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Morphological features and new description of the fossil species *Thalassiosira dolmatovae* (Bacillariophyceae)

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Abstract

Specimens of the Neogene marine diatom *Thalassiosira dolmatovae* have been studied with a scanning electron microscope for the first time. The observations revealed the morphological features typical of this species including arrangement of different kinds of processes. *T. dolmatovae* has one single subcentral strutted process, a ring of marginal strutted processes, a labiate process located at the margin and enclosed by two strutted processes. Marginal strutted processes with outward extensions and without inward extensions have internal openings surrounded by 4 satellite process. The location of a labiate process not on the valve face and the presence of marginal strutted processes with outward extensions indicate that the studied species really belongs to genus *Thalassiosira* not to genus *Shionodiscus*. A valid description of *T. dolmatovae* is given.

Introduction

The diatom species *Thalassiosira dolmatovae* was described (but as a *nodem nudum*, see below) from the Neogene of Karaginsky Island stratigraphic section, northeastern Kamchatka (Fig. 1), by T. Oreshkina (1992) based on material studied with a light microscope (LM). Stratigraphic and paleontological data of the last two decades indicate this fossil diatom is typical of the Neogene marine onshore sequences from Kamchatka and Alaska (Oreshkina 1992; Dolmatova 1992a, b; Marincovich & Gladenkov 1999, 2001; Gladenkov 2003, 2006). Similar taxa are also known to be typical of the Neogene sequences from Sakhalin, Japan, California, and bottom sediments from the North Pacific. Morphology and taxonomy of a number of taxa from oceanic sediments have been studied in detail with a scanning electron microscope (SEM) by Bodén (1993), Shiono (2000, 2001) and Shiono & Koizumi (2000, 2001). As a result, the revision of some species has been carried out and several new species and forms from genus Thalassiosira Cleve (1873: 6) have been described based on a location of rimoportula (labiate process), number and arrangement of fultoportula (strutted processes), structure of strutted processes (operculate, or trifultate), possession of occluded processes, and a presence of central occluded areolae. The stratigraphic occurrence of these new taxa and related species in the northwest Pacific has been also clarified. The obtained results allowed distinguishing Thalassiosira trifulta G. Fryxell in Fryxell & Hasle (1979: 16–19) group with a definition of its three different subgroups, and speculation on the phylogenic evolution of the group (Shiono & Koizumi 2000, 2001).

Data on the stratigraphic occurrence of *T. dolmatovae* indicates this species is a potential biostratigraphic marker for the uppermost Miocene to upper Pliocene sequences in Alaska and Kamchatka ranging within the interval corresponding to the North Pacific *Neodenticula kamtschatica* (Zabelina) Akiba & Yanagisawa (1986: 490–491) diatom Zone to *Neodenticula koizumii* Akiba & Yanagisawa (1986: 491) Zone (Oreshkina 1992; Dolmatova 1992a, b; Gladenkov *et al.* 2002; Gladenkov 2003, 2006). However, detailed morphological features of *T. dolmatovae* including different types of processes, their structure and arrangement remained

unknown because they had never been observed by means of SEM. In order to bridge a gap and compare them with resembling taxa, specimens of *T. dolmatovae* have been studied with SEM for the first time. Moreover, the original description of *T. dolmatovae* by Oreshkina (1992) is invalid because it lacks a holotype, thus the valid description of this taxa should be given.



FIGURE 1: Locations of the Cenozoic stratigraphic sections (black circles) in the North Pacific region where *Thalassiosira dolmatovae* is documented. 1—Karaginsky Island section, northeastern Kamchatka. 2—Sandy Ridge section, the Alaska Peninsula, southwestern Alaska

Materials and Methods

Specimens of *T. dolmatovae* derived from the samples collected from the Neogene Milky River Formation at the Sandy Ridge stratigraphic section of the Alaska Peninsula, southwestern Alaska were studied (Figs. 1, 2). As it was shown by results obtained on diatom stratigraphy (Gladenkov 2003, 2006), *T. dolmatovae* is typical of fossil diatom assemblages from the Milky River Formation occurring consistently and relatively abundantly through the section with an age range of ~5.5 to 4.8 Ma (Figs. 2, 3). Sample material (#CAS 608382, CAS 608400, and CAS 60269-s) is deposited at Geological Institute of Russian Academy of Sciences, Moscow, Russia, and duplicates of strewn slides are deposited at the California Academy of Sciences, San Francisco, USA.



FIGURE 2: Generalized stratigraphic column of the Milky River Formation at the Sandy Ridge stratigraphic section with levels of diatom-bearing samples (after Gladenkov 2003, 2006) and occurrence of *Thalassiosira dolmatovae*. 1—fine- and medium grained sandstones. 2—coarse and very coarse grained sandstones. 3—conglomerates and gritstones. 4—coal. 5—tuff. *T.—Thalassiosira*. *C.—Cosmiodiscus*. Arrows indicate the levels of the first (F) and last (L) occurrences of biostratigraphically important diatom species. The wavy line indicates an angular unconformity separating the Milky River Formation and underlying strata.



FIGURE 3: Correlation of the Milky River Formation at the Sandy Ridge stratigraphic section with the North Pacific diatom zonation based on data of diatom stratigraphy indicating a latest Miocene to early Pliocene age (modified from Gladenkov 2003, 2006). Q— Quaternary. a–c—subzones. Diatom zonation of Barron & Gladenkov (1995) for the last 8 myr correlated to the geochronologic time scale of Berggren *et al.* (1995).

The procedure including a treatment by acetic acid and sodium pyrophosphate, and the following centrifugation with heavy liquid described by Gladenkov (2003) was used to process the samples for SEM and LM. Strewn slides were mounted in Naphrax mounting medium (index of diffraction = 1.74) for LM observation. The LM pictures were taken using Jeneval (Jeiss) and Leica DMRB light microscopes, and the SEM pictures were taken using Hitachi S–520 and LEO 1450 VP scanning electron microscopes at the California Academy of Sciences.

Diatom terminology follows that of Anonymous (1975). Numerical ages, geological epochs and subepochs used herein according to the Cenozoic geochronologic scale after Berggren *et al.* 1995. The North Pacific Neogene diatom zonation follows Barron & Gladenkov (1995).

New species description

Division Bacillariophyta

Class **Coscinodiscophyceae** F.E. Round & R.M. Crawford in Round *et al.* 1990 emend. Medlin & Kaczmarska 2004

Order **Thalassiosirales** Glezer & Makarova 1986 Family **Thalassiosiraceae** Lebour 1930 Genus *Thalassiosira* Cleve (1873: 6)

Thalassiosira dolmatovae Oreshkina ex A. Gladenkov sp. nov. (Figs. 4–29)

- Synonyms:—*Thalassiosira* sp. 9 Dolmatova 1992b (p. 86, pl. 30, figs. 1–5); *Thalassiosira dolmatovae* Oreshkina 1992 (p. 129, pl. XL, figs. 7, 8), invalid species name.
- Valves circular, slightly convex to almost flat, diameter 12–37 µm. On valve face size of the areolae gradually decreases from the centre (3–5 areolae in 10 µm) towards the margin, in irregular, concentric wavy arrangement. Abrapt change in areolae pattern at marginal zone, up to 19–25 areolae in 10 µm near the margin, arranged in sublinear to tangental rows. Margin is hyaline, 0.7–1.5 µm wide. Simple external (occluded) processes are scattered on the valve face between areolae. One single strutted process occurs near the valve center between two areolae, one of which has a smaller size than other central areolae. 4–6 strutted processes in 10 µm are located along the margin zone near the boundary between valve face and low mantle. Internal openings of central and marginal strutted processes are surrounded by 4 satellite pores. External opening of central process as a simple rounded opening, and marginal processes have external extensions. One single labiate process is located at the margin and enclosed by two strutted processes. External opening of labiate process is simple.
- Type:— USA. Alaska: Sandy Ridge stratigraphic section of the Alaska Peninsula, Milky River Formation, 56° 70' N, 159° 92' W, material from 28 m above an angular unconformity with the underlying Bear Lake Formation, (Circled specimen (Fig. 4a–c) on slide *Slide 608382/1, Sample #CAS 608382*, (Geological Institute, Russian Academy of Sciences, Moscow, Russia), holotype, designated here; circled specimen (Fig. 5) on *Slide #608382/2, Sample #CAS 608382*, (Geological Institute, Russian Academy of Sciences, Moscow, Russia), above an angular unconformity with the underlying Bear Lake Formation, circled specimen (Fig. 8a–b) on *Slide #608400/1, Sample #CAS 608400* (Geological Institute, Russian Academy of Sciences, Moscow, Russia), paratype, designated here).

Occurrence:—Marine neritic species. Marine deposits of the latest Miocene to early Pliocene (the North Pacific *Neodenticula kamtschatica* diatom Zone) of the Alaska Peninsula, southwestern Alaska; the latest Miocene to late Pliocene (the *Neodenticula kamtschatica* Zone to *Neodenticula koizumii* Zone) of Karaginsky Island, northeastern Kamchatka.

Remarks:—This species is distinguished from *Thalassiosira baldaufii* Bodén (1993: 68) by the presence of one single central strutted process on the valve face, by the absence of prominent marginal occluded processes, and by areolae pattern. It is similar to *Thalassiosira labimarginata* Bodén (1993: 68) but differs by larger valve diameter, wider hyaline margin, and size of areolae and their arrangement.

Etymology:—The species is named in honour of Dr. Lora M. Dolmatova who studied fossil diatoms from Russian Far East during many years.

Observations

Specimens of *T. dolmatovae* from Alaskan material have circular valves, varying from slightly convex to almost flat (Figs. 4–11, 14–17), with a diameter ranging between 12 and 37 μ m, the majority of observed specimens with diameters around 18–30 μ m. Areolae on valve face showing a rounded-polygonal image in LM with an irregular arrangement to concentrically wavy rows (Figs. 4–8). On the valve face size of the areolae gradually decrease from the centre (3–5 areolae in 10 μ m), with an abrupt change in the size of areolae in the submerginal zone approximately from the boundary between valve face and low mantle where up to 19–25 areolae in 10 μ m near the margin are arranged in sublinear to tangental rows (Figs. 9, 15–17, 28, 29). The internal cribra of areolae seems to be subcircular in outline (Figs. 12, 13), but as a rule cribra is eroded. Most of specimens have external bulges between areolae giving to valve face a relief undulate image in SEM (Figs. 14, 15, 17). In some cases small rounded openings are observed at the top of these projections (Figs. 17, 28) which may be regarded as simple external (occluded) processes. Margin is hyaline, 0.7–1.5 μ m wide.



FIGURES 4–10: *Thalassiosira dolmatovae*, LM (Figs. 4–8), SEM (Figs. 9–10), external views of whole valves. Arrows show central fultoportula. Black line segment is scale bar = 10 μ m for Figs. 4–8. a–c–valve in different focus. Fig. 4. Holotype. Fig. 5. Isotype. Figs. 4–6, 9–10, sample #CAS 608382. Fig. 7, #CAS 60269-s. Fig. 8. Paratype, Sample #CAS 608400.



FIGURES: 11–17: *Thalassiosira dolmatovae*, SEM. Figs. 11, 14–17. External views of whole valves. Fig. 12. Internal view of whole valve with arrow showing the areolae with internal cribra. Fig. 13. Enlargement of areolae with internal cribra. Fig. 14. Black arrows show external extensions of marginal strutted processes, white arrow shows external opening of central strutted process. Fig. 15. Arrows show external extensions of marginal strutted processes. Fig. 17. Short arrows show openings of simple external (occluded) processes scattered on the valve face, long arrow shows external opening of central strutted process. Figs. 11, 16, #CAS 608400. Figs. 12–13, #CAS 60269-s. Figs. 14–15, 17, #CAS 608382.



FIGURES 18–23: *Thalassiosira dolmatovae.* SEM Fig. 18. Internal view of the valve with arrow showing occluded (?) areolae (OA). Fig. 20. Internal view of the valve showing labiate process (LP), copula (C), central fultoportula (CF) and marginal strutted processes (short white arrows) surrounded by 4 satellite pores. Fig. 19, 21, 23. External views of valves center showing opening of central strutted process (long arrows) and occluded (?) areolae (short arrows). Fig. 22. Enlarged fragment of Fig. 18 showing central fultoportula (CF), occluded (?) areolae (OA), and marginal strutted processes (short arrows). Figs. 18–22, #CAS 608382. Fig. 23, #CAS 60269.



FIGURES 24–29: *Thalassiosira dolmatovae*, SEM. Figs. 24, 25 (enlarged fragment of Fig. 18), 27. Internal views of the valves showing central fultoportula (CF) and marginal strutted processes (MF) surrounded by 4 satellite pores, labiate processes (LP), and copula (C). Fig. 26. Internal view of the valve showing broken labiate processes (LP), central fultoportula (CF), and marginal strutted processes (black arrows). Fig. 28 (enlarged fragment of Fig. 17). External view of the valve with white arrows showing openings of simple occluded processes scattered on the valve face, and black arrow showing rounded opening of marginal strutted processes with small rounded openings on their tops. Fig. 24, #CAS 60269-s. Figs. 25–26, 28–29, #CAS 608382. Fig. 27, #CAS 608400.

One single strutted process occurs somewhat away from the valve center between two areolae, closer to the areola having a smaller size than other central areolae (Figs. 4, 6, 9, 10). Central fultoportula has no external extension and discernible as a small rounded opening on the outside of the valve (Figs. 9, 10, 17, 19, 21, 23). Internal opening has the form of slightly raised rim surrounded by 4 satellite pores (Figs. 20, 24, 25, 27). To a certain extent the smaller areolae closer to central strutted process bears resemblance to the internally occluded "occluded areolae" defined by Shiono (2000, 2001). In contrast to external view of valves, internal view of *T. dolmatovae* shows the absence of internal opening of this areolae but the presence of dark circle looks like the occluded areolae (Figs. 18, 22).

Four to 6 strutted processes in 10 µm separated by 3–4 areolae are located at the submarginal zone and positioned at approximately the same distance from the margin near the boundary between the valve face and the mantle where the size of areolae decreases abruptly (Figs. 14, 15, 20, 22, 25–27, 29). The fultoportula's internal openings in the form of slightly raised rims surrounded by 4 satellite pores are observed on the inside of the valve (Figs. 20, 25, 27). Strutted processes have external extensions discernible as knob-like projections with small rounded openings on their tops (Figs. 14, 15, 28, 29). Previously these projections have been regarded as marginal occluded processes by the author (Gladenkov 2010). However, additional study and discussions with colleagues at the 21st International Diatom Symposium held in 2010 allow recognizing them as external extensions of marginal strutted processes. One single labiate process (Figs. 20, 24–26). Externally, the rimoportula appears as a small rounded opening indistinguishable from the areolae. Morphology of the girdle region was not studied, although the copula slitted near the whereabouts of labiate process, and radially "ribbed" copula were observed occasionally on the inside of the valve (Figs. 20, 24, 25, 27).

Discussion

The presence of structure looks like the "occluded areolae" defined by Shiono (2000, 2001) in the valve centre of *T. dolmatovae* is quite surprise. As showed Shiono & Koizumi (2001) occluded areolae (or pore-like structure) are typical of only their *Thalassiosira bipora* Shiono (2000: 139) subgroup from *Thalassiosira trifulta* group. This subgroup comprises of taxa lacking external spines and projections, and having a labiate process located on the valve face. Recently these and related taxa with a rimoportula being distant from the margin, and with long inward and reduced or absent outward extensions, have been transferred from genus *Thalassiosira* to new genus *Shionodiscus* A.J. Alverson, S.-H. Kang & E.C. Theriot (2006: 258). However, occluded areolae were unknown for *Thalassiosia* species having a labiate process located not onto valve face and external projections as *T. dolmatovae* does. So probably, *T. dolmatovae* is the first example of possession of all these morphological features, and its possible relation with "*Thalassiosira bipora*" subgroup may be speculated in the future.

Comparison. *T. dolmatovae* is distinguished from specimens of *T. baldaufii* Bodén by the presence of one single central strutted process on the valve face, by the absence of prominent marginal occluded processes, and by areolae pattern. It differs from *T. labimarginata* Bodén by larger valve diameter, wider hyaline margin, and size of areolae and their arrangement. On an abrupt decrease in the size of areolae at the submarginal zone *T. dolmatovae* resembles some taxa from genus *Shionodiscus* Alverson, Kang *et* Theriot (previously attributed to genus *Thalassiosira*), namely *Shionodiscus biporus* (Shiono) Alverson, Kang *et* Theriot (2006: 259), *S. centrus* (Shiono) Alverson, Kang *et* Theriot (2006: 259), *S. exceptiunculus* (Shiono) Alverson, Kang *et* Theriot (2006: 259), *S. exceptiunculus* (Shiono) Alverson, Kang *et* Theriot (2006: 259), *S. tetraoestrupii* (Bodén) Alverson, Kang *et* Theriot (2006: 260), and *S. tetraoestrupii* var. *reimeri* (Mahood *et* Barron) Alverson, Kang *et* Theriot (2006: 260). However, in contrast to *Shionodiscus* taxa *T. dolmatovae* has marginal strutted processes with outward extensions, a labiate process located at the margin, and occluded processes scattered on the valve face. Thus, *T. dolmatovae* can not be transferred from genus *Thalassiosira* to genus *Shionodiscus*.

Distribution. *T. dolmatovae* is known from the latest Miocene to late Pliocene marine neritic diatom assemblages of northeastern Kamchatka (Oreshkina 1992, Dolmatova 1992a, b) and latest Miocene to early Pliocene assemblages of southwestern Alaska (Gladenkov *et al.* 2002; Gladenkov 2003, 2006). Resembling taxa referred to as *Thalassiosira* cf. *tetraoestrupii* var. *reimeri* Mahood *et* Barron was also documented from the latest Miocene to late Pliocene of southern Sakhalin and northern Hokkaido (Akiba *et al* 2000). Notable, in Northern Hokkaido area it occurs commonly to abundantly just around the boundary between *Neodenticula kamtschiatica* Zone and *Neodenticula koizumii–Neodenticula kamtschatica* Zone, just like a short but very remarkable marker bed (Akiba, personal communication 2010). Moreover, specimens similar to *T. dolmatovae* under LM and referred to as *Thalassiosira* sp. 2 were noted and illustrated from deposits assigned to the uppermost Miocene–lower Pliocene in borehole A–2 drilled in Aiyon Island, the East Siberian Sea (Stepanova 1989). However, further study of mentioned taxa under SEM should finally clarify their taxonomic position because the location of labiate process, the number and structure of strutted processes (operculate, or trifultate) and other morphological features are unknown for the present.

Conclusions

The original description of T. dolmatovae by T. Oreshkina (1992, p. 129) based only on LM observation is in Russian. My English translation of the diagnosis is as follows: "Valve circular, flat, diameter 15–20 µm. Areolae are in rarefied concentrically wavy rows, 3–4 areolae in 10 µm in the valve center, near the margin areolae are considerable smaller, 10–12 in 10 µm. One or several strutted processes are in the center. Distinct marginal strutted processes are located at the boundary between valve face and mantle, 4–5 in 10 µm. Margin hyaline, 2-3 µm in wide". However, data obtained with SEM revealed only subcentral strutted process not "several strutted processes in the center". Possibly, combinations of central strutted process and the nearest areolae of relatively small size, or central fultoportula and adjacent external processes have been interpreted as "central strutted processes" under LM. Also SEM observation shows the presence of simple external (occluded) processes scattered on the valve face. These processes have not been noted in the original description but the presence of "mucous pores" scattered on the whole valve face was mentioned by L. Dolmatova (1992b, p. 86) in her informal description of *Thalassiosira* sp. 9 that is a synonym of T. dolmatovae. Moreover, SEM study revealed smaller sizes of areolae near the margin (up to 19-25 areolae in $10 \,\mu\text{m}$) in comparison with those from the original description (10–12 in 10 μm) and the informal description by Dolmatova (1992b)—up to 15 in 10 µm. Additionally, data obtained with SEM revealed narrower hyaline margin (0.7–1.5 μ m wide) in comparison with the original description (2–3 μ m). However, measurements including width of copulae and/or valvocopula instead of a real margin under LM may have been included and influence the earlier descriptions.

It is important to emphasize that unfortunately, the first species description of *Thalassiosira dolmatovae* Oreshkina is invalid because the rubric "Holotype" is absent and the holotype for the species is not designated in the original description (Oreshkina 1992, p. 192). According to the *International Code of Botanical Nomenclature*, even in 1992 it was compulsory to designate holotypes in descriptions of new species. Hence, instead of *T. dolmatovae* Oreshkina, a new species based on a valid description must be erected. The original description is supplemented with SEM observations, but I retain the name *Thalassiosira dolmatovae* for this new taxon in honour of Russian diatomologist Lora M. Dolmatova, who found it for the first time in Kamchatka but did not publish its formal description.

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References

- Akiba, F., Hiramatsu, C., Tsoy, I.B., Ogasawara, K. & Amano, K. (2000) Diatom biostratigraphy and geologic age of the Maruyama and Kurasi Formations, Southern Sakhalin, and their correlation to the Neogene of the Tempoku Area, Hokkaido. *Journal of Geography* 109: 203–217 (in Japanese). http://dx.doi.org/10.5026/jgeography.109.2 203
- Akiba, F. & Yanagisawa, Y. (1986) Taxonomy, morphology and phylogeny of the Neogene diatom zonal marker species in the middle-to-high latitudes of the North Pacific. *In*: Kagami, H., Karig, D.E., Coulbourn, W.T. *et al.* (Eds.), *Initial Reports of the Deep Sea Drilling Project.* Washington (U.S. Government Printing Office) 87: 483–554, 53 pls.
- Alverson, A.J., Kang, S.-H. & Theriot, E.C. (2006) Cell wall morphology and systematic importance of *Thalassiosira ritscheri* (Hustedt) Hasle, with a description of *Shionodiscus* gen. nov. *Diatom Research* 21: 251–267. http://dx.doi.org/10.1080/0269249X.2006.9705667
- Anonymous (1975) Proposals for a standardization of diatom terminology and diagnoses. *Nova Hedwigia, Beihefte* 53: 323–354.
- Barron, J.A. & Gladenkov, A.Y. (1995) Early Miocene to Pleistocene diatom stratigraphy of Leg 145. *In*: Rea, D.K., Basov, I.A., Scholl, D.W. & Allan, J.F. (Eds.), *Proceedings of the Ocean Drilling Program, Scientific Results, 145.* College Station, TX (Ocean Drilling Program), pp. 3–20.
- Berggren, W.A., Kent, D.V., Swisher III, C.C. & Aubry, M.-P. (1995) A revised Cenozoic geochronology and chronostratigraphy. *SEPM Special Publication* 54: 129–212.
- Bodén, P. (1993) Taxonomy and stratigraphic occurrence of *Thalassiosira tetraoestrupii* sp. nov. and related species in upper Miocene and lower Pliocene sediments from the Norwegian Sea, North Atlantic and North West Pacific. *Terra Nova* 5: 61–75.

http://dx.doi.org/10.1111/j.1365-3121.1993.tb00227.x

- Cleve, P.T. (1873) On Diatoms from the Arctic Sea. *Bihang till Kongliga Svenska Vetenskaps-Akademiens Handlingar*, 1[13]: 1–28, 4 pls.
- Dolmatova, L.M. (1992a) Diatomovye vodorosli. In: Volobueva, V.I., Belaya, B.V., Dolmatova, L.M., Grevtsev, A.V., Minyuk, P.S., Narkhinova, V.E., Polovova, T.L. & Shchiraya, O.A. Opornyi razrez neogena severo-vostoka Azii na o. Karaginsky. Chast' 1 (Stratigraphiya). SVKNII, DVO RAN, Magadan, Russia, pp. 40–53.
- Dolmatova, L.M. (1992b) Diatomovye vodorosli. In: Volobueva, V.I., Belaya, B.V., Dolmatova, L.M., Grevtsev, A.V., Minyuk, P.S., Narkhinova, V.E., Polovova, T.L. & Shchiraya, O.A. Opornyi razrez neogena severo-vostoka Azii na o. Karaginsky. Chast' 2 (Sistematicheskaya chast'). SVKNII, DVO RAN, Magadan, Russia, pp. 70–135, 155–167, plates 21–52.
- Fryxell, G.A. & Hasle, G.R. (1979) The genus *Thalassiosira*: *T. trifulta* sp. nova and other species with tricolumnar supports on strutted processes. *In*: R. Simonsen (Ed.), *Proceedings of the Fifth Symposium on Recent and Fossil Diatoms*, Antwerp, September 3–8, 1978. *Nova Hedwigia, Beihefte* 64: 13–40.
- Gladenkov, A.Yu. (2003) Diatom biostratigraphy of the Neogene Milky River Formation, Alaska Peninsula, southwestern Alaska. *Proceedings of the California Academy of Sciences* 54: 27–64.
- Gladenkov, A.Yu. (2006) Neogene diatoms from the Sandy Ridge Section, Alaska Peninsula: significance for stratigraphic and paleogeographic reconstructions. *Stratigraphy and Geological Correlation* 14 (1): 73–90. http://dx.doi.org/10.1134/S0869593806010059
- Gladenkov, A.Yu. (2010) Morphological features of the fossil marine diatom species *Thalassiosira dolmatovae*. *Abstracts of the 21st International Diatom Symposium*, St. Paul, Minnesota, United States, 29 August to 3 September, 2010, p. 20.
- Gladenkov, A.Yu., Oleinik, A.E., Marincovich, L., Jr. & Barinov, K.B. (2002) A refined age for the earliest opening of Bering Strait. *Palaeogeography, Palaeoclimatology, Palaeoecology* 183: 321–328. http://dx.doi.org/10.1016/S0031-0182(02)00249-3
- Marincovich, L., Jr. & Gladenkov, A.Yu. (1999) Evidence for an early opening of the Bering Strait. *Nature* 397: 149–151.

http://dx.doi.org/10.1038/16446

Marincovich, L., Jr. & Gladenkov, A.Yu. (2001) New evidence for the age of Bering Strait. *Quaternary Science Reviews* 20: 329–335.

http://dx.doi.org/10.1016/S0277-3791(00)00113-X

- Oreshkina, T.V. (1992) Diatomovye. *In*: Gladenkov, Yu.B. & Devjatkin, E.V. (Eds.), *Detal'noe raschleneniye neogena Kamchatki*. Nauka Publishers, Moscow, Russia, pp. 44–55, 129, 167–185, 200–203.
- Shiono, M. (2000) Three new species in the *Thalassiosira trifulta* group in late Neogene sediments from the northwest Pacific Ocean. *Diatom Research* 15: 131–148.

http://dx.doi.org/10.1080/0269249X.2000.9705488

Shiono, M. (2001) Two new species in the *Thalassiosira trifulta* group in late Pliocene sediments of the northwest Pacific Ocean. *Diatom Research* 16: 83–92.

http://dx.doi.org/10.1080/0269249X.2001.9705510

- Shiono, M. & Koizumi, I. (2000) Taxonomy of the *Thalassiosira trifulta* group in late Neogene sediments from the northwest Pacific Ocean. *Diatom Research* 15: 355–382. http://dx.doi.org/10.1080/0269249X.2000.9705502
- Shiono, M. & Koizumi, I. (2001) Phylogenetic evolution of the *Thalassiosira trifulta* group (Bacillariophyceae) in the northwestern Pacific Ocean. *Journal of the Geological Society of Japan* 107: 496–514. http://dx.doi.org/10.5575/geosoc.107.496
- Stepanova, G.V. (1989) Nakhodka morskih neogenovyh diatomei na ostrove Aiyon (Vostochno-Sibirskoe more). In: Kolobova, I.M. & Hosatski, L.I. (Eds.), Ezhegodnik Vsesouznogo Paleontologicheskogo Obshchestva, Volume XXXII. Nauka Publishers, Leningrad, USSR, pp. 200–217.