* to be a synonym of *C. bisecta* (Kanno, 1971; Abbott, 1974; Habe, 1977, 1981; Coan & Scott, 1997; Higo et al., 1999; Coan et al., 2000).

All the authors who thought *C. disjuncta* and *C. bisecta* to be separate species distinguished them only on the basis of shell morphology: different apical angles (larger in *C. bisecta*), a concave outline of the anterior surface and the more prominent beaks in *C. bisecta,* larger sizes and more quadrate shell form in *C. disjuncta*. In addition, Bernard (1972) pointed to a number of anatomical differences between these species. Our studies showed that with regard to shell morphology and gross anatomy all large specimens from the Sea of Okhotsk were identical to *C. disjuncta* (Gabb, 1866; Nakazima, 1958; Okutani, 1962; Bernard, 1972), whereas young specimens were identical to *C. bisecta* (Conrad, 1849; Bernard, 1972). Moreover, some individuals had conchological features of both species. Hence, we believe that conchological and anatomical differences between *C. bisecta* and *C. disjuncta* are due to the age and individual variability of one species, *C. bisecta* (see "Variability" section).

For the recent fauna of Russia this species was erroneously stated as *Thyasira bisecta* (Conrad) solely on the basis of some finding of shell fragments at a depth of 20 m in Posiet Bay (southern Peter the Great Bay, Sea of Japan) (Golikov & Scarlato, 1967). Judging from fragments, the shell was about 70 mm high. Later on, this same material was presented as *Conchocele "disjuncta* Gabb" (Scarlato, 1981). However, in 1984 Ivanova & Moskaletz (1984) described a new species, *Conchocele scarlatoi* Ivanova & Moskaletz, 1984 (holotype shell length 70.9 mm) that was found approximately in the same region (Vityaz Bay, southern Peter the Great Bay) at a depth of 30 m. They stated that shell fragments found by Golikov & Scarlato (1967) in Posiet Bay belong to this species. However, Coan et al. (2000) considered *C. scarlatoi* to be a synonym of *C. bisecta.* We have examined fragments of shells from Posiet Bay, deposited at ZIN, as well as the type and supplementary material (different-aged individuals) of *C. scarlatoi* and also believe that this material represents one and the same, described as *C. scarlatoi*. As distinct from *C. bisecta*, different-aged individuals of this species have a triangular-angular shell, with an apical angle always less than 90°, a slightly convex anterior shell margin, extending dorsally; a straight posterior shell margin; and a well expressed lunule. All these features are rather stable and slightly prone to age and individual variation.

Distribution and habitat in the western Pacific: In the Sea of Okhotsk (Figure 23)-the northeastern Sea of Okhotsk (57°02′N, 152°29′E–57°16′8″N, 152°40′4″E); western Kamchatka (55°00′2″N, 154°06′3″E); Paramushir Island (50°30.88′N, 155°18.14′E) (Kuznetsov et al., 1987, 1989; Galchenko et al., 1988b; Kuznetsov & Levenstein, 1988); northeastern (54°28.5′N, 144°00.0′E; 54°22.5′N, 144°05.0′E; 53°24.0′N, 144°33.0′E) (Biebow & Hütten, 1999), (52°22′9″N, 144°38′4″E) and southeastern (45°53′2″N, 143°53′E; 47°14.8′N, 143°42.7′E) Sakhalin Island. In the Sea of Japan—the southern Primorje, Russia (42°19.6′N, 131°10.6′E); Chuetsu, Niigata Prefecture, Japan (37°48.6′N, 138°42.3′E) (Ito, 1989); Mishima, Yamaguchi Prefecture, Japan (35°27′N, 130°35′E) (Kanno,

Table 1

Conchocele bisecta (Conrad, 1849). Shell measurements (mm) and indices: AA—apical angle; L—shell length, H—height, W—width, A—length of anterior adductor scar, P—width of posterior adductor scar, N—nymph length.

Valve	AA	L	H	W	A	P	N	H/L	W/L	A/L	P/L	N/L
Northeastern Sea of Okhotsk (57°02′N, 152°29′E–57°16.8′N, 152°40.4′E), 482–491 m depth, silty sand + H_2S, bottom temperature 1.65°C												
Left	95	131.8	93.4	38.5	57.2	15.5	65.9	0.71	0.29	0.43	0.12	0.50
Right	95	132.3	92.9	37.6	57.6	16.4	65.9	0.70	0.28	0.44	0.12	0.50
Left	90	146.5	116.6	47.0	67.3	18.5	75.7	0.80	0.32	0.46	0.13	0.52
Right	90	144.8	116.6	45.0	67.5	18.6	75.1	0.81	0.31	0.47	0.13	0.52
Left	90	152.5	113.1	43.8	63.0	20.0	74.5	0.74	0.29	0.41	0.13	0.49
Right	90	152.5	113.0	42.0	60.5	20.0	74.5	0.74	0.28	0.40	0.13	0.49
Left	—	—	—	—	—	—	—	—	—	—	—	—
Right	90	165.4	118.8	46.6	78.9	23.1	79.4	0.72	0.28	0.48	0.14	0.48
West coast of Kamchatka, Sea of Okhotsk (55°00′2″N, 154°06′3″E), 522–531 m depth, mud + H_2S, bottom temperature 2.2°C												
Left	—	—	—	—	—	—	—	—	—	—	—	—
Right	125	46.8	36.5	11.7	21.1	5.5	18.0	0.78	0.25	0.45	0.12	0.39
Left	—	—	—	—	—	—	—	—	—	—	—	—
Right	122	66.8	48.9	14.6	29.1	8.3	24.6	0.73	0.22	0.44	0.12	0.37
Left	115	78.9	56.8	19.4	35.7	9.6	35.3	0.72	0.25	0.45	0.12	0.45
Right	—	—	—	—	—	—	—	—	—	—	—	—
Left	118	87.2	61.0	20.9	38.1	10.5	33.9	0.70	0.24	0.44	0.12	0.39
Right	—	—	—	—	—	—	—	—	—	—	—	—
Left	113	100.0	72.2	25.4	45.4	12.5	33.2	0.72	0.25	0.45	0.13	0.33
Right	—	—	—	—	—	—	—	—	—	—	—	—
Left	118	115.0	82.3	29.3	53.2	13.6	50.2	0.72	0.26	0.46	0.12	0.44
Right	—	—	—	—	—	—	—	—	—	—	—	—
Left	—	—	—	—	—	—	—	—	—	—	—	—
Right	106	117.0	81.4	31.6	54.0	14.4	51.2	0.70	0.27	0.46	0.12	0.44
Left	—	—	—	—	—	—	—	—	—	—	—	—
Right	105	122.5	88.1	33.2	57.3	14.6	57.7	0.72	0.27	0.47	0.12	0.47
Left	100	127.9	90.8	37.0	54.7	18.0	58.5	0.71	0.29	0.43	0.14	0.46
Right	100	127.9	90.8	37.9	54.7	17.0	58.5	0.71	0.30	0.43	0.13	0.46
Left	—	—	—	—	—	—	—	—	—	—	—	—
Right	97	151.5	114.3	45.8	69.5	21.2	64.3	0.75	0.30	0.46	0.14	0.42
Paramushir Island, Sea of Okhotsk (50°30.88′N, 155°18.14′E), 792–804 m depth, mud + H_2S												
Left	100	71.7	53.7	18.6	32.1	8.4	35.1	0.75	0.26	0.45	0.12	0.49
Right	100	72.3	52.8	23.4	32.3	8.7	35.1	0.73	0.32	0.45	0.12	0.49
Left	—	—	—	—	—	—	—	—	—	—	—	—
Right	90	77.5	60.5	23.9	37.3	9.9	40.0	0.78	0.31	0.48	0.13	0.52
Northeastern coast of Sakhalin Island, Sea of Okhotsk (54°26.75′N, 144°04.940′E), 702 m depth, sandy silt + shell fragments												
Left	110	21.4	18.0	5.2	—	—	—	0.84	0.24	—	—	—
Right	—	21.4	18.0	5.2	—	—	—	0.84	0.24	—	—	—
Left	—	—	—	—	—	—	—	—	—	—	—	—
Right	122	39.9	—	—	18.9	—	17.4	—	—	0.47	—	0.44
Sea of Japan (42°19.6′N, 131°10.6′E), 130 m depth, silty sand												
Left	—	—	—	—	—	—	—	—	—	—	—	—
Right	100	108.6	79.5	32.1	47.8	19.2	68.4	0.73	0.30	0.44	0.18	0.63
Left	—	—	—	—	—	—	—	—	—	—	—	—
Right	110	111.3	86.3	29.4	50.8	18.3	57.8	0.78	0.26	0.46	0.16	0.52
Left	105	121.1	88.2	38.6	—	—	62.0	0.73	0.32	—	—	0.51
Right	—	—	—	—	—	—	—	—	—	—	—	—
Left	—	—	—	—	—	—	—	—	—	—	—	—
Right	100	133.3	92.4	44.1	60.8	22.1	79.3	0.69	0.33	0.46	0.17	0.60
Left	—	—	—	—	—	—	—	—	—	—	—	—
Right	95	133.9	98.4	35.2	54.7	28.2	80.0	0.74	0.26	0.41	0.21	0.60
Kyushu-Palau Ridge south of Shikoku Island (Japan), pacific Ocean (24°46′N, 134°93′E–28°03′N, 135°39′E)												
Left	110	131.2	108.1	38.1	55.8	16.1	63.2	0.82	0.29	0.43	0.12	0.48
Right	—	—	—	—	—	—	—	—	—	—	—	—

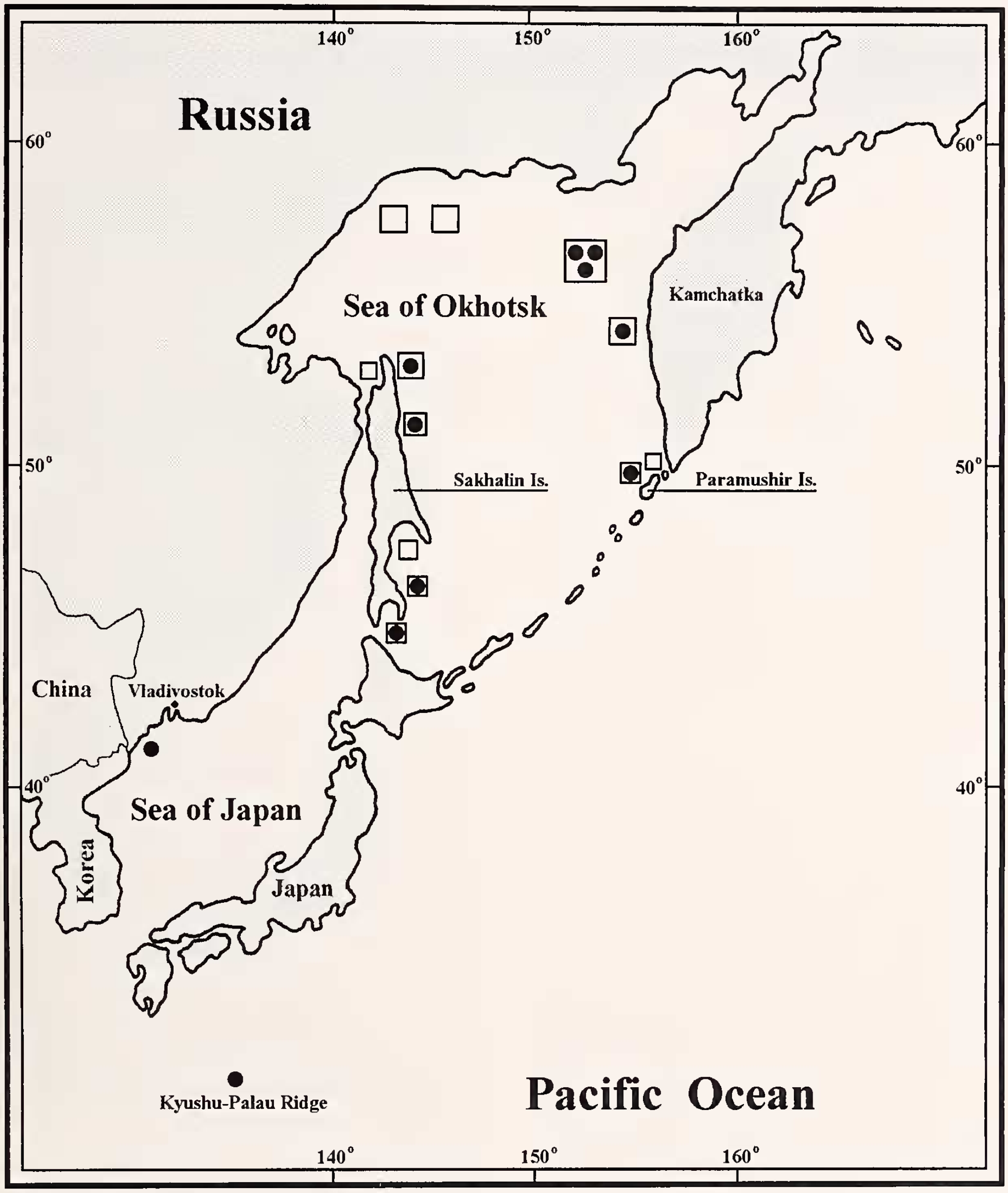

Figure 23. Map showing locations where *Conchocele bisecta* was found (●) and distribution of cold-water methane-rich seep zones in the Sea of Okhotsk (□) (Obzhirov, 1993; Gaedicke et al., 1997; Biebow & Hütten, 1999).

1971); Kasumi, Hyogo Prefecture, Japan (35°44′N, 134°38′E) (Ito, 1967; Kanno, 1971); Oki Island and Shimane Prefecture, Japan (Habe, 1958). In the Pacific Ocean near the coast of Japan—Cape Erimo, Hokkaido (41°40′N, 143°15′E) (Kanno, 1971); Tosa and Sagami Bays (Okutani, 1962); Shikoku (33°10′N, 133°30′E) (Habe, 1964, 1981; Kanno, 1971); south of Shikoku, Kyushu-Palau Ridge.

This species has been recorded at depths from 4 m to 1400 m (Higo et al., 1999). In the Sea of Okhotsk it was found at depths from 300 m (southeastern Sakhalin Island) to 804 m (Paramushir Island) on silty sand and mud+H_2S at a bottom water temperature of 1.65–2.2°C. Near Paramushir Island this species was registered in a zone of methane-rich fluids with concentrations of dissolved methane in bottom water from 180 nL/L to 1000 nL/L at a "normal" bottom-water methane background of 30–40 nL/L (Obzhirov, 1993; Gaedicke et al., 1997). Near the northeastern Sakhalin Island, this species was registered from 385 to 750 m in zones of gas seepage with concentrations of dissolved methane in bottom water from 446 nL/L to 11,076 nL/L (Biebow & Hütten, 1999);

in the Sea of Japan—from 130 m (southern Primorje, Russia) to 350 m (Kasumi, Hyogo Prefecture, Japan) on silty sand and mud at a bottom-water temperature of 1.5°C (Kanno, 1971); in the Pacific Ocean off Japan—from 200 m (Cape Erimo) to 770 m (Sagami Bay) at a bottom-water temperature 2.0–9.8°C (Okutani, 1962; Kanno, 1971). This species was also recorded near Japan at depths of 4 m and 1400 m (Habe, 1977; Higo et al., 1999).

DISCUSSION

As mentioned before, *C. bisecta* dwelling near methane-rich seeps off Paramushir Island has a dual feeding type: suspension feeding and bacterial symbiotrophy. Large amounts (up to $n \cdot 10^9$ per 1 gram wet mass) of intracellular methane- and sulfur-oxidizing symbiotic bacteria were found in the gills of this species (Galchenko et al., 1988a, b; Strizhov et al., 1990; Kuznetsov et al., 1991). It was also shown that bacterial methane-oxidation prevailed significantly over CO_2 fixation. The share of methane carbon in total carbon, assimilated in methane-oxidation and CO_2 fixation, is 68–76% (Galchenko et al., 1988b). Large mollusk size, high population density near methane-rich seeps (up to 15–20 ind/m^2 at a biomass no less than 2.5–3.0 kg/m^2 (Kuznetsov et al., 1987, 1989)), and bacterial symbiotrophy as the main feeding mode enabled Kuznetsov et al. (1987, 1991) to conclude that this species is a typical representative of a highly specialized "specific" fauna of methane seeps, analogous to different species of the genus *Calyptogena* Dall, 1891.

Zones of cold-water methane/sulfide seeps and the associated fauna have been studied in many areas of the Pacific Ocean: subduction zones off Oregon (Suess et al., 1985); Japan (Tenryu Canyon, Japan and Kurile trenches) (Juniper & Sibuet, 1987); and Peru (Olu et al., 1996); Laurentian Fan, Canada (Mayer et al., 1988); Sagami Bay, Japan (Okutani & Egawa, 1985); continental slope off northern California (Kennicutt et al., 1989); Monterey Bay, Southern California (Orange et al., 1994). However, *C. bisecta* was not recorded as a member of cold seep communities in these areas. Nevertheless, a comparison of our materials with the results of geological and gas-chemistry research in the Sea of Okhotsk has shown that *C. bisecta* was found in the Sea of Okhotsk only in areas of cold-water seeps (Figure 23) with abnormally high concentrations on methane (10 times the background ones) in bottom water and sediments (Obzhirov, 1993; Gaedicke et al., 1997; Biebow & Hütten, 1999). In the bottom sediments close to the gas vents, gas hydrates were found. This suggests that gas hydrates are a source of emanating gas.

It is noteworthy that the shelf and bathyal zones of western Kamchatka were repeatedly examined by expeditions of PRIFO. Bottom trawling at a depth over 100 m was carried out in 1997 and 1998 by two different expeditions. Nevertheless, both expeditions found shells and live specimens of *C. bisecta* only in the area corresponding to methane anomaly in bottom water and sediment.

There are vast zones of cold-water methane seeps with gas hydrates in the bottom sediments on the shelf and the bathyal zones of northeastern Sakhalin Island (Obzhirov, 1993). In some zones (Giselle Flare, Obshirov Flare, and Piltunsky Flare), at depths of 385–750 m, large aggregations of shells and live specimens of *Conchocele* sp. were found with the help of video-/camera-sled OFOS (Ocean Floor Observation System) (Biebow & Hütten, 1999). Our studies of valves from these areas have shown them to be *C. bisecta*. It is characteristic that populations of *C. bisecta* resemble narrow strips or spots depending on the form of active methane seepage zones (Obzhirov, personal communication).

Perhaps, in other areas of the Pacific and Atlantic oceans *C. bisecta* also occurs in areas with a high concentration of methane in the bottom sediment. *C. bisecta* was recorded in Sagami Bay, which is characterized by the abundance of cold-water methane seep zones with dense aggregations of different species of the genus *Calyptogena* (Okutani, 1957; 1962; Okutani & Egawa, 1985; Kojima & Ohta, 1997). Also, a species of the genus *Conchocele* with methane-oxidizing symbiotic bacteria was found in the area of hydrothermal vents of Guaymas Basin, the Gulf of California (Galchenko et al., 1988a, b). This species was found in those areas of Guaymas Basin where no traces of recent hydrothermal activity were noted but which had a high methane content in the sediments. Boss (1967) showed that *C. bisecta* was found in Gulf of Darien (Caribbean Sea) in a dredging station together with *Calyptogena* sp., later described as *Calyptogena (Ectenagena) modioliforma* (Boss, 1968) (Boss & Turner, 1980). The presence of a species from the genus *Calyptogena* in this station attests to the presence of hydrothermal vents or cold-water methane/sulfide seeps in this area.

Zones with high dissolved methane concentration in sediments and bottom water are widespread in the world's oceans (Grassle, 1986; Hovland & Judd, 1988) and are favorable for the life of various animals, containing sulfur- and methane-oxidizing endosymbiotic bacteria. This may account for the fact that *C. bisecta* has such a wide geographic distribution and a large depth range. Taking into account the very large size of *C. bisecta* and the considerable contribution of the methane- and sulfur-oxidizing bacteria to the nutrition of mollusks, we conclude that *C. bisecta* may dwell only in organic-rich sediments with high total methane and sulfide concentrations which are specific to cold-water methane-rich seeps. Here it forms dense aggregations and may be indicative of high methane concentration in bottom sediments connected with the location of seeps.

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LITERATURE CITED

Abbott, R. T. 1974. American Seashells. The Marine Mollusca of the Atlantic and Pacific Coasts of North America. Van Nostrand Reinhold Company: New York/Cincinnati/Toronto/London/Melbourne. 663 pp.

Avdeiko, G. P., G. M. Gavrilenko, L. V. Chertkova, V. I. Bondarenko, V. A. Rashidov, V. I. Guseva, V. I. Maltzeva & A. P. Sazonov. 1984. Submarine hydrothermal activity off northwestern Paramushir Island (Kuril Island). Vulkanologiya i Seismologiya (Volcanology and Seismology) 6:66–81. [in Russian]

Bernard, F. R. 1972. The genus *Thyasira* in western Canada (Bivalvia: Lucinacea). Malacologia 11:365–389.

Bernard, F. R. 1983. Catalogue of the living Bivalvia of the eastern Pacific Ocean: Bering Strait to Cape Horn. Canadian Special Publications of Fisheries and Aquatic Sciences 61: 1–102.

Biebow, N. & E. Hütten (eds.). 1999. Cruise reports: KOMEX I and II, RV Professor Gagarinsky Cruise 22, RV Akademik M. A. Lavrentyev Cruise 28. GEOMAR, Research Center for Marine Geosciences Christian Albrechts University in Kiel: Kiel. 146 pp.

Boss, K. J. 1967. *Thyasira disjuncta* (Gabb, 1866) in the Caribbean Sea. Bulletin of Marine Science 17:386–388.

Boss, K. J. & R. D. Turner. 1980. The giant white clam from the Galapagos rift, *Calyptogena magnifica* species novum. Malacologia 20:161–194.

Coan, E. V. & P. H. Scott. 1997. Checklist of the marine bivalves of the Northeastern Pacific Ocean. Santa Barbara Museum of Natural History. Contributions in Science 1:1–28.

Coan, E. V., P. H. Scott & F. N. Bernard. 2000. Bivalve Sea Shells of Western North America. Santa Barbara Museum of Natural History: Santa Barbara, California pp.

Conrad, T. A. 1849. Fossils from northwestern America. Pp. 722–728 (appendix) in J. D. Dana, United States Exploring Expedition. During the years 1838, 1839, 1840, 1841, 1842. Under the command of Charles Wilkes, U. S. N. Atlas. Geology. Vol. 10. C. Sherman, Printer: Philadelphia.

Dall, W. H. 1892. On some new or interesting west American shells obtained from the dredging of the U. S. Fish Commission Steamer Albatross in 1988, and from other sources. Proceedings of the United States National Museum 14:173–191.

Dall, W. H. 1895. Scientific results of exploration by the U.S. Fish Commission Steamer Albatross. 34. Report on Mollusca and Brachiopoda dredged in deep water, chiefly near the Hawaiian Islands, with illustrations of hitherto unfigured species from Northwest America. Proceedings of the United States National Museum 17:675–733.

Dall, W. H. 1901. Synopsis of the Lucinacea and of the American species. Proceedings of the United States National Museum 23:779–833.

Gabb, W. M. 1866. Description of the Tertiary invertebrate fossils. California Geological Survey, Paleontology 2(1) pt. 1: 1–38.

Gaedicke, C., B. V. Baranov, A. I. Obzhirov, E. P. Lelikov, I. N. Belykh & E. I. Basov. 1997. Seismic stratigraphy, BSR distribution, and venting of methane-rich fluids west of Paramushir and Onekotan Islands, northern Kurils. Marine Geology 136:259–276.

Galchenko, V. F., A. Y. Lein, E. M. Galimov & M. V. Ivanov. 1988a. Methane-trophic symbiotic bacteria as a primary link in the food chain in the ocean. Doklady AN SSSR (Proceedings of the Academy of Sciences USSR) 300:717–720. [in Russian]

Galchenko, V. F., S. V. Galkin, A. Y. Lein, L. I. Moskalev & M. V. Ivanov. 1988b. The role of bacteria-symbionts in the nutrition of invertebrates from the regions of active underwater hydrotherms. Okeanologiya (Oceanology) 28:1020–1031. [in Russian, with English summary]

Golikov, A. N. & O. A. Scarlato. 1967. Molluscs of Possiet Bay (Sea of Japan) and their ecology. Pp. 5–154 in Ya. I. Starobogatov (ed.), Molluscs and Their Role in Biocenoses and in the Formation of Faunas. Proceedings of the Zoological Institute, Vol. 42. "Nauka" Publishing House: Leningrad. [in Russian]

Grassle, J. F. 1986. The ecology of deep-sea hydrothermal vent communities. Advances in Marine Biology 23:301–362.

Habe, T. 1958. Report on the mollusca chiefly collected by the S. S. Soyo-Maru of the Imperial Fisheries Experimental Station on the continental shelf bordering Japan during the years 1922–1930. Part 4. Lamellibranchia (2). Publication of the Seto Marine Biological Laboratory 317:19–52.

Habe, T. 1964. Shells of the Western Pacific in Color. Vol. II. Hoikusha: Osaka, 233 pp.

Habe, T. 1977. Systematics of Mollusca in Japan. Bivalvia and Scaphopoda. Tokyo. 372 pp. [in Japanese]

Habe, T. 1981. Bivalvia. Publications of the Seto Marine Biological Laboratory, special publication series "A catalogue of molluscs of Wakayma Prefecture, the Province of Kii. I. Bivalvia, Scaphopoda and Cephalopoda", 7(1):25–224.

Higo, S., P. Callomon & Y. Goto. 1999. Catalogue and Bibliography of the Marine Shell-Bearing Mollusca of Japan. Elle Scientific Publications. 749 pp.

Hovland, M. & A. G. Judd. 1988. Seabed Pockmarks and Seepages. Impact on Geology, Biology and Marine Environment. Graham and Trotman Inc.: London/Dordrecht/Boston. 293 pp.

Ito, K. 1967. A catalogue of the marine molluscan shell-fish collected on the coast of and off Tajima, Hyogo Prefecture.

Bulletin of the Japan Sea Regional Fisheries Research Laboratory 18:39–91.

ITO, K. 1989. Distribution of molluscan shells in the coastal areas of Chuetsu, Kaetsu and Sado Island, Niigata Prefecture, Japan. Bulletin of the Japan Sea Regional Fisheries Research Laboratory 39:37–133.

IVANOVA, M. B. & I. P. MOSKALETZ. 1984. Two new species of bivalve mollusks of the family Thyasiridae from the waters of the Far Eastern State Marine Reserve. Pp. 45–50 in V. S. Levin (ed.), Animal World of the Far Eastern Marine Reserve. DVNC AN SSSR: Vladivostok. [in Russian]

JUNIPER, S. K. & M. SIBUET. 1987. Cold seep benthic communities in Japan subduction zones: spatial organization, trophic strategies and evidence for temporal evolution. Marine Ecology Progress Series 40:115–126.

KANNO, S. 1971. The ecological significance of *Thyasira bisecta* Conrad. The Nautilus 84:96–101.

KEEN, A. M. 1969. Family Thyasiridae. Pp. 508–511 in R. C. Moore (ed.), Treatise on Invertebrate Paleontology. Part N. Mollusca 6 (Bivalvia). The Geological Society of America, Incorporated and The University of Kansas. XXXViii+952 pp.

KENNICUTT, M. C. II, J. M. BROOKS, R. R. BIDIGARE, S. J. MCDONALD & D. L. ADKINSON. 1989. An upper slope "cold" seep community: northern California. Limnology and Oceanography 34:635–640.

KOJIMA, S. & S. OHTA. 1997. *Calyptogena okutanii* n. sp., a sibling species of *Calyptogena soyoae* Okutani, 1957 (Bivalvia: Vesicomyidae). Venus 56:189–195.

KUZNETSOV, A. P., S. V. GALKIN & TH. S. RASS. 1987. A new benthic community based on both photo- and chemosynthetic food (energy) sources. Pp. 6–15 in A. P. Kuznetsov & M. N. Sokolova (eds.), Feeding of Marine Invertebrates and Its Significance in Formation of Communities. Academy of Sciences of the USSR, P. P. Shirshov Institute of Oceanology: Moscow. [in Russian]

KUZNETSOV, A. P. & R. YA. LEVENSTEIN. 1988. *Pavelius ushakovi* Gen. et sp. n. (Polychaeta, Ampharetidae) from Paramushir gas hydrate spring in the Sea of Okhotsk. Zoologicheskiy Zhurnal (Zoological Journal) 57:819–825. [in Russian, with English summary]

KUZNETSOV, A. P., TH. S. RASS & S. V. GALKIN. 1989. Benthic community of Paramushir gas hydrated source. Zoologicheskiy Zhurnal (Zoological Journal) 58:5–14. [in Russian, with English summary]

KUZNETSOV, A. P., TH. S. RASS & S. V. GALKIN. 1989. Benthic community of Paramushir gas hydrated source. Zoologicheskiy Zhurnal (Zoological Journal) 58:5–14. [in Russian, with English summary]

KUZNETSOV, A. P., V. P. STRISHOV & S. I. KIJASHKO. 1991. Respiratory and digestive systems in *Conchocele sp.* from the Paramushir gas-hydrite vent (The Sea of Okhotsk) conditioned by the bacterial biochemosynthesis. Izvestija Akademii Nauk SSSR. Seria Biologicheskaya (News of the Academy of Sciences USSR. Biological Series) 3:445–457. [in Russian, with English summary]

MAYER, L. A., A. N. SHOR, C. J. HUGHES & D. J. W. PIPER. 1988. Dense biological communities at 3850 m on the Laurentian Fan and their relationship to the deposits of the 1929 Grand Banks earthquake. Deep-Sea Research 35:1235–1246.

MOORE, E. J. 1963. Miocene marine mollusks from the Astoria formation in Oregon. Geological Survey Professional Paper 419. United States Government Printing Office: Washington. 109 pp.

NAKAZIMA, M. 1958. Notes on gross anatomy of *Conchocele disjuncta*. Venus 20:186–197.

OBZHIROV, A. I. 1993. Gasogeochemical Fields of Marginal Seas and Oceans. Nauka Press: Moscow. 139 pp. [in Russian, with English summary]

OKUTANI, T. 1957. Two new species of bivalves from the deep waters in Sagami Bay collected by the R. V. *Soyou-Maru*. Bulletin of the Tokai Regional Fisheries Research Laboratory 17:27–30.

OKUTANI, T. 1962. Report on the archibenthal and abyssal lamellibranchiate Mollusca mainly collected from Sagami Bay and adjacent waters by the R. V. *Soyou-Maru* during the years 1955–1960. Bulletin of the Tokai Regional Fisheries Research Laboratory 32:1–40.

OKUTANI, T. & K. EGAWA. 1985. The first underwater observation on living habit and thanatocoenoses of *Calyptogena soyoae* in bathyal depth of Sagami Bay. Venus 44:285–289.

OLDROYD, I. S. 1924. The Marine Shells of the West coast of North America. Vol. 1. Pelecypoda and Brachiopoda. Stanford University Publications, Geological Sciences 1:1–248.

OLU, K., A. DUPERRET, M. SIBUET, J. P. FOUCHER & A. FIALA-MEDIONI. 1996. Structure and distribution of cold seep communities along the Peruvian active margin: relations to geological and fluid patterns. Marine Ecology Progress Series 132:109–125.

ORANGE, D. L., H. G. GREENE, J. BARRY & R. KOCHEVAR. 1994. ROV investigations of cold seeps along fault zones and mud volcanoes in Monterey Bay. 1994. spring meeting, Baltimore, Maryland. EOS 75:324.

SCARLATO, O. A. 1981. Bivalve Mollusks of Temperate Waters of the Northwestern Pacific. Nauka Press: Leningrad. 480 pp. [in Russian]

STRIZHOV, V. P., A. P. KUZNETSOV & N. V. GURINA. 1990. Compounds of early diagenesis of sediments as energy source in food web of bottom community of *Conchocele* sp. (Bivalvia) around gasohydrate vents near the Paramushir Island (the Sea of Okhotsk). Okeanologia (Oceanology) 30:666–671. [in Russian, with English summary]

SUESS, E., B. CARSON, S. D. RITGER, J. C. MOORE, M. L. JONES, L. D. KULM & G. R. COCHRANE. 1985. Biological communities at vent sites along the subduction zone off Oregon. Bulletin of the Biological Society of Washington 6:475–484.

TEGLAND, N. M. 1928. *Thyasira disjuncta* Gabb not *Thyasira bisecta* Conrad, the Recent West Coast Shell. The Nautilus 41:129–131.