



# Prosobranch Family Velutinidae (Gastropoda) in Cold and Temperate Waters of the Northern Hemisphere: History, Biogeography, Evolution and Chorology

V. V. Gulbin

Institute of Marine Biology, Russian Academy of Sciences, Palchevskogo Str. 17, Vladivostok 690041, Russia

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**Abstract** – The history of investigation of the family Velutinidae from 1776 to the present day is briefly described in the last part of this review; the contemporary system of the family, consisting of 39 species and subspecies, belonging to 17 genera and subgenera, and three subfamilies, is presented here. A biogeographic analysis of the fauna has been made, the history of origin and development of the family, vertical distribution and relation to substrates have been described in this work.

**Key words** – Gastropoda, Velutinidae, biogeography, chorology, evolution

## 1. Introduction

The first valid velutinid species were described in 1776 by Müller (1776) under the name *Bulla plicatilis* and *Bulla velutina* (*Helix laevigatus* L. 1758, described by Linnaeus, is nomen nudum). As an independent genus, *Velutina* was described by Fleming (1821), and in 1842, it was related to an independent family Velutinidae by Gray (Gray 1842). It was Gray who later (1847) described the genus *Velutella*, and then (Gray in Gray 1850, cited from: Wenz 1938-1944) the genus *Marsenina*. Genera *Onchidiopsis* (Bergh 1853) and *Limmeria* (Adams and Adams 1853) were described in 1853. Altogether, by the end of the 19<sup>th</sup> century, more than 35 taxa of various ranks of species, related to the Velutinidae family in its contemporary interpretation, had been described, and less than one third of the species proved valid.

Odhner (1913) was one of the first researchers who attempted to compile a guide list for recent velutin species, which were included and described in detail, including 6 species of *Velutina* and 3 species of *Onchidiopsis*.

The first system of the family Lamelliariidae (where

earlier velutin was also attributed) and its position in the general system of Gastropoda, was proposed by Thiele (1929). He related the family Lamelliariidae to the tribe Lamelliariacea of the Mesogastropoda order and subdivided this species into three subfamilies: 1-Velutininae of the genera *Capulacmaea* Sars 1859 (= *Pilidium* Middendorff, 1851, non Forbes, 1849; = *Piliscus* Lovén, 1859), *Velutina* Fleming, 1822 (of the subgenera *Velutina* s.s., *Limmeria* H. et A. Adams, 1853 and *Velutella* Gray, 1847) and *Onchidiopsis* Berg, 1853 (with sections *Atlantolimax* Dall, 1917 and *Onchidiopsis* s.s.); 2-Marsenininae of the genus *Marsenia* Gray, 1850; 3-Lamelliariinae of the genera *Marseniopsis* Bergh, 1850; *Lamelliariopsis* Vogssiere, 1906 and *Galidoniella* Souverbie, 1869.

A rather different system was proposed by Wenz (1936-1944). He included the family Lamelliariidae into the superfamily Cypraeacea and related it to the order Mesogastropoda. He recognized two subfamilies under this genus: 1-Lamelliariinae of the genera *Marseniopsis* Berg, 1886, *Mysticoncha* Allan, 1936, and *Lamellaria* Montagu, 1815; 2-Velutininae of the genera *Marsenia* Gray, 1850, *Velutina* Fleming, 1812 (of the subgenera *Velutella* Gray, 1847, *Velutina* s.s., *Limmeria* H. et A. Adams, 1853), *Onchidiopsis* Berg, 1853 (of the subgenera *Onchidiopsis* s.s. and *Atlantolimax* Dall, 1917) and *Capulacmaea* M. Sars, 1859. Thus, Wenz did not single out the subfamily Marsenininae, as Thiele did, but integrated it into the subfamily Velutininae.

In 1937, Derjugin undertook the successful attempt to revise the genus *Onchidiopsis*. He examined and described eleven species under this genus, eight of which turned out to be newly discovered species. At the same time, Derjugin began to revise the data on the genus *Velutina* as well, but his early death did not allow him to complete this work. Nevertheless, his unfinished posthumous work on revision of the *Velutina* genus, in which 16 species

\*Corresponding author. E-mail: inmarbio@mail.primorye.ru

**Table 1.** List of species

Species	Biogeographical group	Depth (m)	Substratum
Class Gastropoda			
Order Cerithiiformes Ferrusac, 1819			
Suborder Calyptraeioidea Lamarck, 1809			
Family Velutinidae Gray, 1842			
Subfamily Capulacmaeinae Golikov et Gulbin, 1990			
Genus <i>Piliscus</i> Lovén, 1859			
1. <i>P. commodus</i> (Middendorff 1849)	wb	int-500	sa, r, co.
2. <i>P. radiatus</i> M.Sars, 1859	a	1-930	mu, sa, co
3. <i>P. rostratus</i> Golikov et Gulbin, 1990	hb	140-160	co
4. <i>P. undulatus</i> Golikov et Gulbin, 1990	lb	600	pe
Genus <i>Cilifera</i> Golikov et Gulbin, 1990			
5. <i>C. ciliata</i> Golikov et Gulbin, 1990	hb	58	mu-co, pe
Subfamily Velutinae Gray, 1842			
Genus <i>Limneria</i> H. et A.Adams, 1853			
Subgenus <i>Limneria</i> s.str.			
6. <i>L. (L.) undata undata</i> (Brown 1838)	ba	8-1187	mu-sa-co
7. <i>L. (L.) undata ochotensis</i> (Derjugin 1950)	hb	24-218	r, co, pe, mu, sa
8. <i>L. (L.) undata bifasciata</i> (Derjugin 1950)	lb	33-414	sa, mu-sa-pe
9. <i>L. (L.) insculpta</i> (Odhner 1913)	a	30-50	r, co, pe, mu, sa
Subgenus <i>Conivelutina</i> Golikov et Gulbin, 1990			
10. <i>L. (C.) prolongata</i> (Carpenter 1865)	wb	int-920	r, co, pe, mu, sa
Genus <i>Ciliatovelutina</i> Golikov et Gulbin, 1990			
11. <i>C. lanigera</i> (Möller 1862)	ba	10-500	sa-she, mu-sa, r, co
12. <i>C. capillata</i> (Derjugin 1950)	wb	int-116	r, co, sa-pe, mu-sa
13. <i>C. lanata</i> (Derjugin 1950)	hb	3-51	r, co, pe, mu-sa
14. <i>C. nana</i> (Bartsch in Derjugin 1950)	wb	7-340	mu-sa, r, co
Genus <i>Velutina</i> Fleming, 1821			
Subgenus <i>Velutina</i> s.str.			
15. <i>V. (V.) velutina</i> (Müller 1776)	ba	0.5-408	mu-sa, mu-pe
16. <i>V. (V.) schneideri</i> Friele, 1886	ba	7-350	mu-sa-co
17. <i>V. (V.) pulchella</i> Derjugin, 1950	wb	int-140	mu-sa-she, pe, co
Subgenus <i>Margaritavelutina</i> Golikov et Gulbin, 1990			
18. <i>V. (M.) tarasovi</i> Derjugin, 1950	lb	int-30	r, co
Subgenus <i>Corneovelutina</i> Golikov et Gulbin, 1990			
19. <i>V. (C.) coriacea</i> Pallas, 1788	wb	int-400	mu-sa-she, mu-co
20. <i>V. (C.) bartschi</i> Derjugin, 1950	wb	int-37	r, co, sa
Genus <i>Velutella</i> Gray, 1867			
21. <i>V. plicatilis</i> (Müller, 1776)	ba	int-430	mu-sa-pe, r, co
Genus <i>Cartilagovelutina</i> Golikov et Gulbin, 1990			
22. <i>C. beringensis</i> (Derjugin 1950)	wb	int-145	sr, pe, sa
23. <i>C. chondrina</i> (Bartsch in Derjugin 1950)	wb	int-150	sa, mu-sa-pe, co
24. <i>C. cristata</i> (Derjugin 1950)	wb	30-240	sa, mu-sa, pe
Genus <i>Marsenina</i> Gray, 1850			
25. <i>M. glabra</i> Couthouy, 1838	ba	23-1222	mu-sa-pe
26. <i>M. rhombica</i> (Dall 1871)	wb	int-130	mu-sa-pe, r, co
27. <i>M. ushidai</i> (Habe 1958)	wb	int-150	r, co, sa-she
28. <i>M. stearnsii</i> (Dall 1871)	wb	int-8	-
Subfamily Onchidiopsinae Golikov et Gulbin, 1990			
Genus <i>Onchidiopsis</i> Bergh, 1853			
Subgenus <i>Onchidiopsis</i> s.str.			

(Table 1. Continued)

Species	Biogeographical group	Depth (m)	Substratum
29. <i>O. (O.) groenlandica</i> (Bergh 1853)	ba	5-365	mu, mu-sa, mu-pe
30. <i>O. (O.) variegata</i> Derjugin, 1937	wb	25-1000	mu-sa-pe
31. <i>O. (O.) zachsi</i> Derjugin, 1937	ba	23-84	sa, mu-sa, mu-pe, co
Subgenus <i>Rostronchidiopsis</i> Golikov et Gulbin, 1990			
32. <i>O. (R.) glacialis</i> (M.Sars 1851)	ba	28-134	mu-sa-pe
33. <i>O. (R.) gurjanovae</i> Derjugin, 1937	wb	20-180	co, pe, mu-sa
34. <i>O. (R.) carnea</i> (Kroeyer 1847)	ba	5-500	mu-sa-pe
35. <i>O. (R.) longipes</i> Derjugin 1937	hb	210-664	mu, mu-sa-pe
36. <i>O. (R.) brevipes</i> Derjugin, 1937	ba	8-207	sa, mu-sa-pe
Subgenus <i>Bullonchidiopsis</i> Golikov et Gulbin, 1990			
37. <i>O. (B.) maculata</i> Derjugin, 1937	wb	5-80	mu-sa, mu-co
38. <i>O. (B.) nadinae</i> Derjugin, 1937	wb	14-100	mu-sa, co
39. <i>O. (B.) ushakovi</i> Derjugin, 1937	hb	16-195	mu,sa,mu-sa

Abbreviations. a - Arctic species, ba - boreal-arctic species, hb - high-boreal species, wb - widespread boreal species, lb - low-boreal species; int intertidal zone; r - rock, co - cobble, sa - sand, she shells, mu - mud, pe - pebble ground.

were examined, 9 of them newly discovered species, was published in 1950 (Derjugin 1950). K.M. Derjugin was one of the first researchers who applied not only the shape of the shell and radula, but also the morphology of the soft body (the reproductive organ, shape of the foot, mantle complex of organs) for species diagnosis of these genera.

Over the last 40 years in the seas of the Northern Hemisphere, only *Marsenina uschidai* (Habe 1958) and four species of the *Velutina* genus, were reassigned by us to the same genus (*V. glabra* Golikov et Kussakin, 1962, *V. fraudatrix* Golikov et Kussakin, 1962, *V. litoralis* Golikov et Kussakin in Golikov et Scarlato, 1967, and *V. ventricosa* Golikov in Golikov et Scarlato, 1985), were described as newly discovered species. A small number of works published in that period, were devoted to some issues of ecology and the anatomy of velutins (Diehl 1956; Thompson 1959; Fretter and Graham 1962, etc.), or to faunistic reports on specific water areas, where velutins were also represented to a certain extent. As for taxonomic works, only that of Behrens (1980) is worth mentioning, as it was devoted to a review of Lamelliariidae from the northwestern Pacific, which, together with three species of *Lamellaria* genus, *Marsenia stearnsii* (Dall 1971), *M. rhombica* (Dall 1971) and *Marseniopsis sharonae* (Willet 1939) were also considered, though they are related to the subfamily Lamelliariinae. A little later, Warén (1989) established the priority of the generic name *Piliscus* Lovén 1859, with respect to *Capulacmaea* M. Sars 1851, and identified the new velutinid genus and the species *Pseudotorelia fragilis*, but we have reassigned it to a separate genus.

We have attempted to revise our categorization of the Velutinidae family, taking into account the present state of the issue (Gulbin and Golikov 1997, 1998, 1999, 2000,

2001). As a result of the revision of the Velutinidae genus, Gray, in 1842, examines the matter in the following way (Table 1).

## 2. Biogeographical Analysis and History of the Family

The following types of natural habitats can be singled out for velutinid, distributed only in cold and temperate waters of the Northern Hemisphere:

### Arctic species

1. Eurasian arctic species, distributed only near the Arctic coasts of Europe and Asia (1 species) - *Limneria insculpta*.

2. Circumarctic species, distributed near the arctic coasts of Europe, Asia and America (1 species) *Piliscus radiatus*.

### Boreal-arctic species

1. Widespread boreal-arctic species, distributed in the boreal waters of the Pacific and Atlantic Oceans and along the entire Arctic coastline (4 species) - *Limneria undata undata*, *Velutina velutina*, *Velutella plicatilis*, *Onchidiopsis groenlandica*.

2. Asian high-boreal Arctic species, dwelling in the high-boreal waters of Asia and along the entire Arctic coastline (4 species) - *Velutina schneideri*, *Onchidiopsis zachsi*, *O. carnea*, *O. glacialis*.

3. Atlantic high-boreal Arctic species, dwelling in the high-boreal waters of the Atlantic Ocean and along the entire Arctic coastline (1 species) - *Marsenina glabra*.

4. Asian wide-boreal Arctic species, dwelling in the boreal waters near the coasts of Asia and Arctic coastline (2 species) - *Ciliatovelutina lanigera*, *Onchidiopsis brevipes*.

### Pacific boreal species

1. Pacific boreal species are widespread, inhabiting boreal waters near the Pacific coasts of Asia and America (2 species) - *Limneria prolongata*, *Marsenia rhombica*.

2. Asian-wide boreal species, inhabiting boreal waters only along Asian coasts (14 species) - *Piliscus commodus*, *Ciliatovelutina nana*, *C. capillata*, *Velutina cariaceae*, *V. bartschi*, *V. pulchella*, *Cartilagovelutina cristata*, *C. chondrina*, *C. beringensis*, *Marsenina uschidai*, *Onchidiopsis nadinae*, *O. maculata*, *O. gurjanovi*, *O. variegata*.

3. Pacific American-wide boreal species, inhabiting only boreal waters of the Pacific coast of America (1 species) - *Marsenina sternsii*.

4. Asian high-boreal species, inhabiting only high-boreal waters of Asia (6 species) - *Piliscus rostratus*, *Cilifera ciliata*, *Limneria undata ochotensis*, *Ciliatovelutina lanata*, *Onchidiopsis longipes*, *O. uschakovi*.

5. Asian low-boreal species, inhabiting only low-boreal waters of Asia (3 species) - *Piliscus undulatus*, *Limneria undata bifasciata*, *Velutina tarasovi*.

The Pacific boreal waters imply an area of water from the East Sea (the Sea of Japan), north-eastern Honshu, Hokkaido Island and California all the way to the north end of the Bering Strait; high-boreal waters - from the Sea of Okhotsk (except its southern part) and Vancouver all the way to the north end of the Bering Strait; low-boreal waters - from the southern border of the boreal waters up to the southern border of high-boreal waters. In the Atlantic Ocean, boreal waters include water areas north off Cape Hatteras and English Channel, and those of the high-boreal region - from Cape Cod and Scotland. Such a scheme of zonality is generally accepted in special literature, and is most frequently used in biogeography.

Thus, all fauna of velutinids, according to natural habitat,

can be divided into 11 zonal geographical specie's groups.

It is noticeable that species inhabiting the Pacific Ocean, and mainly its Asian coastal waters, are most dominant: they are 36, or 92.2% of the total number of species. They are, in the first turn, Asian wide-boreal (14, or 35.9%) and Asian high-boreal species. At the same time, the majority of velutinid species are widespread. There are only 2 Arctic species (5.2%), dwelling only in the Arctic Ocean. There are no Pacific American high- and low-boreal species, or Atlantic boreal species, and the fauna of these regions is represented only by widespread species.

To analyze the distribution of velutinids, it is advisable to consider the degree of similarity between different species of fauna from different distribution areas (Simpson 1943; Sørensen 1948).

$$I_{sim} = \frac{C}{A + C}, B \geq C \quad (1)$$

$$I_{spr} = \frac{2C}{A + B} \quad (2)$$

$A$  - number species in the 1<sup>st</sup> list;  $B$  - number species in the 2<sup>nd</sup> list;  $C$  - number common species

Simpson index (1) has a numerical value from 0 (the compared lists have no species in common) to 1, or 100% (the shorter list is fully covered by the longer one). Sørensen index (2) also varies from 0 (the lists have no common species) to 1, or 100% (the compared lists do not differ).

The largest number of velutinid species (28) inhabit the waters of the Sea of Okhotsk (Table 2), and representatives of all genera and subfamilies of Velutinidae family are found here. Species, inhabiting other seas of the Far East, comprise 87-95% of the Sea of Okhotsk fauna. Three species

**Table 2.** Comparison of species composition of Velutinidae among different parts of the family range.

Area	D <sub>1</sub>	D <sub>2</sub>	D <sub>3</sub>	D <sub>4</sub>	D <sub>5</sub>	D <sub>6</sub>	D <sub>7</sub>	D <sub>8</sub>	D <sub>9</sub>	D <sub>10</sub>	D <sub>11</sub>	D <sub>12</sub>
D <sub>1</sub>	<b>18</b>	89	50	60	67	40	60	30	44	31	27	30
D <sub>2</sub>	69	<b>28</b>	95	87	87	40	60	50	33	31	45	60
D <sub>3</sub>	49	76	<b>19</b>	73	53	100	80	60	55	69	64	60
D <sub>4</sub>	54	60	65	<b>15</b>	60	40	40	20	22	23	27	30
D <sub>5</sub>	61	60	48	60	<b>15</b>	20	40	30	22	27	27	30
D <sub>6</sub>	29	21	69	32	16	<b>10</b>	80	50	30	60	50	50
D <sub>7</sub>	26	26	33	20	20	53	<b>5</b>	100	80	100	100	100
D <sub>8</sub>	21	36	41	16	24	50	67	<b>10</b>	89	100	90	80
D <sub>9</sub>	30	16	36	17	17	30	71	84	<b>9</b>	100	100	78
D <sub>10</sub>	26	20	56	21	23	52	55	87	82	<b>13</b>	100	90
D <sub>11</sub>	21	26	47	23	23	46	62	86	90	92	<b>11</b>	100
D <sub>12</sub>	21	32	41	24	24	50	67	80	70	78	95	<b>10</b>

Note. the marked numbers on a diagonal line of the table designate the number of species in each district. Districts: D<sub>1</sub> - the East Sea (Sea of Japan), D<sub>2</sub> - the Sea of Okhotsk, D<sub>3</sub> - Bering the sea, D<sub>4</sub> - near Hokkaido and South Kuril islands, D<sub>5</sub> - near the Middle and Northern Kuril Islands and for eastern Kamchatka, D<sub>6</sub> - Chukchi Sea, D<sub>7</sub> - East Siberian Sea, D<sub>8</sub> - Laptev Sea, D<sub>9</sub> - Kara sea, D<sub>10</sub> - Barents Sea, D<sub>11</sub> - Norwegian Sea, D<sub>12</sub> - Greenland Sea. In the upper right part of the table - Simpson's index of association, in the inferior left part of the table - Sørensen's (in %).

(*Cilifera ciliata*, *Onchidiopsis longipes* and *O. uschakovi*) seem to be endemic for the Sea of Okhotsk.

The East Sea (the Sea of Japan) fauna is less rich: 18 species, comprising all genera and subfamilies of velutinids, dwell here. 50-67% of their composition are comprised of fauna from the Kuril Islands, as well as fauna of the Pacific coasts of Kamchatka and Bering Sea. 19 species, including all fauna of the Chuckchee Sea, were found in the Bering Sea, and 80% of them are formed of depleted fauna of the East Siberian Sea.

15 species, differing substantially according to composition (index of association -60%), were found both near the southern and northern Kuril Islands.

10 species were found in the Chuckchee Sea, 80% of which were formed of the fauna of the East Siberian Sea. All species of the East Siberian Sea also inhabit the Laptev, Bering, Barents, Norwegian and Greenland Seas.

10 species dwell in the Laptev Sea, and 80-100% of them share common features to those of the fauna of other seas of the Arctic Ocean. The same can be applied to the fauna of the Kara Sea, which does not differ from the Barents and Norwegian Seas according to velutinid composition.

In comparing fauna likenesses, we performed a cluster analysis of the species composition of velutinids from different areas of cold and temperate waters in the Northern Hemisphere (Fig. 1). Faunas of Norwegian and Greenland Seas are the most similar. They are followed by faunas of

the Barents, Kara and Laptev Seas, as the level of their likeness exceeds 80%. Depleted fauna of the East Siberian Sea is less similar to that of the mentioned seas, but is similar to that of the Chuckchee Sea with a degree of likeness as high as 48%.

Another block of dendrogram is formed in the sea fauna of the Far Eastern, which is similar to that of the Arctic seas at the level of 25-30%. The fauna of the Sea of Okhotsk and the Bering Sea are the closest in terms of composition. They are followed by the fauna of the southern Kuril Islands and Hokkaido Island, which, in turn, is more than 50% similar to that of the northern and middle Kuril Islands and southeastern Kamchatka.

Thus, though velutinids are widely spread, cluster analysis shows reliable distinctions in composition of Pacific boreal and Arctic fauna. In fact, the sea fauna of the Far East, having greater meridional length, display greater diversity of genus and species than that of some Arctic seas. Within the limits of the Pacific boreal region, faunas of the Sea of Okhotsk and the Bering Sea, related to the high-boreal subregion, are the closest. The fauna of the Sea of Japan reveals greater likenesses to the fauna of the Kuril Islands, where 3 species (*Piliscus undulatus*, *Limmeria undata bifasciata* and *Velutina tarasovi*) are endemics of the low-boreal subregion.

Six species (*Piliscus rostratus*, *Cilifera ciliata*, *Limmeria undata ochotensis*, *Ciliatovelutina lanata*, *Onchidiopsis longipes*, and *O. ushidai*) are endemic for the high-boreal Pacific subregion.

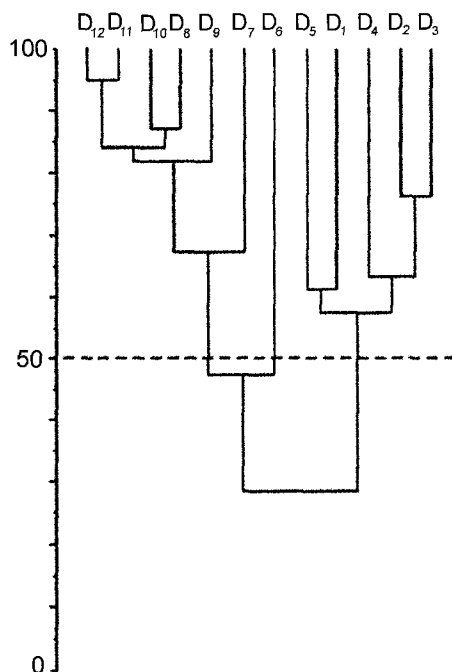


Fig. 1. Dendrogram of similarity (Sørensen index, %) of the species composition of velutinids in different parts of the family's ranges (notations as in Table 2).

### 3. The History of Velutinidae Fauna Formation

Unfortunately, Velutinidae shells are very poorly calcified or not calcified at all, which does not allow them to be preserved in a fossilized state. The absence of paleontologic data impelled us to apply an ecological method of evolutionary tracing (Golikov and Tzvetkova 1972) based on the close relationship between the development of the present faunas and the history of climate and relief changes, in order to reconstruct the ways in which velutinid fauna are formed in the Northern Hemisphere. This relationship is determined by the vital effect of physico-chemical factors on the processes of species and fauna formation, as well as on their subsequent distribution. Presently available data on paleofloras and paleofaunas enable us to picture a sufficiently legible pattern of climate changes in the Northern Hemisphere during the recent geological epochs (Krishtophovich 1932; Berg 1947; Schwarzbach 1955; Gekker 1957; Markov 1960; Sinitzin 1965, 1972; Braycev and Melekescev 1974; etc.). Comparison of data on ecology (in the first turn on thermopathy) and recent species distribution with the data on the history of climate and paleogeography development

enables us to suspect an ecological situation in which these species lived in the past, and to predict corresponding distribution patterns. This procedure also allows the research team to estimate the possible time and place of origin of the considered species. It was successfully applied in the reconstruction of the history of fauna preserved in a fossilized state (*Bivalvia*, *Gastropoda*) and not preserved ones (*Amphipoda*) (Golikov and Tzvetkova 1972; Scarlato 1981).

Analysis of the morphological likeness of velutinid species, identifying the trend of their morphogenesis, scant data on paleontology and paleoecological methods of evolutionary tracing enable us to suppose the following space-time evolutionary pattern for this family of specimens.

Velutinids could develop in the northwestern Pacific in the depths of Cenozoic era from common ancestors with *Capulidae* and *Trichotropidae* families. Representatives of the *Capulacmaeinae* subfamily, in which development of periostracum resulted in the appearance of setae (*Cilifera* genus), have the greatest likeness to the *Capulidae* family. *Limneria* genus originated from the same *Capulid-Trichotropid* ancestors, and gave rise to two trends in morphogenesis. The first trend followed the manner whereby the substitution of the shell calcareous layer for the periostracum, in the process of which, in the same way as for *Capulacmaeinae* specimens was achieved, setae developed on periostracum initially (*Ciliatovelutina* genus), and then the calcareous layer being replaced by the periostracum in the evolutionary line *Velutina-Velutella-Cartilagovelutina*.

Another trend in evolutionary morphogenesis concerned the covering of a shell by a mantle while the surface area of the shell was progressively reduced. It seemed to result in the development of *Marsenina*-like ancestors, which later on gave rise to the *Marsenina* genus, specimens which have a shell, partially closed by mantle flaps, and also led to the development of a highly deviated branch of *Onchidiopsis*-like ancestors, from which the present subfamily *Onchidiopsis* originated, specimens which have strongly reduced shells, completely closed by the intergrown mantle flaps.

The absence of velutinids in Mediterranean-Lusitanian waters testifies to the development of this family near the Asian coasts of the Pacific Ocean. At that, this development happened after isolation of the Eurasian sector of the Tethys Sea from the East-Asian sector in subtropical waters. The late Eocene-Early Oligocene turned out to be the optimum time for the appearance and development of this family. At that time, a substantial drop in temperature occurred on the Earth, which resulted in the relatively psychrophilic nature of the existing families of specimens. The most primitive in the family is the subfamily *Capulacmaeinae*, in which the Pacific Asian species *P. commodus* is distinguished for its relatively plesiomorphous

features (terminology of Hennig, 1950). It could originate even in the absence of clear hydrological borders between low-boreal and high-boreal waters of the Pacific Ocean, but in the presence of essential distinctions in the hydrology of Asian and American waters and in the presence of deep-water barriers between the Asian and American continents in high-boreal waters. It might have happened evidently in the period of Boreocene (Golikov 1985), 10-12 million years ago (Fig. 2).

Approximately at the same time, relatively ancient specimens of the other evolutionary lines of the family could originate in the temperate Asian waters of the Pacific Ocean: *Ciliatovelutina nana*, *Velutina coriacea* and *Onchidiopsis variegata*.

The origin of these species is timed to the Nuvoc transgression, which could facilitate a wide vertical distribution of these species.

A little later, during the ocean regression, *Velutina barschi*, *V. pulchella*, *Cartilagovelutina chondrina*, *Marsenina uchidai* and *Onchidiopsis gurjanovae*, which have a similar geographic distribution but a narrower vertical distribution range, could originate.

*Limneria prolongata*, which is notable for a number of primitive morphological features and the widest distribution range in the Pacific boreal region, seems to be the most ancient specimen of the present Velutinidae. This species seems to have developed in the early Boreocene, when there were no clear geomorphological and hydrological barriers between the Asian and American shelves.

Pacific species with a limited low- and high-boreal distribution originated much later, when clear hydrological barriers between low-boreal and high-boreal waters had already existed. Pacific Asian low-boreal *Velutina tarasovi* and *Onchidiopsis maculata*, and Pacific high-boreal *Piliscus rostratus*, *Ciliatovelutina capillata*, *C. lanigera*, *Cartilagovelutina beringensis*, *Marsenina rhombica*, *Onchidiopsis zaschi* and *O. nadinae* could develop from those species under the conditions of the late Boreocene-early Pliocene regression in shallow waters.

*Piliscus undulatus* and *Onchidiopsis longipes* could originate in the upper bathyal zones at the same time or a little earlier, and they continue to inhabit these depths up to the present time. A species, undoubtedly related to *Velutina* genus (*V. tokyensis*), was found in the Pliocene deposits in Japan.

A powerful transgression occurred in the middle of the Pliocene, about 3.5 million years ago, which allowed a number of widespread boreal species to penetrate, mainly underwater along the coastlines of Canada to the northern Atlantic waters. There are no modern velutinid species with purely Atlantic-like boreal distribution, but fossil shells of *Limneria* genus are found in the Pliocene deposits of England.

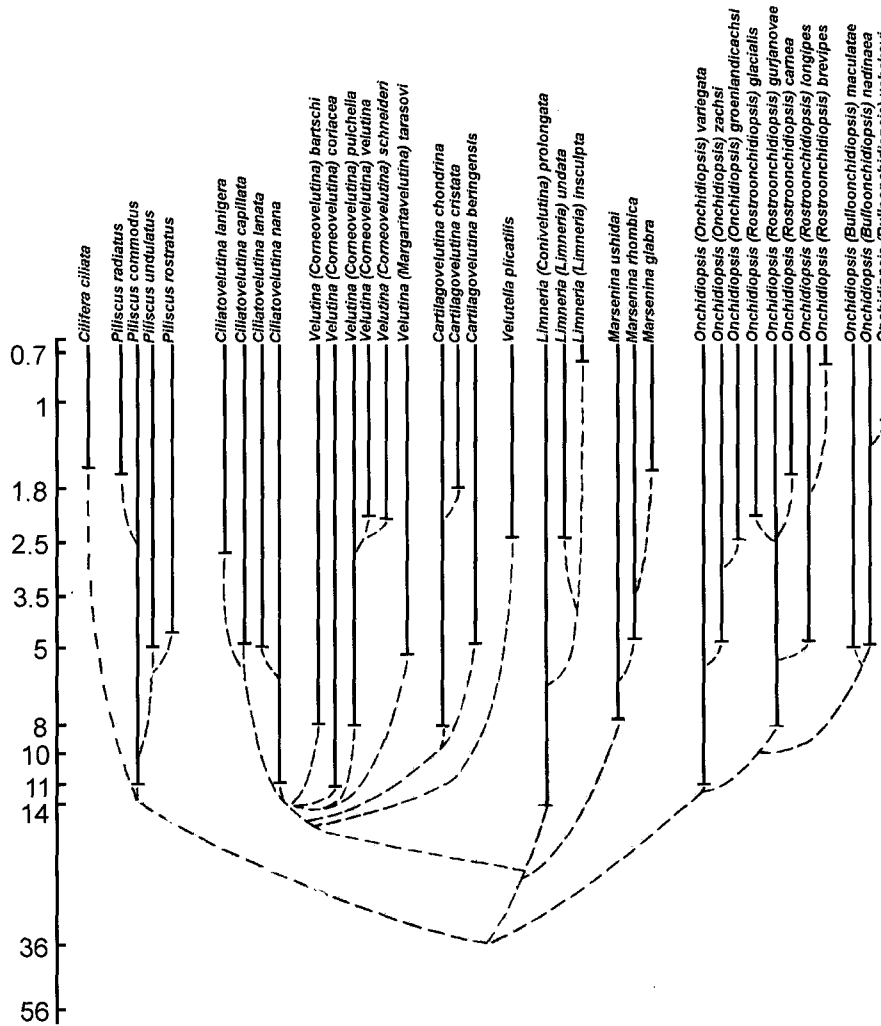


Fig. 2. Diagram of evolution of the family Velutinidae. Ordinate axis - time (million. years on log. Scale).

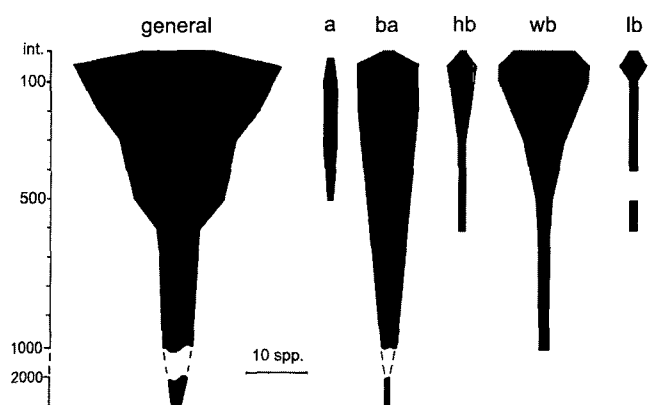
About 2.5 million years ago, due to the increased cooling in the northern Atlantic region, seemingly in the Norwegian Sea, Atlantic boreal Arctic species with a mainly Eurasian natural habitat - *Piliscus radiatus* and *Marsenina glabra* - descended from species close to the Pacific boreal type, which had penetrated there earlier. They have a wide vertical distribution range and seem to have developed already in Pleistocene under the conditions of progressive glaciation. At the same time, *Onchidiopsis carnea*, a Pacific boreal Arctic species with mainly American-Asian distribution, could develop in the northern Bering Sea. A little later, about 2.5 million years ago, *Ciliatovelutina lanigera*, *Limneria undata undata*, *Velutina plicatilis* and *Onchidiopsis groenlandica*, a widespread Arctic boreal species, could originate seemingly in the northern Bering Sea. High-boreal Arctic species *Velutina velutina* and *Onchidiopsis glacialis* developed after them, probably in the same place. Endemic to the Sea of Okhotsk, the genus

*Cilifera* with a single species *C. ciliata*, related to *Cartilagovelutina chondrina* - *C. cristata*, and *Onchidiopsis nadinae* *O. uschidai*, - could develop in the Pleistocene, when the western Sea of Okhotsk and the glacial Sea of Okhotsk was formed.

After the formation of Arctic surface waters during the glacial development and ocean regression, resulted in partial isolation of the Eurasian sector of the Arctic from the American-Asian sector, *L. insculpta* could descend from *Limneria undata* in the first case, and *O. brevipes* from *Onchidiopsis longipes* in the second case.

#### 4. Relation to Depths

Velutinidae have a wide range of depth distribution: from the intertidal zone to the bottom bathyal zone (Fig. 3). *Limneria undata undata* has a maximal reliably recorded habitat depth of 1187 m (Clarke 1963, cited from Macpherson



**Fig. 3.** Vertical distribution of velutinids: Abscissa - number of species; ordinate axis - depth, m. Abbreviations: a - Arctic species, ba - boreal-arctic species, hb - high-boreal species, wb - widespread boreal species, lb - low-boreal species; int - intertidal zone.

1971).

Analysis of depth distribution of the studied species allows us to single out the following main groups:

#### Stenobathic species, having a relatively small range of habitat depths

1. Littoral-circalittoral species<sup>1</sup> (5): *Cilifera ciliata* (8-58 m), *Ciliatovelutina lanata* (3-51 m), *Velutina bartschi* (intertidal zone-37 m), *V. tarasovi* (intertidal zone-28 m), *Marsenina sternsii* (intertidal zone-8 m).

2. Circalittoral-medial species (3): *Onchidiopsis zachsi* (23-84 m), *O. maculata* (5-80 m), *O. uschakovi* (16-95 m).

3. Inframedial species (1): *Piliscus rostratus* (139-160 m).

4. Bathyal species (2): *Piliscus undulatus* (600 m), *Onchidiopsis longipes* (210-664 m).

#### Eurybathic species, having a very wide range of habitat depths

1. Littoral-inframedial species (6): *Ciliatovelutina capillata* (intertidal zone-116 m), *Velutina pulchella* (intertidal zone-140 m), *Cartilagovelutina beringensis* (intertidal zone-145 m), *C. chondrina* (intertidal zone-150 m), *Marsenina uschidai* (intertidal zone-150 m), *M. rhombica* (intertidal zone-103 m).

2. Circalittoral-inframedial species (6): *Limneria undata ochotensis* (24-218 m), *Cartilagovelutina cristata* (30-240 m), *Onchidiopsis glacialis* (28-34 m), *O. brevipes* (8-207 m), *O. nadinae* (14-100 m), *O. gurjanovae* (20-180 m).

3. Littoral-bathyal species (4): *Piliscus commodus* (intertidal zone-500 m), *Limneria prolongata* (intertidal zone-920 m), *Velutina coriacea* (intertidal zone-414 m), *Velutella plicatilis* (intertidal zone-430 m).

4. Circalittoral-bathyal species (12): *Piliscus radiatus* (1-930 m), *Limneria undata undata* (8-1187 m), *L. undata bifasciata* (33-414 m), *L. insculpta* (30-500 m), *Ciliatovelutina nana* (7-340 m), *L. lanigera* (10-500 m), *Velutina schneideri* (7-350 m), *V. velutina* (0.5-1000 m), *Marsenina glabra* (22-1222 m), *Onchidiopsis variegata* (25-1000 m), *O. groenlandica* (5-365 m), *O. carnea* (5-500 m).

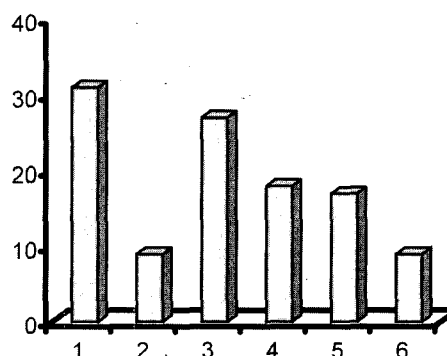
The general picture of vertical distribution of velutinid species is given on Fig. 3. The greatest species number (35, or 89.7%) was found at the depths of about 50 m, which corresponds to the boundary between circalittoral and medial zones (or sublittoral proper and eulittoral, according to Kjelman, 1877). At greater depths, a rapid reduction in species number occurs, which slightly decreases in the upper bathyal, and then increases again in the lower bathyal.

It is remarkable, that despite a wide vertical distribution of velutinids, the greatest number of them is attributed to shallow depths, which seems to testify to the shallow water origin of this group. Analysis of the vertical distribution of various subfamily species showed the same pattern as that of the family as a whole.

Biogeographical composition of velutinids changes with depth increases (Table 3). 77.9% of all species, found in the intertidal zone, fall at widespread boreal ones. The other species are presented by an approximately equal proportion of other biogeographic groups.

A portion of high-boreal, boreal arctic and arctic species rapidly rises with the depth increase. Species number peaks at depths of 50 m determined mainly by wide-boreal (42.9%) and boreal arctic (31.5%) species.

At greater depths, a portion of Arctic boreal species increases up to 54.5% at depths of 400-500 m, and at depths of more than 1000 m they already amount to 100% of the fauna. A portion of Arctic species is the greatest at



**Fig. 4.** Relation of velutinids to terrain. Ordinate axis number of species; abscissa axis - grounds: 1 - rock-cobble, 2 - cobble-sand-shells, 3 - mud-sand-cobble, 4 - sand, 5 - mud-sand, 6 - mud.

<sup>1</sup>Names of vertical zones are given according to Forbes and Hanley (1853)



**Table 3.** Biogeographical composition of velutinids at different depths (percentage of total species at this depth).

Depth, m	Number species and subspecies	Arctic	Boreal-arctic	High-boreal	Wide-spread boreal	Low-boreal
intertidal	12	0	7.5	7.5	77.5	7.5
0-10	23	4.2	29.2	12.4	50	4.2
11-50	35	5.8	31.3	14.3	42.8	5.8
51-100	32	6.1	33.3	12.1	45.5	3.0
101-200	27	7.4	37.0	11.1	40.8	3.7
201-300	19	11.1	44.4	5.6	33.3	5.6
301-400	17	11.8	47.0	5.9	29.4	5.9
401-500	15	9.1	54.4	9.1	27.4	0
501-600	7	0	42.9	14.3	28.5	14.3
601-700	6	0	50	16.7	33.3	0
701-1000	5	0	60	0	40	0
1002-2000	2	0	100	0	0	0

depths of 300-400 m, where they make up 11.8% of all velutinid fauna at these depths. At depths greater than 600 m, they disappear and are replaced by boreal species. The number of low-boreal species is not high at all depths, but at depths of 500-600 m, they comprise 14.3% of all velutinids, though represented by only one bathyal species *Piliscus undulatus*.

The greatest range of vertical distribution is occupied by species, having the widest natural habitat areas (widespread boreal and boreal arctic species): *Piliscus commodus*, *P. radiatus*, *Limmeria prolongata*, *Ciliatovelutina lanigera*, etc. Species, having a narrow natural habitat range (low- and high-boreal), are confined as a rule to a narrow depth range: *Ciliatovelutina lanata*, *Velutina tarasovi*, *Onchidiopsis uschakovi*, etc.

## 5. Relation to Grounds

The overwhelming majority of velutinid species are eurytopic, and can live on extremely diverse terrain. Most often they settle on rocky and stony ground (Fig. 4), usually among algae, sea grasses, hydroids, sponges and ascidians, with which their way of life is closely connected. As a rule, these are species and populations inhabiting shallow depths. At greater depths, where tough terrain is absent, they prefer a mixed cobble-sandy-muddy surface. Rather less frequently velutinids can be found on sandy and muddy-sandy terrain, and much less frequently on cobble-sandy terrain and pure mud.

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