



UDC 595.182.4 (261)

When did the first species of the genera *Tonicella* Carpenter, 1873 and *Boreochiton* G.O. Sars, 1878 (Mollusca, Polyplacophora) appear in the Atlantic Ocean?

B.I. Sirenko^{1*} and B. Dell'Angelo²

¹ Zoological Institute, Russian Academy of Sciences, Universitetskaya Emb. 1, 199034 Saint Petersburg, Russia; e-mail: marine@zin.ru

² Via Briscata 16/6, 16154 Genova, Italy; e-mail: bruno.dellangelo@chitons.it

Submitted November 11, 2022; revised January 23, 2023; accepted February 20, 2023.

ABSTRACT

It is assumed that the species of the genera *Boreochiton* G.O. Sars, 1878 and *Tonicella* Carpenter, 1873 originated in the North Pacific Ocean. The first representatives of these genera apparently penetrated into the northern part of the Atlantic Ocean not earlier than the Pliocene. Fossil representatives from the Late Cenozoic deposits of Europe, belonging to the genus *Tonicella*, have a sculpture of a tegmentum closer to the species of the genus *Lepidochitona* Gray, 1821, which suggests their transfer to this genus.

Key words: Cenozoic, fossil chitons, *Lepidochitona*, Tonicellidae

Когда первые виды родов *Tonicella* Carpenter, 1873 и *Boreochiton* G.O. Sars, 1878 (Mollusca, Polyplacophora) появились в Атлантическом океане?

Б.И. Сиренко^{1*} и Б. Делл'Анджело²

¹ Зоологический институт Российской академии наук, Университетская наб. 1, 199034 Санкт Петербург, Россия; e-mail: marine@zin.ru

² Via Briscata 16/6, 16154 Genova, Italy; e-mail: bruno.dellangelo@chitons.it

Представлена 11 ноября 2022; после доработки 23 января 2023; принята 20 февраля 2023.

РЕЗЮМЕ

Предполагается, что виды родов *Boreochiton* G.O. Sars, 1878 и *Tonicella* Carpenter, 1873 возникли в северной части Тихого океана. Первые представители этих родов, по-видимому, проникли в северную часть Атлантического Океана не ранее плиоцена. Ископаемые представители, из позднекайнозойских отложений Европы, относимые к роду *Tonicella*, имеют скульптуру тегмента более близкую к видам рода *Lepidochitona* Gray, 1821, что предполагает перенесение их в этот род.

Ключевые слова: Cenozoic, ископаемые хитоны, *Lepidochitona*, Tonicellidae

* Corresponding author / Автор-корреспондент

INTRODUCTION

All species of genera *Boreochiton* G.O. Sars, 1878 and *Tonicella* Carpenter, 1873 live in the Boreal and Arctic regions, in the northern parts of the Pacific and Atlantic Oceans and in the Arctic Ocean. The largest number of species of these genera lives in the north Pacific, from Japan and Baja California to the Chukchi Peninsula in the Bering Sea (Kaas and Van Belle 1985; Clark 1999; Vendrasco et al. 2012). There are three species and one subspecies of the genus *Boreochiton*: *B. beringensis beringensis* (Jakovleva, 1952), *B. beringensis lucidus* (Sirenko, 1975), *B. granulatus* (Jakovleva, 1952), *B. jakovlevae* Sirenko, 2016 and nine species of the genus *Tonicella*: *T. marmorea* (Fabricius, 1780), *T. squamigera* Thiele, 1909, *T. submarmorea* (Middendorff, 1847), *T. zotini* Jakovleva, 1952, *T. undocaerulea* Sirenko, 1973, *T. lokii* Clark, 1999, *T. venusta* Clark, 1999, *T. insignis* (Reeve, 1847), *T. lineata* (Wood, 1815) in the northern Pacific. Only two species of these genera, *B. ruber* (Linnaeus, 1767) and *T. marmorea*, inhabit the Atlantic and Arctic oceans. Such an uneven distribution of the species of these two genera, with a clear predominance of the number of chiton species in the Pacific Ocean, most likely indicates the origin of the first species of both genera in the Pacific Ocean. In fossil deposits of the Pacific fauna, species of the genus *Tonicella* were found in California (*Tonicella* sp. cf. *T. venusta*) in Pliocene beds (Vendrasco et al. 2012) and in Pleistocene beds (*T. lokii*, *T.* sp.: Muhs et al. 2006, 2012), and in Japan (*T. lineata*, *Tonicella* sp.), in Pleistocene, Pliocene and Miocene beds (Itoigawa et al. 1976, 1978, 1981, 1982), which also indicates their sufficient antiquity.

The genus *Tonicella* has been mentioned in the list of fossil chitons of Europe since 1978, when Janssen (1978) moved *Chiton tenuissimus* Sandberger, 1859 (Rupelian, Middle Oligocene, Germany) to the genus *Tonicella*. Since then seven fossil species have been transferred to the genus or described as species of this genus: *Tonicella tenuissima*, *T. modesta* (Rolle, 1862), *T. implumis* Bielokrysz, 1999, *T. lira* Cherns et Schwabe, 2017, *T. redoniensis* Dell'Angelo, Landau, Dingenen et Ceulemans, 2018, *T. nuda* Dell'Angelo, Lesport, Cluzaud et Sosso, 2020 and *T. adunca* Dell'Angelo, Lesport, Cluzaud et Sosso, 2020. All these seven species have been found ranging from Eocene to Miocene deposits. A comparison of the number of modern species of these genera in the Pacific and Atlantic

Oceans indicates a significant dominance of Pacific species, and it is most logical to assume the settlement of the Atlantic by Pacific migrants. However, a comparison of fossil chitons that lived off the Atlantic and Pacific coasts indicates an earlier appearance of species of these genera in the Atlantic, rather than in the Pacific Ocean. This article discusses this problem and suggests a solution.

MATERIAL AND METHODS

The materials for this article were collections of fossil mollusks from different parts of Europe and recent mollusks in the Barents Sea and from near the Pacific coast of Mexico. The fossil valves of *B. ruber* were collected in Late Quaternary biocenoses, between Corsica and the Island of Capraia in the Mediterranean Sea, at depth 350–500 m (Dell'Angelo and Giusti 1997). The fossil valves of *Tonicella redoniensis* were collected in Miocene (Tortonian) deposits in Saint-Clément-de-la-Place, France by B. Dell'Angelo. The fossil valves of *T. implumis* were collected in Upper Eocene (Mandrikovka Beds) deposits, in Dnepropetrovsk, Ukraine by B. Sirenko. The fossil valves of *Tonicella tenuissima* were collected in Oligocene deposits, Germany by B. Dell'Angelo. The specimen of *B. ruber* was collected in Yarnishnaya Inlet, Murman coast, the Barents Sea, at 4–6 m depth by B. Sirenko. The specimen of *Tonicella marmorea* was collected in Yarnishnaya Inlet, Murman coast, the Barents Sea, at 18–20 m depth by B. Sirenko. The specimen of *Lepidochitona salvadorensis* was collected in Mahahua, Acapulco, Guerrero, Mexico, at 4–5 m depth by A. Reyes-Gómez (Centro Universitario de Ciencias Biológicas y Agropecuarias, Departamento de Ecología Universidad de Guadalajara, México).

The recent specimens chosen for examination under a scanning electron microscope (SEM) were boiled in 7% KOH for 5–7 minutes and then boiled twice in fresh water. After that, several valves (usually valves I, II, IV, V and VIII) were dried and examined under a FEI SEM Quanta 250 scanning electron microscope. The valves of fossil species after brushing were also examined under the electron scanning microscope.

RESULTS AND DISCUSSION

Given the significant predominance of the number of species of both genera in the Pacific Ocean

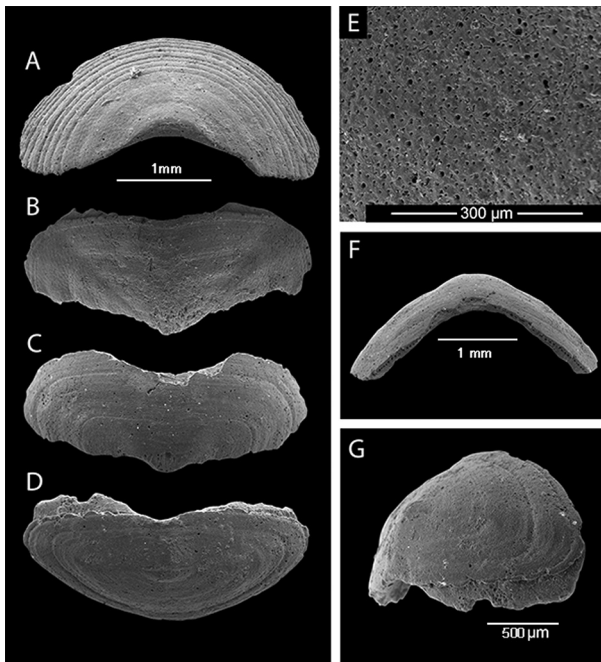


Fig. 1. *Boreochiton ruber*, Late Quaternary biocenoses between Corsica and the Island of Capraia, the Mediterranean Sea, 350–500 m. A – valve I, dorsal view; B, C – intermediate valve, dorsal view; D – valve VIII, dorsal view; E – intermediate valve, structure of tegmentum in central area; F – intermediate valve, rostral view; G – valve VIII, lateral view.

compared to the Atlantic Ocean, which was noted in the introduction, it is logical to assume the appearance of species of these two genera in the Atlantic as a result of their migration from the Pacific Ocean (Sirenko 1974). In this regard, it is worth discussing the question of the time of this penetration. According to data on other species of mollusks, Pacific settlers were first found in Red Craggs beds of England (Chatwin 1954; Gladenkov 1978; Dixon 1979; Golikov 1980) in the Pliocene. Earlier penetrations of Pacific settlers into the Atlantic Ocean have not been noted. It is assumed that Pacific migrants entered the Atlantic Ocean through the Bering Strait along the north of North America (Hopkins 1972). The oldest find of *B. ruber* (Fig. 1) was recorded in Late Quaternary biocenoses in the Mediterranean Sea (Dell'Angelo and Giusti 1997), which does not contradict the assumption about the penetration of the ancestors of this species in the Pliocene from the Pacific Ocean.

Recent species of *Boreochiton* and *Tonicella* are easily distinguishable from each other by the presence of a large fenestral gland located under the posterior

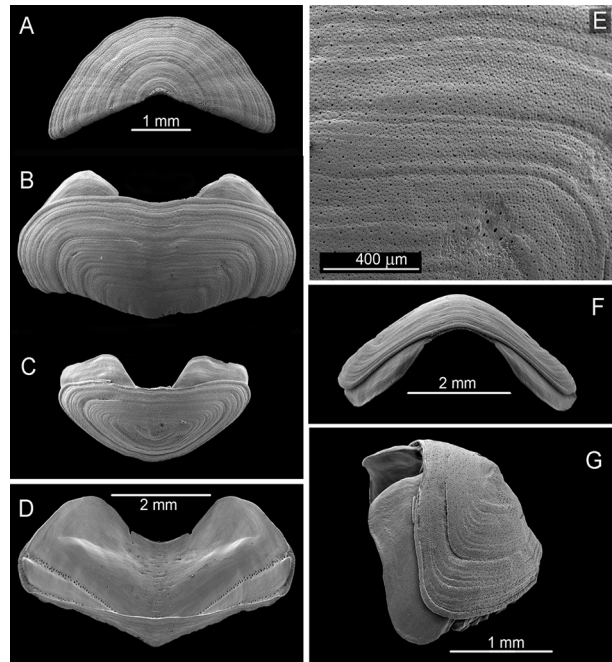


Fig. 2. *Boreochiton ruber*, Jarnishnaja Inlet, Murman coast, the Barents Sea, 4–6 m depth. A – valve I, dorsal view; B – intermediate valve, dorsal view; C – valve VIII, dorsal view; D – intermediate valve, ventral view; E – intermediate valve, structure of tegmentum in central and lateral areas; F – intermediate valve, rostral view; G – valve VIII, lateral view.

valves in the first genus and its absence in the second genus. The valves of the species of both genera, by which it is possible to determine whether they belong to a particular species, especially in fossil species, have very slight differences. In both genera there are species with a granular and smooth tegmentum. One of the important feature of the tegmentum in species of both genera is a well-marked difference in size of the pore of megal aesthetes and micra aesthetes (Figs 2, 3).

The shape of the valves of seven fossil European chitons belonging to the genus *Tonicella* (see Introduction) is similar to the shape of the valves of modern species of *Boreochiton* and *Tonicella*. However, the microsculpture of the tegmentum in these seven European species differs markedly from that of recent species of these two genera. In European fossils of *Tonicella*, all the pores of aesthetes have approximately the same diameter (Figs 4–6), while in recent species of *Tonicella* and *Boreochiton* there is a noticeable difference between the large pores of megal aesthetes and the small pores of micra aesthetes

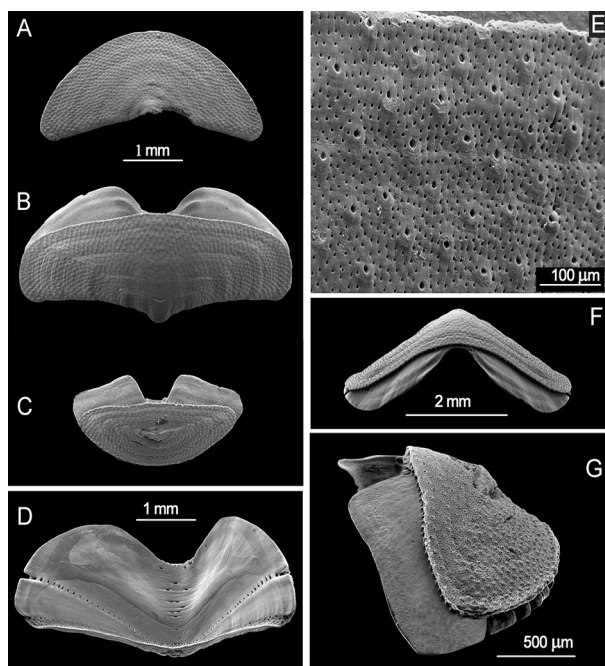


Fig. 3. *Tonicella marmorea*, Yarnishnaya Inlet, Murman coast, the Barents Sea, 18–20 m depth. A – valve I, dorsal view; B – intermediate valve, dorsal view; C – valve VIII, dorsal view; D – intermediate valve, ventral view; E – intermediate valve, structure of tegmentum in central area; F – intermediate valve, rostral view; G – valve VIII, lateral view.

(Figs 2, 3). It should be noted that the fossil species of the genus *Tonicella* have a valve shape similar to the species of the genus *Lepidochitona*, known since the Eocene in Europe. Moreover, in some species of the latter genus, for example *L. salvadorensis* García-Ríos, 2006 (Fig. 7) with a smooth tegmentum, there is no difference in the pore sizes of megal aesthetes and micraesthetes. Recent representatives of the genus *Lepidochitona* include species with both granular and smooth tegmentum, while all fossil European species have only a granular tegmentum. And where did the fossil species of *Lepidochitona* with a smooth tegmentum go? Apparently these are the seven fossil species that have been assigned to *Tonicella* and in which, unlike other real species of *Tonicella*, there is no difference in the size of the pores of megal aesthetes and micraesthetes. We propose to transfer these seven known fossil species, with a smooth tegmentum and with no difference in pore sizes of megal aesthetes and micraesthetes, to the genus *Lepidochitona*.

The system of recent chitons is based on the use of both external (the shape and sculpture of the shell

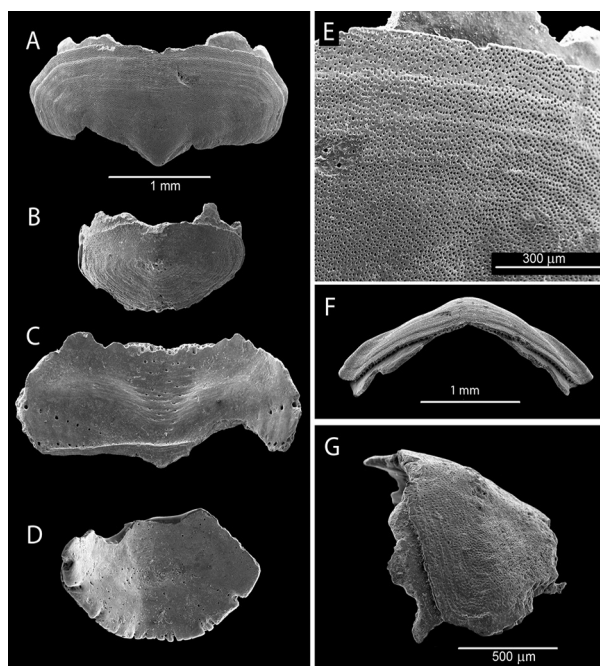


Fig. 4. *Tonicella redoniensis*, Miocene, (Tortonian). Saint-Clément-de-la-Place, France. A – intermediate valve, dorsal view; B – valve VIII, dorsal view; C – intermediate valve, ventral view; D – valve VIII, ventral view; E – intermediate valve, structure of tegmentum in central and lateral areas; F – intermediate valve, rostral view; G – valve VIII, lateral view.

valves, the armament of the perinotum and hyponotum, the number and location of the gills, the location of the gonopore and nephridiopore) and internal morphological features (apophyses, insertion plates and slits of the articulamentum, number and the shape of the teeth of the radula) (Bergenhayn 1930; Van Belle 1983; Sirenko 2006). In fossil chitons, unfortunately, of all the above set of features, only those associated with the shell remain (the shape and sculpture of the valves as well as apophyses, insertion plates and slits of articulamentum). Until recently, these features were actively used, and it should be noted that only macrosculpture was used in the sculpture of shell valves (all kinds of ribs, pits, furrows, borrows, grains, pustules, etc.). With the use of the scanning electron microscope, it became possible to study the microsculpture of various parts of the shell of chitons. This microsculpture is created by numerous pores of megal aesthetes and micraesthetes and associated apical and subsidiary caps (Boyle 1974; Baxter and Jones 1981, 1987; Gowlett-Holmes and Jones 1992; Sirenko 1992; Eernisse and Reynold 1994).

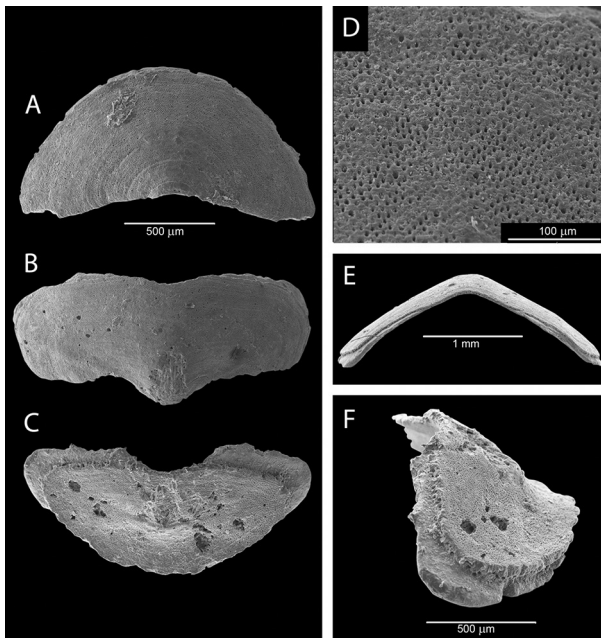


Fig. 5. *Tonicella implumis*, Upper Eocene, Mandrikovka Beds, Dnepropetrovsk, Ukraine. A – valve I, dorsal view; B – intermediate valve, dorsal view; C – valve VIII, dorsal view; D – intermediate valve, structure of tegmentum in central area; E – intermediate valve, rostral view; F – valve VIII, lateral view.

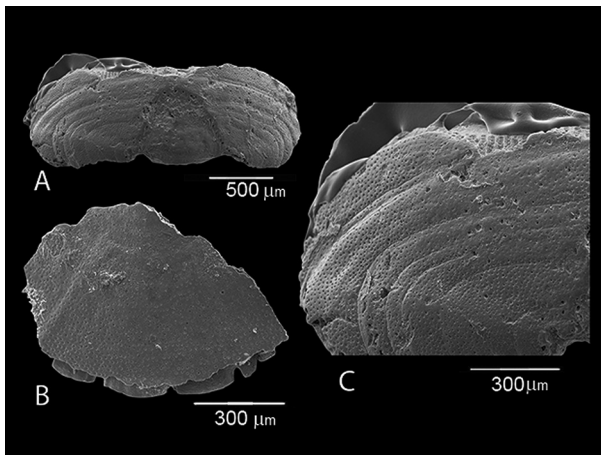


Fig. 6. *Tonicella tenuissima*, Oligocene, Germany. A – intermediate valve, dorsal view; B – part of valve VIII, lateral view; C – intermediate valve, structure of tegmentum in central and lateral areas.

In the class Polyplacophora there are many species of various genera (*Ferreiraella* Sirenko, 1988, *Leptochiton* Gray, 1847, *Parachiton* Thiele, 1909, *Ischnochiton* Gray, 1947, *Stenosemus* Middendorff, 1847, *Tonicina* Thiele, 1906, *Chaetopleura* Shuttle-

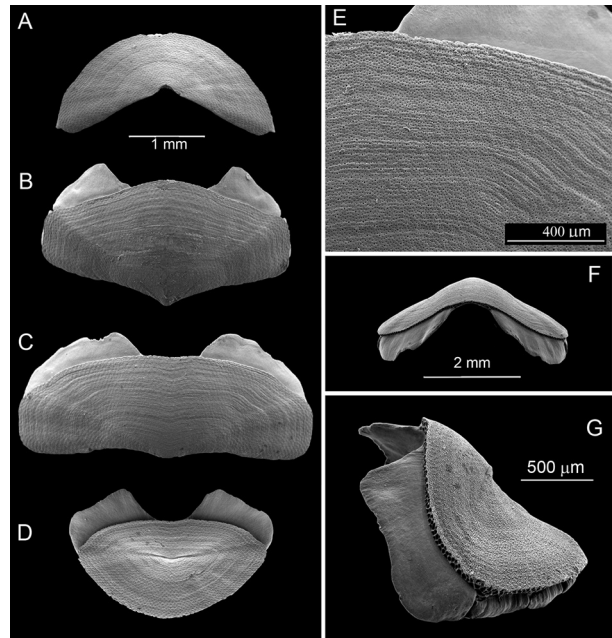


Fig. 7. *Lepidochitona salvadorensis*, Majahua, Acapulco, Guerrero, Mexico, 4–5 m. A – valve I, dorsal view; B – valve II, dorsal view; C – valve V, dorsal view; D – valve VIII, dorsal view; E – valve V, tegmentum sculpture in central and lateral areas; F – valve V, rostral view; G – valve VIII, lateral view.

worth, 1853, *Lepidochitona* Gray, 1821, *Boreochiton* Sars, 1878, *Tonicella* Carpenter, 1873) with the so-called smooth tegmentum. Such recent species that have a sufficient number of external and internal distinguishing features are not difficult to differentiate. As our research has shown, in contrast to the recent species, the definition of fossil species with a smooth tegmentum is quite difficult if the features of microsculpture of the tegmentum are not used.

Doug Eernisse (pers. comm.) rightly believes that North Atlantic *T. marmorea* and *B. ruber* are so similar to their counterpart species in the North Pacific that they are likely to be Pacific/Atlantic sister species pairs and this helps reinforce the claim that the two extant species have only recently invaded the North Atlantic.

In conclusion, it should be emphasized that the Eocene, Oligocene and Miocene European fossil species previously attributed to the genus *Tonicella* should be included in the genus *Lepidochitona*, which, since the Eocene, was widespread in the Tethys Ocean, and the first true representatives of the *Tonicella* and *Boreochiton* genera were able to penetrate from the Pacific Ocean to the Atlantic Ocean only in the Pliocene.

ACKNOWLEDGEMENTS

We would like to thank, Doug Eernisse (California State University Fullerton, Fullerton, CA, USA), Bruce Marshall (Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand), Wellington) and Anatoly Petrov (ZIN) for their careful review of the manuscript, Floyd Sandford (Coe College, Cedar Rapids, IA, USA) for polishing our English, Alexey Miroljubov (ZIN) for his technical assistance with SEM procedures, and Evgenia Goncharova (ZIN) for preparing the plates of illustrations. This research was performed using the equipment of the “Taxon” Research Resource Centre (<http://www.ckp-rf.ru/ckp/3038/>) of ZIN. This work is based on the taxonomic collection of ZIN and was supported by the State Research Assignment of Russian Federation “Taxonomy, biodiversity and ecology of invertebrates from Russian and adjacent waters of World Ocean, continental water bodies and damped areas”, No. 122031100275-4.

REFERENCES

- Baxter J. M. and Jones A.M. 1981.** Valve structure and growth in the chiton *Lepidochitona cinereus* (Polyplacophora: Ischnochitonidae). *Journal of the Marine Biological Association UK*, **61**: 65–78. <https://doi.org/10.1017/S0025315400045914>
- Baxter J. M. and Jones A.M. 1987.** The ultrastructure of aesthetes in *Tonicella marmorea* (Polyplacophora: Ischnochitonina) and a new functional hypothesis. *Journal of Zoology*, **211**: 589–604. <https://doi.org/10.1111/j.1469-7998.1987.tb04473.x>
- Bergenhayn J.R.M. 1930.** Kurze Bemerkungen zur Kenntnis der Schalenstruktur und Systematik der Loricaten. *Kungliga Svenska Vetenskapsakademiens Handlingar*, **3**(9): 3–54, pls 1–10.
- Boyle P.R. 1974.** The aesthetes of chitons. 2. Fine structure in *Lepidochitona cinerea* (L.). *Cell Tissue Research*, **153**: 383–398. <https://doi.org/10.1007/BF00229166>
- Chatwin C.P. 1954.** British Regional Geology: East Anglia and adjoining areas. 3rd Edition. Department of Scientific and Industrial Research: Geological Survey and Museum, London, 100 p.
- Clark R.N. 1999.** The *Tonicella lineata* (Wood, 1815) species complex (Polyplacophora: Tonicellidae), with descriptions of two new species. *American Malacological Bulletin*, **15**(1): 33–46.
- Dell’Angelo B. and Giusti F. 1997.** I Polyplacophora di una tafocenosi profonda. *La Conchiglia*, **29**(283): 51–58.
- Dixon R.G. 1979.** Sedimentary facies in Red Crag (Lower Pleistocene, East Anglia). *Proceedings of the Geologists’ Association*, **90**(3): 117–132. [https://doi.org/10.1016/S0016-7878\(79\)80014-0](https://doi.org/10.1016/S0016-7878(79)80014-0)
- Eernisse D.J. and Reynold P.D. 1994.** Polyplacophora. In: F.W. Harrison (Ed.). *Microscopic Anatomy of Invertebrates*, Vol. 5: Mollusca I. Wiley-Liss, New York, 390 p.
- Gladenkov Yu.B. 1978.** Marine Upper Cenozoic of the northern regions. *Proceedings of the Geological Institute of the Academy of Sciences of the USSR*, **313**: 1–194. [In Russian].
- Golikov A.N. 1980.** Molluscs Buccininae of the World Ocean. Fauna of USSR, Molluscs, Vol. **5**(2). Leningrad, Nauka, 466 p. [In Russian].
- Gowlett-Holmes K.L. and Jones A.M. 1992.** Xylochitonidae fam. n., a new family of deep-water chitons, with descriptions of a new genus and species from New Zealand (Polyplacophora: Lepidopleurina). *Journal of the Malacological Society of Australia*, **13**: 35–44. <https://doi.org/10.1080/00852988.1992.10674032>
- Hopkins D.M. 1972.** The paleogeography and climatic history of Beringia during late Cenozoic time. *Inter-nord*, **12**: 121–150.
- Itoigawa J., Kuroda M., Naruse A. and Nishimoto H. 1976.** Polyplacophora assemblages from the Pleistocene formations of Boso and Miura Peninsulas, environs of Tokyo, Japan. *Bulletin of the Mizunami Fossil Museum*, **3**: 171–204.
- Itoigawa J., Kuroda M., Naruse A., Nishimoto H., Asada T., Tatsuya I. and Kiyokazu H. 1978.** Polyplacophora assemblages from the Pleistocene formations of Kisarazu, Ichihara and their environs, Boso Peninsula, Japan. *Bulletin of the Mizunami Fossil Museum*, **5**: 143–153.
- Itoigawa J., Shibata H., Nishimoto H. and Okumura Y. 1981.** Miocene fossils of the Mizunami group, central Japan. 2. Molluscs. *Monograph of the Mizunami Fossil Museum*, **3-A**: 1–53, pls 1–52.
- Itoigawa J., Shibata H., Nishimoto H. and Okumura Y. 1982.** Miocene fossils of the Mizunami group, central Japan. 2. Molluscs (Continued). *Monograph of the Mizunami Fossil Museum*, **3-B**: 303–311.
- Janssen R. 1978.** Revision der Polyplacophora des Oligozäns in Mitteleuropa. *Archiv für Molluskenkunde*, **108**(4–6): 215–235.
- Kaas P. and Van Belle R.A. 1985.** Monograph of living chitons (Mollusca: Polyplacophora). Vol. 2. Suborder Ischnochitonina. Ischnochitonidae: Schizoplacinae, Callochitoninae & Lepidochitoninae. E.J. Brill, W. Backhuys, Leiden, 198 pp. <https://doi.org/10.1163/9789004431683>
- Muhs L.R., Simmons K.R., Kennedy G.L., Ludwig K.F. and Groves L.T. 2006.** A cool eastern Pacific Ocean at the close of the Last Interglacial complex. *Quaternary Science Reviews*, **25**: 235–262. <https://doi.org/10.1016/j.quascirev.2005.03.014>

- Muhs L.R., Simmons K.R., Schumann R.R., Groves L.T., Mitrovica J.X. and Laurel D. 2012.** Sea-level history during the Last Interglacial complex on San Nicolas Island, California: implications for glacial isostatic adjustment processes, paleo-zoogeography and tectonics. *Quaternary Science Reviews*, **37**: 1–25. <https://doi.org/10.1016/j.quascirev.2012.01.010>
- Sirenko B.I. 1974.** Evolution of chitons of the genus *Tonicea* Carpenter (Ischnochitonina, Ischnochitonidae). *Vestnik Leningradskogo Universiteta, Seriya 9. Biologiya*, **2**: 138–140. [In Russian].
- Sirenko B.I. 1992.** Nierstraszellidae fam. nov. – a new family of chitons (Polyplacophora, Lepidopleurida) from the bathyal Western Pacific. *Ruthenica*, **2**: 81–90. [In Russian].
- Sirenko B.I. 2006.** New outlook on the system of chitons (Mollusca: Polyplacophora). *Venus*, **65**: 27–49.
- Van Belle R.A. 1983.** The systematic classification of the chitons (Mollusca: Polyplacophora). *Informations de la Société Belge de Malacologie*, **11**: 1–179.
- Vendrasco M.J., Eernisse D.J., Powell C.L.I. and Fernandez C.Z. 2012.** Polyplacophora (Mollusca) from the San Diego Formation: a remarkable assemblage of fossil chitons from the Pliocene of Southern California. *Natural History Museum of Los Angeles County Contributions in Science*, **520**: 15–72. <https://doi.org/10.5962/p.241291>