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Schizoplax brandtii (Middendorff, 1847) (Mollusca: Polyplacophora) – an example of «explosive speciation»?

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The close relationship of *Schizoplax brandtii* (Middendorff, 1847) and *Lepidochitona dentiens* (Gould, 1846) is proposed on the basis of morphological comparison and molecular investigations. The advantages of *S. brandtii* which were conducive to occupying the northern Pacific and its origin as a result of «explosive speciation» is discussed. The family Schizoplacidae is considered as a junior synonym of the family Tonicellidae.

Key words: *Schizoplax brandtii* (Middendorff, 1847), *Lepidochitona dentiens* (Gould, 1846), morphology, molecular analysis, speciation, origin, Schizoplacidae, Tonicellidae.

Schizoplax brandtii (Middendorff, 1847) (Mollusca: Polyplacophora) – пример «внезапного видообразования»?

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Близкое родство *Schizoplax brandtii* (Middendorff, 1847) и *Lepidochitona dentiens* (Gould, 1846) предполагается на основе морфологических и молекулярных исследований. Обсуждаются преимущества *S. brandtii*, которые способствовали его широкому расселению в северной Пацифике и происхождение этого вида, как результат «внезапного видообразования». Семейство Schizoplacidae предложено рассматривать в качестве младшего синонима Tonicellidae.

Ключевые слова: *Schizoplax brandtii* (Middendorff, 1847), *Lepidochitona dentiens* (Gould, 1846), морфология, молекулярный анализ, видообразование, происхождение, Schizoplacidae, Tonicellidae.

Schizoplax brandtii (Middendorff, 1847) is the sole member of the genus and family. Among chitons, only *S. brandtii* possesses intermediate valves of its shell that consists of two portions connected by ligament. This feature allowed Dall [1878] to describe a new genus *Schizoplax* Dall, 1878, and Bergenhayn [1955] – a new family Schizoplacidae. Such an essential feature is absent in other Recent and fossil chitons. All other features of the shell important in the taxonomy of chitons, i.e., the radula and perinotum, are very similar to those of the genus *Lepidochitona* Gray, 1821. If we ignore the ligament in *S. brandtii*, we can wrongly place this species in the genus *Lepidochitona* of the family Tonicellidae.

Molecular markers that were used in the studies on chitonids include nuclear ribosomal genes (18S rRNA, fragment of 28S rRNA), nuclear protein coding gene histone H3 and mitochondrial protein coding cytochrome oxidase subunit 1 (CO1) and mitochondrial ribosome gene 16S RNA [Okusu et al., 2003; Kelly et al., 2007; Kelly, Eernisse, 2008]. The application of these molecular markers was not resulted in a robust tree neither with individual genes nor with concatenated matrix and phylogenetic relations within chitons above the species level remain uncertain. Meanwhile the greatest amount of sequences for chitons is represented by CO1, the fragment of the gene used for the DNA barcoding (BOLD). But even though the total number of sequences of CO1 is over 700, data on *S. brandtii* are still absent. Here, we start our molecular investigation of *S. brandtii* with CO1 as this is the most widely used marker and thus it is easy to assemble material for comparison, then it would contribute to the DNA barcoding initiative and to future phylogeographic studies, and finally we can make a first step towards testing our ideas on phylogenetic relationships of this chiton and its probable closeness to *Lepidochitona*. Therewith, we clearly understand that CO1 is not the appropriate molecular marker for above species level phylogenetic analysis due to extremely high saturation, but obtained results may be used as a preliminary data mining and some independent evidence alongside with non-molecular data. Thus, this paper is aimed at testing the hypothesis on phylogenetic relationships of *S. brandtii*, and in particular we want to test whether molecular data confirm or reject the phylogenetic closeness of genera *Schizoplax* and *Lepidochitona*.

Material and methods

Samples

For molecular analysis, material fixed in 75–80% ethanol was used. Tissue samples were taken from the following species: *S. brandtii*, *Lepidochitona dentiens* (Gould, 1846), *L. keepiana* Berry, 1848, *Spongioradsia aleutica* Dall, 1878, *Boreochiton beringensis* (Yakovleva, 1952), *Tonicella marmorea* (Fabricius, 1780) and *T. submarmorea* (Middendorff, 1847); samples are stored in the collection of the Zoological Institute, Russian Academy of Sciences. Accession numbers, abbreviations and geographic origin of original material sequenced in this study are given in Table 1. The comparative material for analysis retrieved from the Genbank was composed in a following way: first we analyzed the data set focusing on genera of the suborder Acanthochitonina using representatives of the suborder Chitonina (*Callistochiton antiquus* (Reeve, 1847) and *Stenoplax alata* (Sowerby, 1841)) as an outgroup. Therewith, almost all genera of the first suborder, referred to all currently recognized families were represented. Secondly, we used the same data set but as an outgroup, we used instead *Laevipilina hyaline* McLean, 1979 from the class Monoplacophora. The complete list of species used in the analysis and their accession numbers are given in Tables 1 and 2. In this paper, the old genus *Lepidochitona* instead of *Cyanoplax* Pilsbry, 1892 is used. *Cyanoplax* was described as a subgenus of

Table 1

Specimens used in molecular studies by the authors

Species	Abbreviation	Date	Location	Depth	Acc. No.
Schizoplax brandtii	1C	17.08.1982	Sea of Japan, Chikhacheva Bay	Intertidal	KC776925
S. brandtii	5C	28.07.1990	Commander Isls., Bering Isl.	Intertidal	KC776926
S. brandtii	5N	06.06.2006	Aleutian Isls., Unalaska Isl.	Intertidal	KC776927
Lepidochitona dentiens	2C	27.08.1999	Oregon, San Juan Isl., FHL	Intertidal	KC776928
L. keepiana	3C	12.04.1995	California, Santa Barbara	Intertidal	KC776929
Spongioradsia aleutica	6C	28.07.1990	Commander Isls., Bering Isl.	Intertidal	KC776924
Boreochiton beringensis	7C	06.06.2006	Aleutian Isls., Unalaska Isl.	Intertidal	KC776930
Tonicella. marmorea	6N	19.10.1996	Norwegian Sea, Tromso	Intertidal	KC776931

the genus *Tonicella* Carpenter, 1873 by Pilsbry [1892–1893] who included two species (*Tonicella* (*Cyanoplax*) *hartwegii* Carpenter, 1855 and *T.* (*C.*) *bipunctata* Sowerby, 1832) in the subgenus. No typical features of *Cyanoplax* which differ it from *Lepidochitona* are known. Therefore, we agree with Van Belle (1983–1985) who considered *Cyanoplax* as a junior synonym of the genus *Lepidochitona*.

DNA isolation, Polymerase chain reaction and sequencing

Genomic DNA was isolated from ethanol-fixed muscles by Proteinase K digestion, phenol-chloroform deproteinization and isopropanol precipitation [Fritsch et al., 1989]. A fragment of mitochondrial gene Cytochrome Oxidase subunit I (COI) 629 bp in length was amplified by PCR using universal COI primers HCO2198 and LCO1490 [Folmer et al., 1994]. Polymerase chain reaction (PCR) entailed 30–35 thermal cycles as follows: 30 s denaturation at 94°C, 1 min annealing at 57–62°C and 1 min extension at 72°C. All PCR experiments include negative controls. PCR products were visualized on 1.5% agarose gel and then purified using Omnix purification kit according to manufacturers instructions. Approximately 10–40 ng of the purified PCR product was used for sequencing with each primer by autosequencing system ABI 3130-Avant using ABI PRISM®BigDye™ Terminator v. 3.1.

Sequences were aligned using Clustal W algorithm implemented in BIOEDIT 7.0 [Hall, 1999] and edited manually.

Table 2

Sequences of CO1 retrieved from GENBANK

Species	Genbank Acc. No., geographic origin	Source
Cyanoplax keepiana	EF201204	Kelly et al., 2007
Cyanoplax hartwegii	EF201149	Kelly et al., 2007
Cyanoplax dentiens	EF201086	Kelly et al., 2007
Nuttallina californica	EF201251	Kelly et al., 2007
Nuttallina fluxa	EF201349	Kelly et al., 2007
Nuttallochiton mirandus	AY377705	Okusu et al., 2003
Mopalia acuta	EF159671	Kelly et al., 2007
Mopalia muscosa	EF159580	Kelly et al., 2007
Mopalia hindsii	|EF159594	Kelly et al., 2007
Mopalia ciliata	EF159588	Kelly et al., 2007
Acanthochitona crinita	AF120627	Girbet, Wheeler, 2002
Crypthochiton stelleri	EF159619	Kelly et al., 2007
Placiphorella velata	EF159593	Kelly et al., 2007
Cryptoplax japonica	FJ445780	Wilson et al., 2010
Katharina tunicata	U09810	Boore, Brown, 1994
Tonicella lineata	EF201596	Kelly et al., 2007
Stenoplax alata	AY377711	Okusu et al., 2003
Stenoplax conspicua	EF200980	Kelly et al., 2007
Callistochiton antiquus	AY377712	Okusu et al., 2003
Callistochiton crassicostatus	EF200762	Kelly et al., 2007
Laevipilina hyalina	FJ445781	Wilson et al., 2010

Phylogenetic analysis and tree reconstruction

Phylogenetic and molecular evolutionary analyses were conducted using *MEGA* version 5 [Tamura et al., 2011]. To reconstruct the ML tree, appropriate models of sequence evolution were chosen as implemented in Modeltest version 3.7 [Posada, Crandall, 1998] based on Akaike Information Criterion (AIC). Rate heterogeneity among sites was modeled assuming gamma distribution for substitution rates (discrete approximation, 5 categories) invoking proportion of invariant sites. Twenty random trees obtained with 'Generate Start Trees' procedure were

used as the starting trees. The MP tree was obtained using the Close-Neighbor-Interchange algorithm with search level 2 in which the initial trees were obtained with the random addition of sequences. Bootstrap analysis (500 pseudoreplicates) was performed. In the data set with Chitonina as an outgroup to Acanthochitonina following the recommendations of Modeltest, we used Hasegawa–Kishino–Yano (HKY) model, (G=0.5461) performing maximum likelihood analysis. While analyzing the data set using Monoplacophora as an outgroup the GTR+I model was used with proportion of invariant sites 0.528; Ts/Tv=1.86.

The data on temperature were taken from Gorshkov [1974] and from own observations. The systematic classification follows Sirenko [2006].

Results

Molecular data

The final alignment included 627 bp or 209 amino acid residues. Among this, 309 and 65 sites respectively were variable, 262 and 37 were parsimony informative. Most substitutions were transitions of the third positions.

Analyzing the first data set maximum likelihood and parsimony analyses produced trees of practically identical topologies. While generally there is very poor resolution at the obtained trees it noteworthy that we have two distinct clusters within Acanthochitonina, one of which has a very strong support and unites genera *Lepidochitona* (=*Cyanoplax*), *Nuttallina* Dall, 1871 (family Tonicellidae) and *Schizoplax* and another, poorly supported cluster, unites most genera of the families Mopaliidae (Fig. 1), Acanthochitonidae and Cryptoplacidae, therewith the representatives of the latter tend to be united in one cluster. The same topology was reproduced also in an analysis of translated sequences (not shown). No resolution of generic relationships within these two clusters of Acanthochitonina was thus obtained.

The data set with Monoplacophora as an outgroup generally showed the same results with only difference that in this case we have only one well supported cluster within the order Chitonida both in analysis of nucleotide sequence and translated sequences and this is again the cluster uniting genera of the family Tonicellidae and *S. brandtii* (Fig. 2).

Morphological and ecological data

Of all groups of chitons, *S. brandtii* is most similar to species of the genus *Lepidochitona*. Species of the latter genus are tropical, subtropical and rare in boreal environments, and are not adapted to temperatures as low as *S. brandtii* encounters in the north Pacific. *Lepidochitona* species are distributed worldwide in water temperature above 0°C where the intertidal zone never freezes, except *Lepidochitona cinerea* (L., 1767), which is able to withstand short-term cooling to −1°C in the intertidal pools on coast in north Norway [Sirenko, 1998]. The distribution of the genus *Lepidochitona* is disjunctive as they are found in five different areas: the Black and Medi-

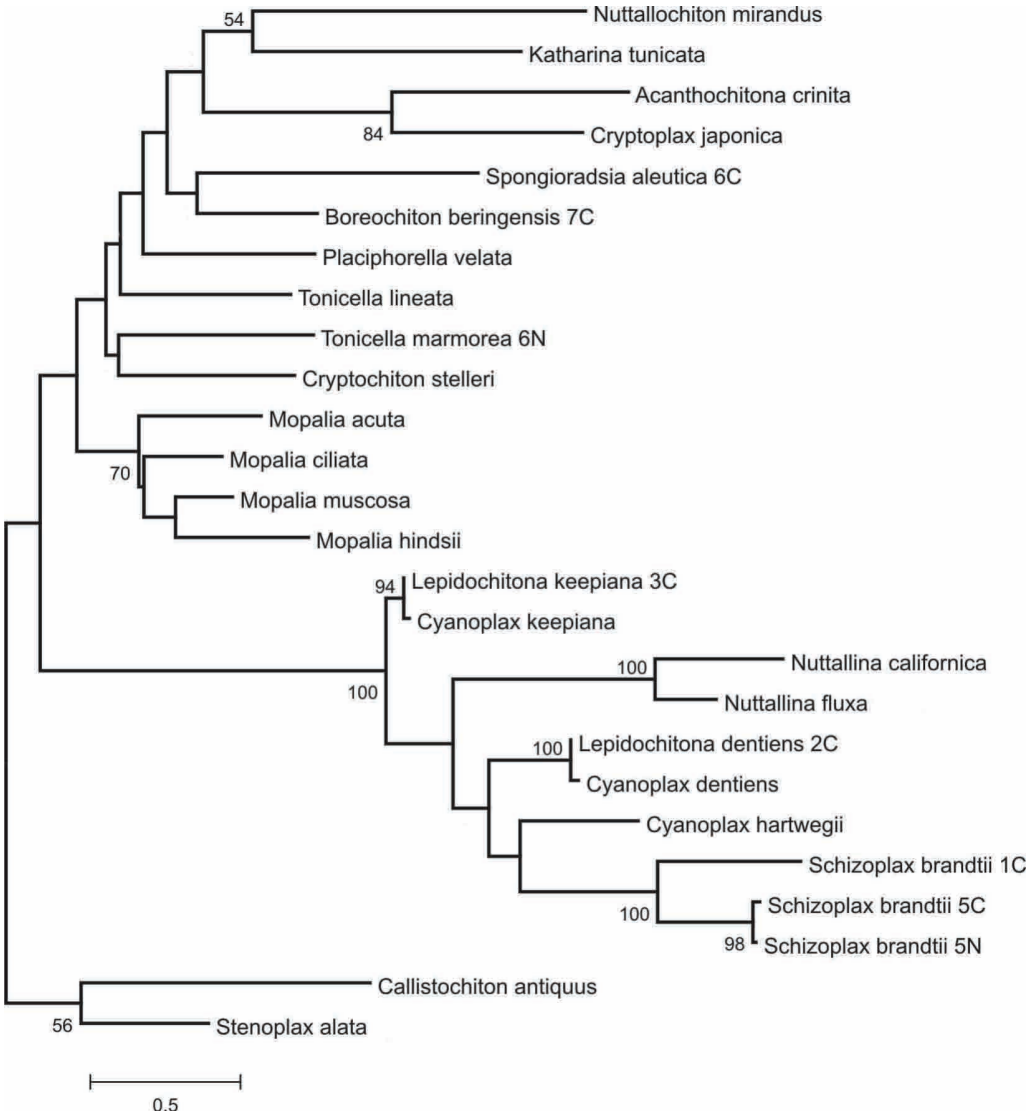

Fig. 1. Maximum likelihood tree of cytochrome oxidase 1 sequences based on the Hasegawa–Kishino–Yano model with representatives of Chitonina (*Stenoplax alata* and *Callistochiton antiquus*) as an outgroup. Numbers on the branches correspond to ML support > 50%. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site.

terranean seas and the north-east Atlantic Ocean from Morocco to north Norway, the Red Sea and north Arabian Sea, off South Africa, the Caribbean Sea and adjacent waters of the Atlantic Ocean, eastern part of the Pacific Ocean from Peru to Alaska Bay [Kaas, Van Belle, 1989; author's data].

L. dentiens is most similar in morphology to *Schizoplax brandtii*, and it inhabits the intertidal zone from Hinchinbrook Island, Alaska to Baja California, Mexico [Ferreira, 1982; Eernisse, 1986]. These two species live in similar biotopes. However, *S. brandtii* is widely distributed in

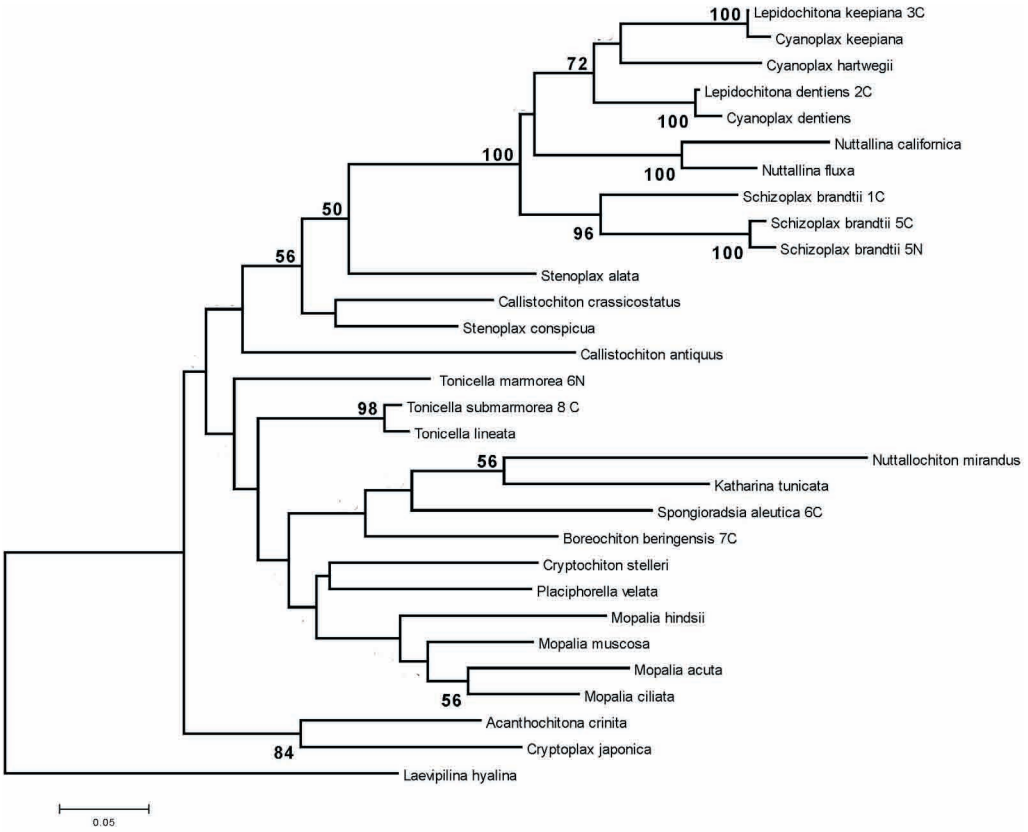

Fig. 2. Maximum likelihood tree of cytochrome oxidase 1 sequences based on GTR+I model rooted with *Laevipilina hyaline.*

the north Pacific (Fig. 3), unlike species of the genus *Lepidochitona*, *S. brandtii* is common near Asian coasts from north Japan [Saito, 1994] to Cross and Plover bays in the Chukchi Peninsula. This species is abundant near the Commander, Aleutian and Pribilova Islands. It has penetrated to the north of the Vancouver Island [Ferreira, 1982]. *S. brandtii* penetrated to the south-eastern Chukchi Sea [Sirenko, 2009]. As *S. brandtii* lives from the intertidal zone to a depth of 40 m, it is most abundant in the low horizon of the intertidal zone and in intertidal pools, where chitons attach to sides and bottoms of stones buried in muddy sand.

S. brandtii inhabits waters with temperatures from −1.8°C (in winter) to +18°C (in summer near south-western Sakhalin Island and Hokkaido Island) and to +16°C (in summer, near British Columbia), and with salinity 25–33‰. Data on number and biomass shown in Table 3 indicate that *S. brandtii* thrives in the intertidal zone of the north Pacific where it is one of the most abundant species of chitons.

Another characteristic feature of *S. brandtii* is related to its juvenile development. Females of this species brood eggs and embryos up to formation of 8 valves in juveniles in the pallial groove [Kussakin, 1960]. The secondary egg hull

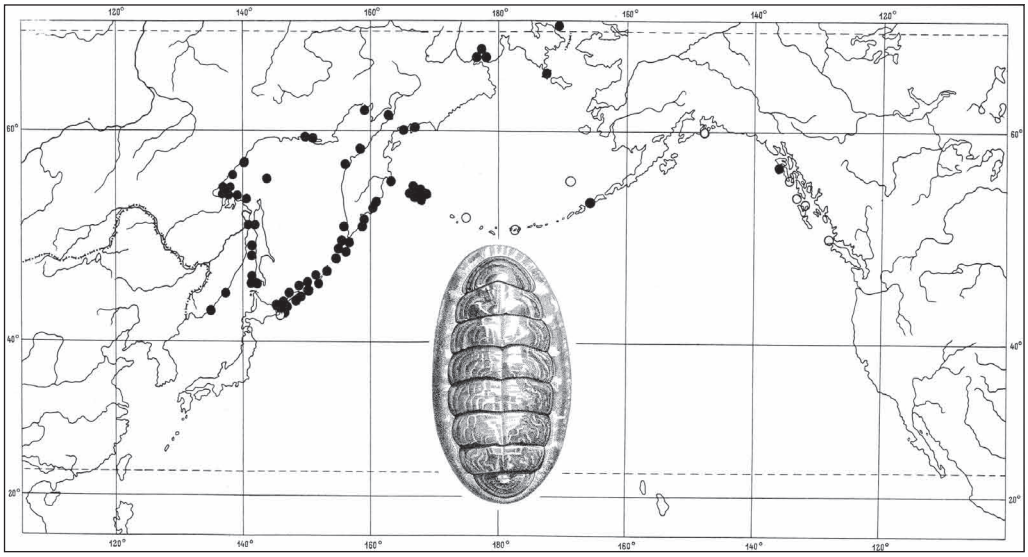

Fig. 3. Distribution of *Schizoplax brandtii*. Black circles – studied by authors, empty circles – literature data.

Table 3

Maximal and average abundance and biomass of *Schizoplax brandtii* in different regions of western Pacific

Region, depth (m)	Abundance (ind./m²)		Biomass (g/m²)	
	maximal	average	maximal	average
Plover Bay, Bering Sea (2–7)	220	20	30.0	2.5
Cross Bay, Bering Sea (intertidal)	200	–	29.0	–
Eastern Kamchatka (2–5)	–	15	–	1.5
Paramushir Isl. (intertidal)	300	12	32.5	0.5
Iona Isl. (Okhotsk Sea) (5)	55	10	22.7	3.0
Simushir Isl. (intertidal)	150	–	3.8	–
Iturup Isl. (intertidal)	200	–	11.0	–
South-western Sakhalin (intertidal – 0.5)	80	–	2.6	–

has thin long appendices curved in the distal part, which apparently assists egg retention in the pallial groove, where the eggs are separated by small spaces through which water flows. This feature of development is similar to *Lepidochitona*, in which about ten species show brooding embryos in the pallial groove. However, this adaptation has developed absolutely independently in several tens of genera of chitons belonging to different families and orders [Strack, 1987; our data].

Morphological similarities between *S. brandtii* and *L. dentiens* are shown in Figs. 4–6 and are compared in Table 4. Most features listed are either similar or slightly different. Moreover, the differences fit within the boundaries of feature variability in north Pacific species of *Lepidochitona* listed by Eernisse [1986]. There are two clear-cut differences between these species: bristles in perinotum and ligament connecting the two halves of the intermediate valves in *S. brandtii.* Admittedly, the first feature has low value because it is highly variable in *S. brandtii*: from hardly visible short single bristles to long bristles sometimes assembled together as a tuft. At the same time, several species of *Lepidochitona* have long sensitive spicules on the perinotum that are rested on short chitinous cups that we consider as homologous to sensitive bristles of *S. brandtii.* Thus, ligament remains the only distinct feature distinguishing *S. brandtii* from *L. dentiens*, all species of *Lepidochitona* and from all other chitons.

Discussion

We have presented very preliminary and modest molecular data on *S. brandtii*, species that was not studied with molecular approach until now. We already mentioned in introduction that this study does not intend to review of phylogenetic relationships and systematics of Chitonida as a whole, or Acantochitonina particular. We clearly understand that not only the DNA barcoding fragment is not sufficient for this purpose, but such revision could not be carried out on the base of one locus. Therefore, we omitted a number of usually common sophisticated statistical procedures and do not see any point in applying molecular clock analysis to this marker and calculate divergence distances as the taxa under analysis evidently evolve beyond the point at which CO1 synonymous substitutions have become saturated due to multiple hits. However, it is impossible to ignore the fact that anyway in all combinations and with any taxa of chitons and any outgroup chosen (we do not present here other variants with inclusion of almost all chitons genera and representatives of Bivalvia as outgroup), the only highly supported monophyletic group was always formed by genera *Lepidochitona*, *Nuttalina* and *Schizoplax*. Taking together with the high similarity that exists in the majority of morphological characters between genera *Schizoplax* and *Lepidochitona* with molecular data presented here, it is a solid basis for inclusion of the former genus into the family Tonicellidae as it is clear evidence that all named genera share common ancestry. The separation of the genus *Schizoplax* into monotypic family thus makes it paraphyletic related to Tonicellidae and so this justifies considering the family Schizoplacidae as a junior synonym of family Tonicellidae.

Our opinion coincides with conclusion of Eernisse [2009] about relationship of *Schizoplax*, *Nuttallina* and *Cyanoplax*.

Fossil *S. brandtii* is not found in neither Pleistocene nor Pliocene deposits, nor in earlier deposits. It is not possible to confuse *Schizoplax* with any other species of chitons because of its distinctive valves that are divided into two portions. The species probably appeared at the end of the Pleistocene or even in the Holocene,

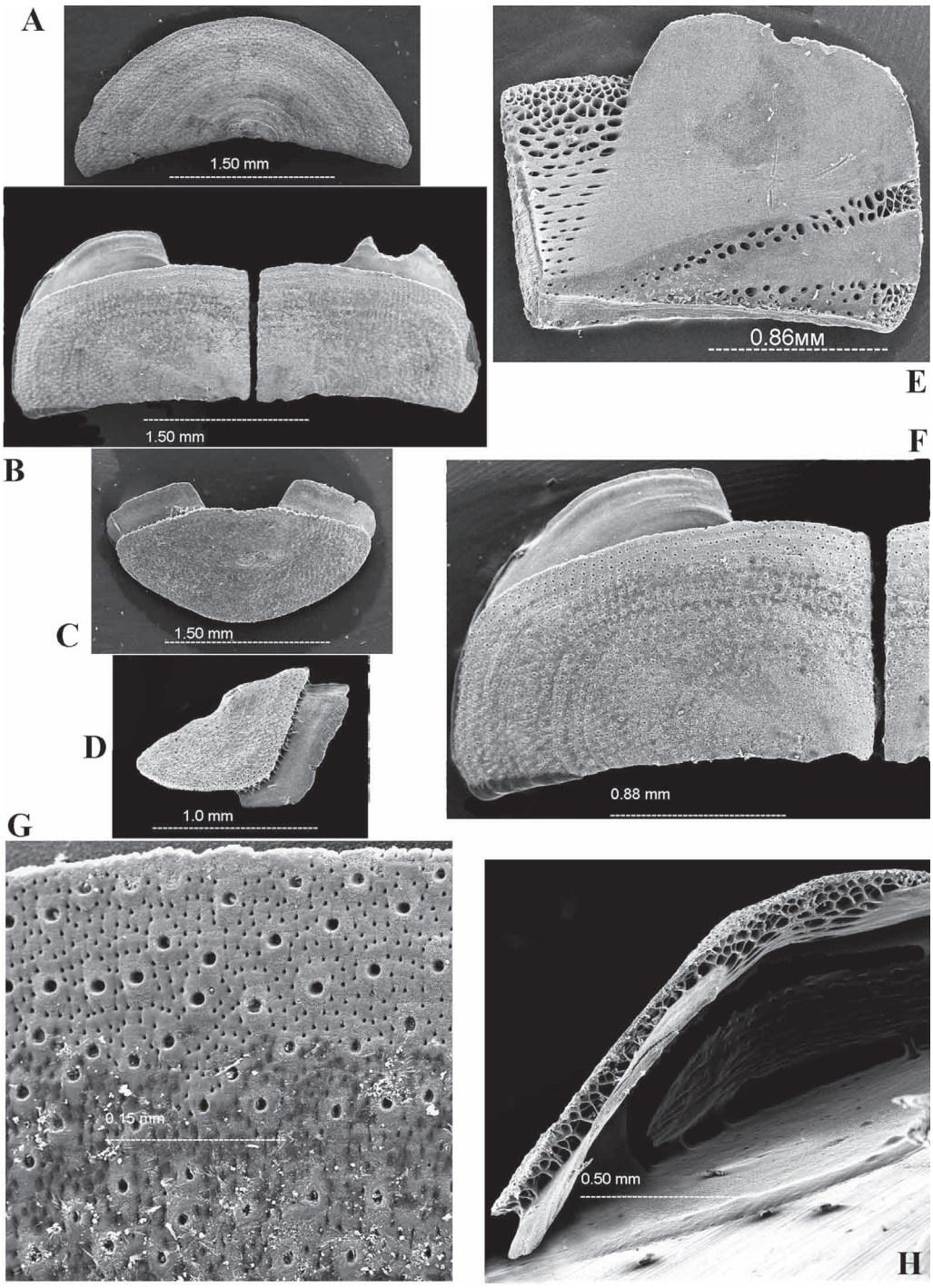

Fig. 4. *Schizoplax brandtii*, body length 8.5 mm, Unalaska Isl., Aleutian, depth 1 m. **A**, **B**, **C** – valves I, V and VIII, dorsal view; **D** – valve VIII lateral view; **E** – valve IV, ventral view; **F** – valve V, dorsal view; **G** – valve V, tegmentum surface; **H** – valve III, rostral view.

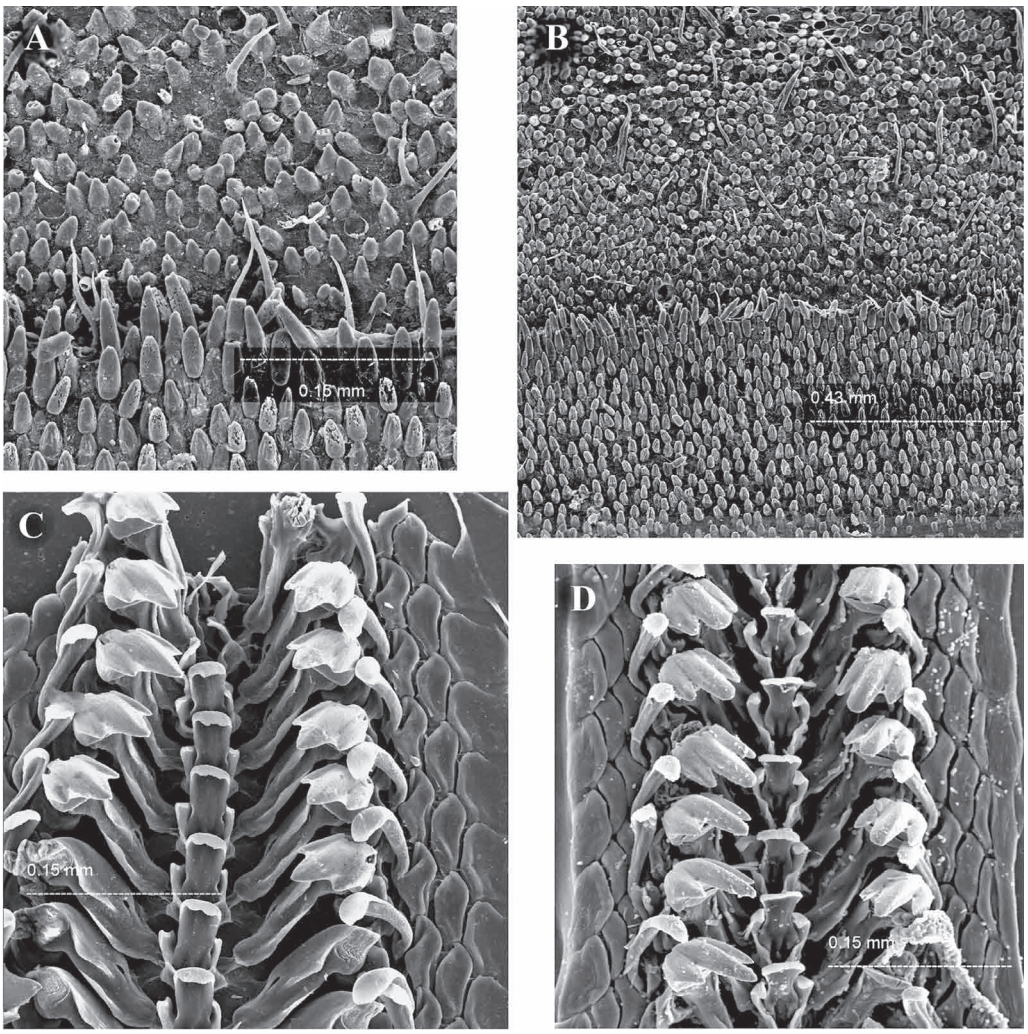

Fig. 5. *Schizoplax brandtii* (**A**, **B**, **C**) and *Lepidochitona dentiens* (**D**). **A**, **B** – dorsal, marginal and ventral spicules, **C**, **D** – radula.

several tens of thousands years ago and then quickly spread to occupy a large area in the north Pacific (see Fig. 3).

Apparently we are dealing with a case of «sudden speciation» according to Huxley [1958] or «genetic speciation» by Vorontsov [1960], who assumed that there are two ways of speciation in nature: 1, «common» gradual, speciation that begins with spatial isolation, changes in frequency of alleles and ends with reproductive isolation; and 2, «genetic» that begins with chromosomal rearrangement with formation of reproductive isolation and ends with divergence in frequency of alleles and phenotypic divergence. It is conceivable that the origin of *S. brandtii* was brought about by mutations, as considered by Goldschmidt [1940]. Mutations change the course of ontogenesis and as a result of these mutations, a «promising monster» is formed. It seems that we really

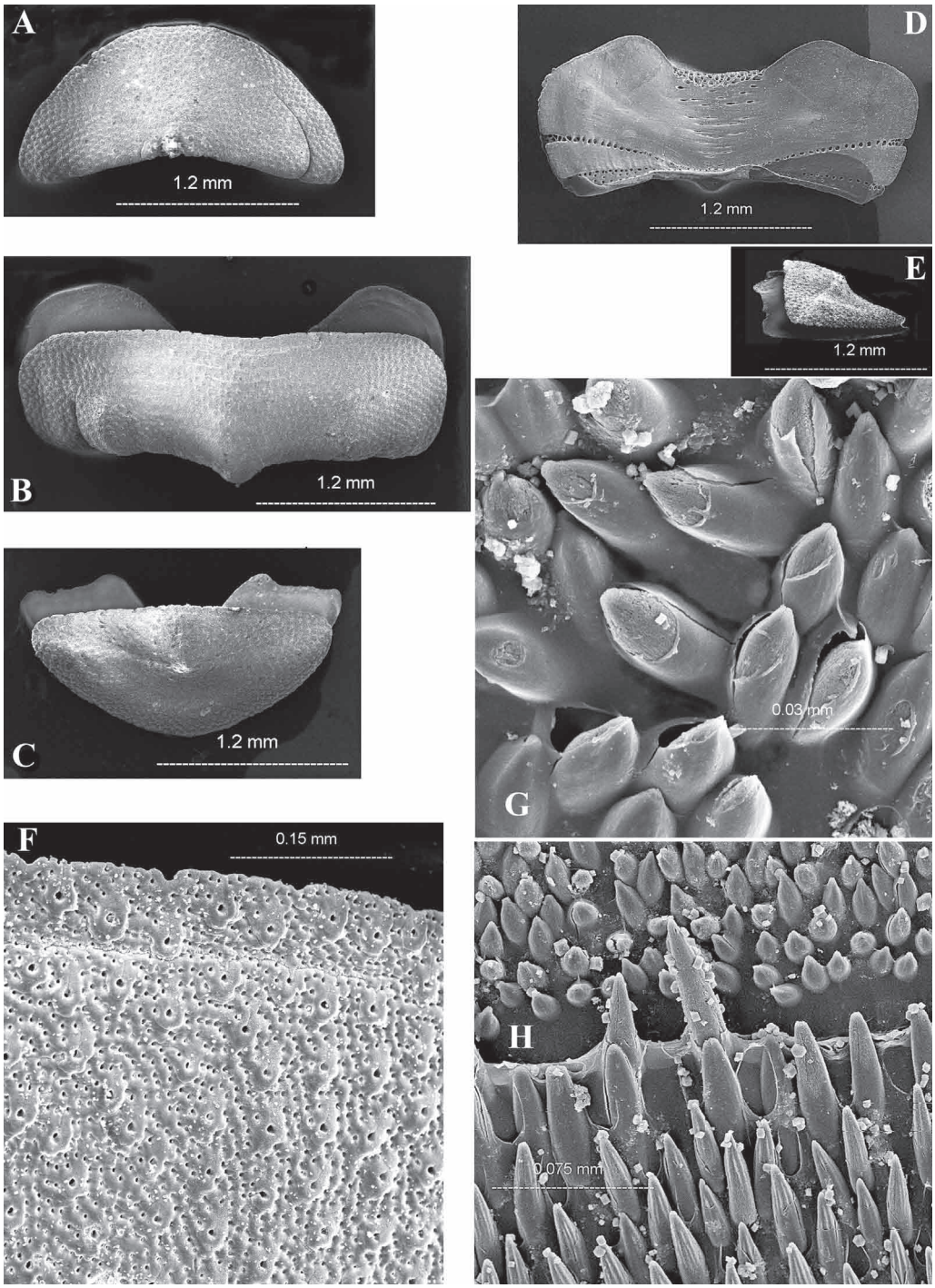

Fig. 6. *Lepidochitona dentiens*, body length 7.8 mm, Friday Harbor Laboratories, San Juan Isl., intertidal pool. **A**, **B**, **C** – valves I, V, VIII, dorsal view; **D** – valve IV, ventral view; **E** – valve VIII, lateral view; **F** – valve V, tegmentum surface; **G** – dorsal spicules; **H** – dorsal, marginal and ventral spicules.

Table 4

Comparison of morphological features in *Schizoplax brandtii* and *Lepidochitona dentiens*

Morphological features	*Schizoplax brandtii*	*Lepidochitona dentiens*
Ratio between width of head and tail valves	1.16–1.26	1.08–1.13
Ratio between width and length of intermediate valves	3.3	3.3
Ratio between length of antemucronal and postmucronal area of tail valve	1.0–1.2	1.08–1.2
Dorsal elevation	0.27–0	0.3
Ligament in intermediate valves	Yes	No
Distance between megalaesthetes	50–70 μm	50–70 μm
Ratio between width of apophyses and jugal simus	1.6–1.8	1.4–1.6
Slit formula	10–12/1/10–13	7–11/1/7–13
Size of pores in eaves	cc. 80 μm	cc. 50 μm
Number of transverse rows of mature teath	30	32
Number of denticles of cusp in major lateral tooth	Three	Three
Size of dorsal spicules of girdle	45	44
Bristles in girdle	Yes	No
Size of marginal spicules	56	120–124
Number of gills	18–26	23–25

have a fact of a relatively rapid origin of a new species that was placed in a separate genus and even in a separate family. *S. brandtii* as a result of a «explosive speciation» has gained advantages over its predecessors. The advantages allow it to occupy a wide range that was beyond the reach for its ancestors. Three advantages are presented below.

1. Owing to elastic ligament connecting the two halves of the intermediate valves, the shell of *S. brandtii* can flatten, which allows the species to a quicker, easier, and deeper push under stones lying on sand and in various crevices that the mollusk uses for shelter from predators. In the intertidal zone during the low tide where sea birds search for food (birds actively feed on chitons [Moore, 1975; Smith, 1977]), such an advantage can turn out to be the key factor for survival under conditions of sharp predatory pressure.

2. This species is extremely eurythermal and can tolerate both hard short-term increase of temperature (to 26°C in intertidal zone during low tide) and considerable cooling during winter period (to −2°C and below) [Kussakin, 1960]. No any other species of the genus *Lepidochitona* that we consider to be close to *Schizoplax* possess such advantages.

3. The optimal water temperature for spawning of *S. brandtii* defined as winter minimal temperature in the south of area and summer maximal temperature in the north of area [Golikov, Scarlato, 1973] are rather low (2–7°C for the Asian coast and 8–9°C for the American coast). The low temperature tolerance allows *S. brandtii* to spread very widely in the north Pacific and north of Chukchi Peninsula, noticeably north of areas of *Lepidochitona* species.

It is noteworthy that within the whole vast distributional range of the genus *Lepidochitona*, *S. brandtii* originated only in the north eastern Pacific and not in the Atlantic Ocean. This may be due to the gradual latitudinal changes of water temperature in the north eastern Pacific. In that area, summer surface waters temperature from Alaska to California varies from 12 to 17°C, and winter temperature from 7 to 13°C. Compared to many other areas of the Northern Hemisphere both in the Pacific and in Atlantic oceans, the difference between the summer and winter water temperature is lowest in the northeastern Pacific. Seemingly, with gradual change of water temperature the species best adapt to low temperature either with conservation of species status or with origin of new species. The latter took place with the origin of *S. brandtii.*

The separation of valves into two halves can be considered a kind of deformity often observed in nature. Finding chitons with 7, 6, even 5 or more rarely with 9 valves or with incomplete valves instead of common 8 valves are a matter of common knowledge [Dell' Angelo, Tursi, 1990; authors data]. Individuals with underdeveloped valves occur as well. Most often these anomalies occurred during larval development with disturbances of conditions normal for ontogenesis. Notable temperature changes that are very common in the intertidal zone during low tide could have been responsible for such disturbance. Cases of mass appearance of chiton deformities in the form either of fragmentary composition of valves, or incomplete development of valves or of the total absence of several valves during cultivation [Sirenko, Kashenko, 1990] are known. Naturally, such monsters with incomplete valves have less chance to survive than normally developed individuals, and most perish, although some can live up to adult stages and produce normal generations without deformity. Such examples show the possibility of chiton survival with anomalous shell.

Brooding of juveniles in the pallial groove allow chitons to produce offspring, which either settle near maternal population or are carried away on floating algae by currents into other regions where young chitons settle after they find suitable substrate. Main food of *S. brandtii* is macroalgae and sea grass detritus that abundantly accumulates in the surf zone between stones. The upper sublittoral zone at depths 5–20 m in the north Pacific was occupied by the second active consumer of plant detritus, the giant chiton *Cryptochiton stelleri* Middendorff, 1847 having originated in the Pliocene [Berry, 1922]. Howerer a similar niche in the intertidal zone was relatively free and *S. brandtii* quickly adapted to new conditions and spread widely along to whole coastal zone of the north Pacific in the Boreal biogeographical region. *S. brandtii* benefitted from surface water currents and spread at first with the Alaska current to the eastern Aleutian Islands and penetrated in the Bering Sea, then later with Kamtchatka and Kurile currents to be distributed along the Asian coast and northward to Hokkaido Island.

Conclusion

In conclusion, we propose a possible scenario of the origin of *S. brandtii*. This could have happened during the last maximum of the Würm–Valdai–Wisconsin Glaciation 18–20 thousand years ago, when a large glacier was situated in the Northern Hemisphere in northern Europe and North America and the biogeographical borders shifted towards the equator. At that time, mass extinction of warm-water species began in the zone of change of temperature factor of the environment. The extinction freed ecological niches and opened new adaptive zones, which was conducive to acceleration of evolution rate. A population of *L. dentiens* inhabiting the intertidal zone experienced extreme temperature conditions, which could have provoked an outburst of genetical alterations and a relatively rapid origin of new species with dimidiate valves. Along with the dimidiate valves the new species acquired much greater tolerance to low temperatures than in the ancestor species, which allowed it to penetrate far to the north Pacific, where it successfully assimilated an ecological niche in the intertidal communities.

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