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The ancient origin and persistence of chitons (Mollusca, Polyplacophora) that live and feed on deep submerged land plant matter (xylophages)

Boris Sirenko

B. Sirenko, Zoological Institute, Russian Academy of Sciences,199034 St. Petersburg, Russia.

ABSTRACT There are 23 species of chitons that live and feed on sunken land plant remains. They belong to three genera *Ferreiraella*, *Leptochiton*, and *Nierstraszella*. In the Carboniferous chitons changed their common food on a cellulose several times independently. Most of the species that live on sunken land plants are distributed along the tropical west and east coasts of the Pacific Ocean and in the Caribbean Sea, which was one of the portions of Pantalassa in the past geological ages. All these species of chitons belong to families that have mostly deep water members with generally plesiomorphic morphology. One can assume that the deep waters off southern Japan, Philippines, Indonesia, New Caledonia, Vanuatu, New Zealand from the western part of Pacific, and off Baja California and the Panama Basin from the eastern Pacific, as well as the Caribbean Sea are all regions where species with primitive character states have accumulated and persisted over geological time. In the future, one would expect a number of other "living fossil" species to be found in these deep water areas of Pantalassa remaining to the present time.

RIASSUNTO Sono note 23 specie di poliplacofori che vivono su legni sommersi, appartenenti ai tre generi *Ferreiraella* (*F.caribbensis, F.plana, F.scrippsiana, F.bartletti, F.taki, F.xylophaga xylophaga e F.xylophaga karenae), Leptochiton (L.kurnilatus, L.benthedi, L.habei, L.vietnamensis, L.saitoi, L.torishimensis, L.juvenis, L.foresti, L.boucheti, L.vitjazi, L.vanbellei, L.thandari, L.deforgesi, L.cancelloides* e *L.binghami*) e *Nierstraszella* (*N.lineata*). Queste specie xilofaghe sono state raccolte su legni rinvenuti a profondità comprese tra 130 e 7657 metri. Nel Carbonifero i chitoni hanno cambiato diverse volte indipendentemente la loro modalità di alimentazione, utilizzando la cellulosa. Molte specie che vivono su residui di piante terrestri sommerse sono distribuite lungo le coste tropicali dell'Oceano Pacifico occidentale ed orientale e dei Carabi, che era una delle porzioni della Pantalassa nei periodi geologici passati. Tutte queste specie di chitoni appartengono a famiglie che comprendono prevalentemente specie di acque profonde con una morfologia generalmente plesiomorfica. Si puo' ipotizzare che le acque profonde del Giappone meridionale, Filippine, Indonesia, Nuova Caledonia, Vanuatu, Nuova Zelanda dalla parte del Pacifico occidentale, Baja California e Bacino di Panama del Pacifico orientale e Mar dei Carabi siano tutte regioni dove specie con morfologia relativamente conservativa (caratteri primitivi) si sono mantenute durante il tempo geologico. In futuro, è lecito aspettarsi il ritrovamento di altre specie con simili caratteristiche di "relitti viventi" nelle acque profonde di queste regioni, che rappresentano le aree di Pantalassa ancora rimaste ai nostri giorni.

KEY WORDS: chitons, xylophages, feeding, origin.

INTRODUCTION

Most members of the molluscan class, Polyplacophora Gray, 1821, live on hard substrates: mainly stones, rocks, pebbles, or shells. However, some chitons live on unusual substrates, namely sunken wood and leaves of terrestrial origin that have come to lie on the muddy sea floor. More than 200 other species of different animals inhabit plant remains mainly in the deep sea (Wolff, 1979). About 50 species have been found to primarily make use of plant remains as a substrate, whereas a smaller number are known to both live and feed on plant remains. Chitons are one of the numerous groups of invertebrates living on sunken wood or leaves, but their diet has not been previously investigated. It is very interesting to study the species composition of this assemblage of chitons in order to infer how and where they adapted to live on the remains of terrestrial plants.

MATERIALS AND METHODS

I researched the published literature for references to chitons living on remains of sunken terrestrial plants. Moreover, I studied stomach and gut contents of 18 xylophagous species of chitons (Table 1). The chitons were opened ventrally and each digestive tract was removed and divided into stomach and intestine. Then the contents of the stomach and gut were spread out on a slide or petri dish for microscopic examination.

Most of the materials for this article were preserved chitons that were part of the collection of the Zoological Institute of Russian Academy of Sciences, St. Petersburg, or sent to Zoological Institute from Museum National d'Histoire Naturelle, Paris. Others were studied in United States National Museum of Natural History, Smithsonian Institution, Washington D.C. Species of chitons used for this study are from different parts of the World Ocean, mainly from the Caribbean Sea, Gulf of Mexico, Panama Basin, New Caledonia, off South Japan, South Vietnam, Vanuatu, Fiji, New Zealand, The Solomon Sea, Reunion Id., and Glorieuses Id.

RESULTS

Species composition.

At the present time, 23 species or subspecies of chitons are xylophages: they are known to live on sunken plants (Table 1). The group includes members of three genera: *Ferreiraella* Sirenko, 1988, *Nierstraszella* Sirenko, 1992 and *Leptochiton* Gray, 1847. These genera belong to three different families: Fer-

Table1. Species of chitons which live and feed on sunken wood and leaves
Tab.1. Specie di poliplacofori che vivono su legni sommersi

species	distribution and depth (m)	substrate	sources
Ferreiraella caribbensis Sirenko, 1988	Cayman Trench, Caribbean Sea, 6740-6780	wood	Sirenko, 1988, 1997
F. plana (Nierstrasz, 1905)	off Celebes Is. and New Caledonia. 650-2053	wood	Sirenko, 1997, 2001
F. scrippsiana (Ferreira, 1980)	off Baja California and Panama Basin. 2891-4000	wood	Sirenko, 1997
F. bartletti (Ferreira, 1986)	Venezuela Basin, Caribbean Sea. 3516-5046	wood	Ferreira, 1986
F. taki (Wu et Okutani, 1984)	off Mikura Is., Japan and South Vietnam. 700-1200	wood	Wu, Okutani, 1984; Sirenko, 1988, 1997, Saito, 2001
F. xylophaga xylophaga (Gowlett-Holmes et Jones, 1992)	off New Zealand. 1045-1180	wood 1997	Gowlett-Holmes, Jones, 1992; Sirenko
F. x. karenae Sirenko 2001	off Vanuatu. 740-798	wood	Sirenko, 1997, 2001
Nierstraszella lineata (Nierstrasz, 1905)	off South Japan, South Vietnam, Philippines, Indonesia, Andaman Ids., Vanuatu, Fiji, 177-1660	wood and leaves	Sirenko, 1992, 2001 Saito, 1997, 2001
Leptochiton kurnilatus Kaas, 1985	off Reunion Is, Indian Ocean. 270-1850	wood	Sirenko, 1998
L. benthedi (Leloup, 1981)	off Glorieuses Is., Mozambique Channel. 3700-3716	wood	Leloup, 1981; Sirenko, 1998
L. habei Saito, 1997	Suruga Bay, Japan, Vanuatu. 200-350	wood	Saito, 1997, 2001, Sirenko, 2001
L. vietnamensis Sirenko, 1988 (Syn. *L. longispinus* Saito, 2001)	Tosa Bay, Japan, off South Vietnam, Molucca Sea, New Caledonia, Vanuatu. 316-768	wood	Sirenko, 1998, Sirenko, 2001, Saito, 2001
L. saitoi Sirenko, 2001	off New Caledonia. 210-580	leaves	Sirenko, 2001
L. torishimensis (Wu et Okutani, 1984)	off Torishima Is. and Suruga Bay, Japan. 200-350	wood	Saito, 1997, 2001
L. juvenis (Leloup, 1981)	off Philippines and Vanuatu. 459-488	wood	—— / ——
L. foresti Leloup, 1981	Philippines. 150-484	wood	—— / ——
L. boucheti Sirenko, 2001	off Vanuatu. 522-527	leaves	—— / ——
L. vitjazi (Sirenko, 1977)	Bougenville trough, Solomon Sea. 6920-7657	wood	Sirenko, 1977
L. vanbellei Sirenko, 2001	off New Caledonia and Vanuatu. 748-1620	wood	—— / ——
L. thandari Sirenko, 2001	off Vanuatu. 765-780	wood	—— / ——
L. deforgesi Sirenko, 2001	off Vanuatu. 522-527	leaves	—— / ——
L. cancelloides Kaas, 1982	Philippines. 130-199	wood	P.Bouchet com.pers.
L. binghami Boone, 1928	Caribbean Sea, Gulf of Mexico. 300-912	wood	Author's data

reiraellidae Dell'Angelo et Palazzi, 1991, Nierstraszellidae Sirenko, 1992, and Leptochitonidae Dall, 1889, respectively.

Distribution. Known xylophagous chitons have been collected from mainly deep water from 130 to 7657 m. All species of genus *Ferreiraella* live in deep water (650-6780 m). Species of genus *Leptochiton* are very different. Most of them live in relatively shallow water or on the shelf but those that live on sunken wood or leaves inhabit depths from 130 to 7657 m. The only species of genus *Nierstraszella*, *N. lineata* (Nierstrasz, 1906), lives at depths from 177 to 1660 m.

Xylophagous chitons are relatively cold-water animals, although they live in the tropics. Most of them inhabit waters with temperature less than 100 C. Species of the genus *Ferreiraella* live in deepwater at temperatures 1.7-6.00 C (Sirenko, 1988).

Xylophagous chitons have a very interesting geographical distribution. *Ferreiraella* has a disjunctive distribution range consisting of three portions: the west Pacific from southern Japan to New Zealand, the eastern Pacific from Baja California to Panama Basin, and the Caribbean Sea (Fig. 1). Xylophages of the genus *Leptochiton* are also distributed in three different areas: the western Pacific, the Caribbean Sea to the Gulf of Mexico, and the western part of the Indian Ocean (Fig. 2). The only species of genus *Nierstraszella* has a wide distribution in the western Pacific from southern Japan to Vanuatu and Fiji (Fig 2).

Morphological features. Ten species (all six members of the genus, *Ferreiraella*, as well as *Leptochiton vietnamensis*, *L. boucheti* and *Nierstraszella lineata*) out of the 23 xylophagous chitons have

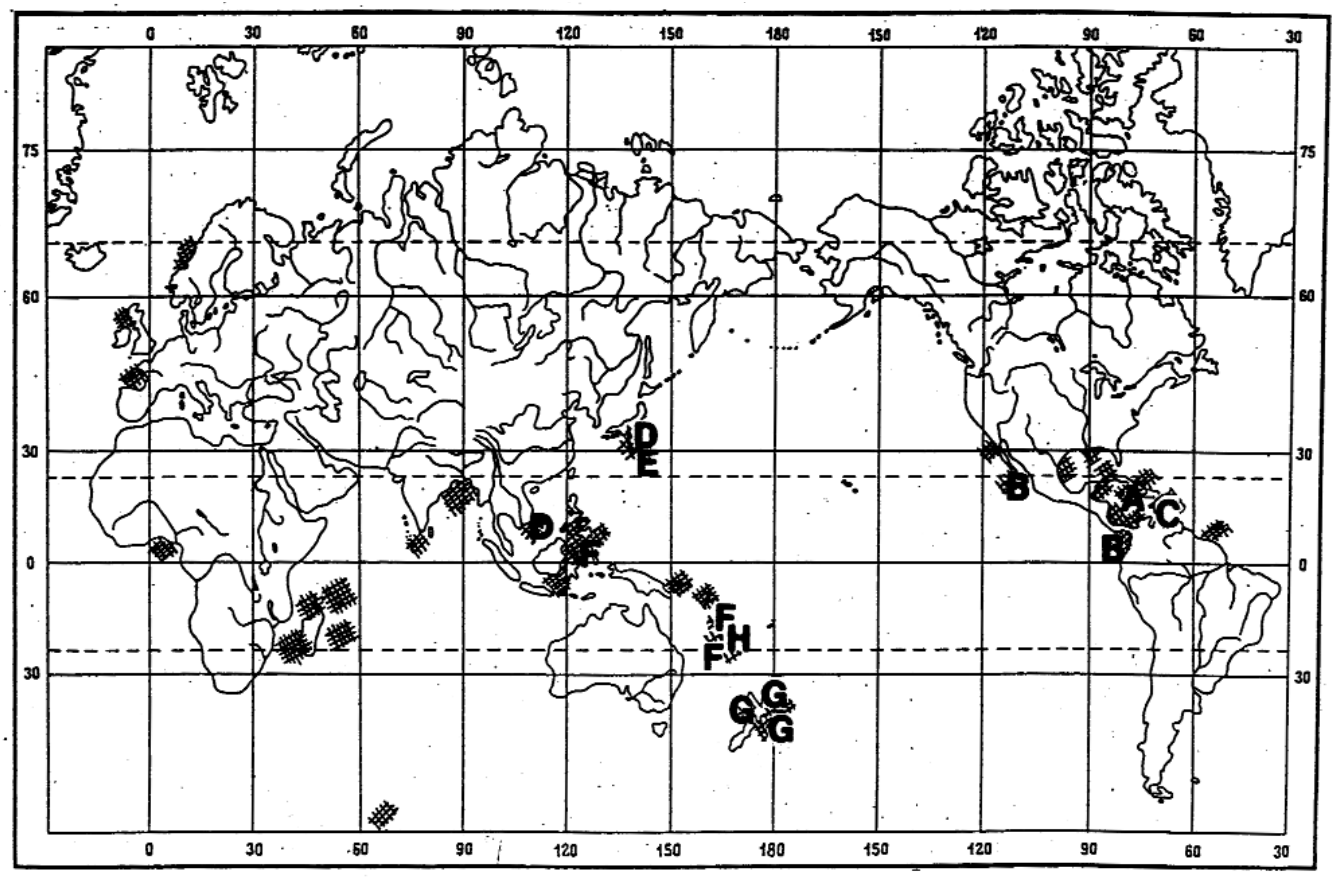

Fig. 1. Areas of accumulation of sunken wood and leaves (net) (after Wolff, 1979 with author's additions) and the distribution of species of *Ferreiraella*: *F. caribbensis* (A); *F. scrippsiana* (B); *F. bartletti* (C); *F. taki* (D); *F. soyomaruae* (E); *F. plana* (F); *F. xylophaga xylophaga* (G); *F. xylophaga karenae* (H).

Fig. 1. Aree di accumulo di legni e foglie sommersi (graticole) (da Wolff, 1979 con aggiunte dell'Autore) e distribuzione delle specie di *Ferreiraella*: *F. caribbensis* (A); *F. scrippsiana* (B); *F. bartletti* (C); *F. taki* (D); *F. soyomaruae* (E); *F. plana* (F); *F. xylophaga xylophaga* (G); *F. xylophaga karenae* (H).

a very interesting feature: erect subsidiary caps on the micraesthetes. These erect caps are absent in other chitons. The function of these subsidiary caps is still unknown. Species of genus *Ferreiraella* are diagnosed by several atypical chiton features: the absence of armature on ventral side of girdle; the presence of groups of erect subsidiary caps of aesthetes which protrude from tegmentum; central tooth of radula with a cross-shaped base; intermediate tooth with shaped like tulip buds processes; the spatulate uncine teeth with a rake-like blade. More typical stable features include each major lateral tooth with a tricuspid head and 18-21 ctenidia on each side of the foot.

Members of *Leptochiton* have less in common than for the case of *Ferreiraella*. Some of them have erect subsidiary caps but most of them have short ones. The major lateral tooth has a uni-, bi-, or tricuspid head, and the number of gills varies considerably in different species, from 4 to 14 ctenidia on each side.

Nierstraszella lineata has a unique arrangement of the elements of tegmental sculpture in which one megalaesthete is surrounded with more than 40 micraesthetes, with erect subsidiary caps present. The major lateral tooth of the radula has a bicuspid head, and there are 15-18 ctenidia on each side.

Feeding. The analysis of contents of the digestive tracts of xylophagous chitons showed that they are usually full of the particles of sunken wood or leaves. Moreover, their stomachs have many small white particles (size about 10 µm) besides particles of wood whereas their posterior intestines contain the particles of wood only. These white particles are probably cellulose-fermenting bacteria or fungi.

I studied the relationship between length of the digestive tract and content of food in chitons from different trophic groups (Fig. 3). As far as I used ratio between length of the body of chiton and length of the digestive tract of the same chiton, I had a relative figure that did not depend on size of a chiton. The longest digestive tract was found in herbivorous chitons, group of *Cryptochiton stelleri* (Middendorff, 1847) (ratio between length of body and length of digestive tract is 4.3-6.7). Eurifagous, detrivorous-herbivorous and detrivorous have a ratio from 2.6-3.1 to 2.2. Epizoophagous and carnivorous chitons have a ratio from 1.3 to 1.2-1.5. It is interesting that xylophagous chitons have a ratio of 2.1, which is very close to the ratio of chitons that consume detritus. Perhaps this closeness confirms their similarity in feeding because one of the general components of detritus is bacteria.

Seven species and subspecies of genus *Ferreiraella* were found on sunken wood. Only *F. soyomaruae* (Wu et Okutani, 1984) is the exception because this species was found on pumice. Species of *Ferreiraella* were sometimes found in abundance in a trawl catch: *F. caribbensis* at the type locality (34 specimens), *F. xylophaga*

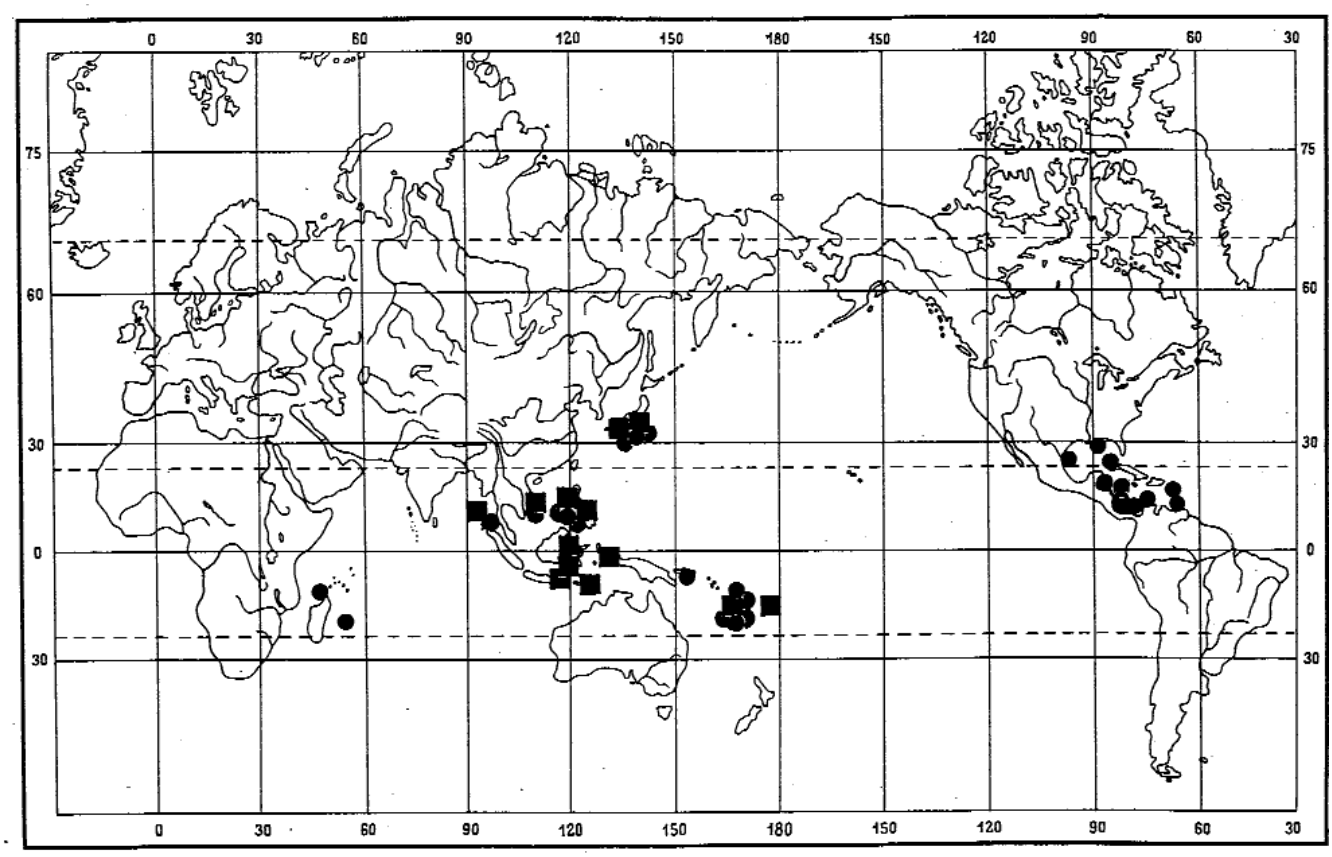

Fig. 2. Distribution of species of genera *Leptochiton* (black circle) and *Nierstraszella* (black square).

Fig. 2. Distribuzione delle specie appartenenti ai generi *Leptochiton* (cerchio nero) e *Nierstraszella* (quadrato nero).

xylophaga at the type locality (34 specimens), *F. xylophaga karenae* at the type locality (82 specimens).
Species of *Leptochiton* and *Nierstraszella* have been found on both sunken wood and leaves.

DISCUSSION

Origin of xylophagous chitons.

There are groups of species that differ substantially from each other among those chitons that are xylophagous. The first group consists of species of genus *Ferreiraella*. Members of this group have similar morphological characteristics, which indicates a likely close relationship exists among all species of this genus.
One can divide *Leptochiton* species-xylophages into several groups, each with similar features that may be of common origin:

1. Group of *Leptochiton vitjazi*
L. vitjazi
L. vanbellei
L. thandari
L. deforgesi

2. Group of *Leptochiton saitoi*
L. saitoi
L. torishimensis
L. juvenis
L. foresti

3. Group of *Leptochiton kurnilatus*
L. kurnilatus
L. benthedi.

Other *Leptochiton* species *(L. boucheti, L. habei, L. vietnamensis, L. binghami* and *L. cancelloides*) have some similarities with species from these groups but they have more differences from those species as well.
Nierstraszella lineata is a species with particular characteristics.
I speculate that these groups of chitons chose sunken land plant remains as a substrate and food independently. In other words, *Ferreiraella spp*., *Nierstraszella lineata*, and several groups of genus *Leptochiton* probably originated independently.
Perhaps, the first species that lived and fed on sunken land plant remains was the species of Pennsylvanian genus *Glaphurochiton* Raymond, 1910. The species of this genus were found in Pennsylvanian localities in the Appalachian basin, eastern interior basin and mid-continent region. Five species of genus *Glaphurochiton* are known: *G. carbonarius* (Stevens, 1858), *G. concinnus* (Richardson, 1956), *G. elimatus* (Hoare et Mapes, 1986), *G. subcirculus* (Hoare et Mapes, 1986), and *G. riddlei* (Frederickson, 1962). The first two species, *G. carbonarius*, and *G. concinnus* were the most abundant. The species of this genus were found in black to dark gray shales (Hoare, Mapes, 1992). Black and dark shales

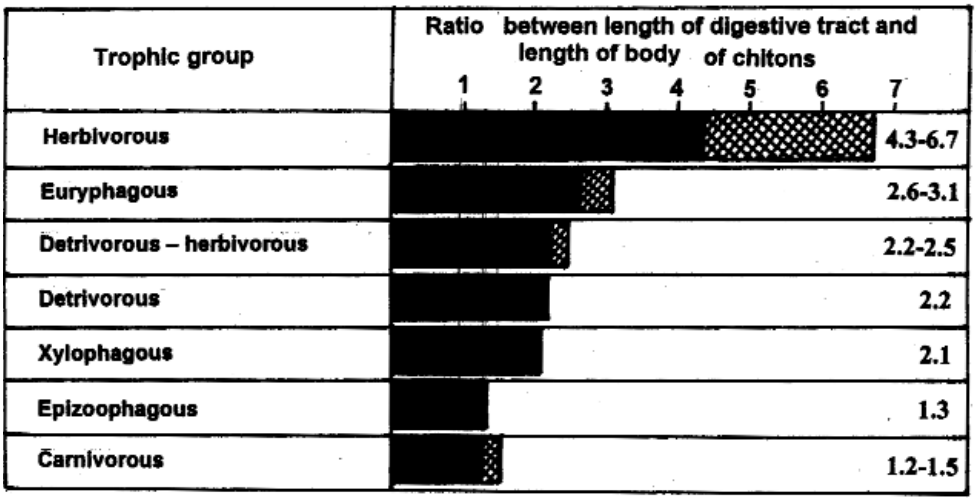

Fig. 3. Relationship between length of digestive tract and length of body in chitons from different trophic groups.

Fig. 3. Relazione tra la lunghezza del tratto digestivo e la lunghezza del corpo in chitoni di differenti gruppi trofici.

originated from muddy grounds that were rich in organic remains. It is likely that the organic remains in the Pennsylvanian were sunken land plant remains. In that time about 300 million years ago there were mostly pteridophytes (ferns) on the land. Recent chitons live on sunken wood, primarily phanerophytes. But bacteria or fungi, which are likely the main real food of chiton-xylophages can break down the cellulose of both phanerophytes and pteridophytes. Therefore we can suppose that the first xylophagous chitons were species of the genus *Glaphurochiton*. The extant genus, *Ferreiraella*, is so similar to the carboniferous *Glaphurochiton* that it seems plausible to me that it is a direct descendant of this same lineage. Species of *Ferreiraella* and *Glaphurochiton* have very similar form of valves of their shells, shape of apophyses and sculpture of tegmentum as well. *Ferreiraella caribbensis* is particularly similar to species of *Glaphurochiton*, furthermore, it lives in the Caribbean Sea, which is not so far from the former distribution of *Glaphurochiton*. Species of *Ferreiraella* have likely continued to inhabit places where sunken land plant remains have accumulated, given their specialized diet of cellulose. The range of Ferreiraella could have been separated into two parts by the formation of continent Pangea in the Permian. The disintegration of Pangea, which began in the Jurassic, split Pangea into separate continents. Species of *Ferreiraella* living near the continents moved with them. Further moving of continents divided the range of *Ferreiraella* into three parts, leading eventually to its present distribution near the continents that were ones united coasts of Pangea (Sirenko, 1997).

Species of genus *Leptochiton* probably originated later than *Ferreiraella* because they have the armature on the dorsal side of their girdle as in all other extant chitons except *Ferreiraella*. The absence of xylophagous members of Leptochiton in the Atlantic Ocean proper (excluding the Carribean Sea and the Gulf of Mexico, which were old gulfs of Pantalassa) implies that these originated after the Jurassic, after the Atlantic Ocean was essentially isolated. It is difficult to say when each *Leptochiton* subgroup originated. However taking into consideration their primary distribution in the western Pacific, with 12 out of 15 xylophagous members of *Leptochiton* inhabiting the western Pacific, one can suppose that the first xylophagous species of *Leptochiton* originated in that region. Two groups of *L. vitjazi* and *L. saitoi* that are distributed in the western Pacific probably originated independently because they have many morphological differences. Moreover the *L. vitjazi* species group lives deeper than the *L. saitoi* species group (Table 1). The *L. kurnilatus* species group in the western Indian Ocean (*L. kurnilatus* and *L. benthedi*), one species from the Caribbean Sea and the Gulf of Mexico (*L. binghami*), and the four remaining species *L. boucheti*, *L. habei*, *L. vietnamensis*, and *L. cancelloides*, each could have had independent origins as well.

Finally, *Nierstraszella lineata* is a curious chiton with quite derived characteristics, especially its broad sutural laminae and very complicated elements of tegmental structure (Sirenko, 1992). It is likely that it originated near the end of the Mesosoic in the western Pacific, after the range of the other xylophagous chitons was already distinct.

Distribution of chitons-xylophages.

Eight species (*Ferreiraella plana, F. scrippsiana, F. taki, Nierstraszella lineata, Leptochiton habei, L vietnamensis, L. juvenis* and *L. binghami*) have comparatively broad distribution whereas the others are known from few localities, or the type locality only. Usually the range size depends on the longevity of a species and its dispersal capabilities. The oldest species have had more time to disperse. However, shallow- water younger species can have a broader range than the old species either because they more successfully disperse during their planktonic larval stage or because they have rafted as adults on floating algae. Unfortunately, we have very little information about the dispersal ability of deepwater chitons. Perhaps all species of genus *Ferreiraella* have demersal larvae. I previously estimated that *F. caribbensis* has large (about 650 µm) and few (about 10) eggs in its gonad (Sirenko, 1988), which is more consistent with demersal rather than planktonic development. The limited range of most species that live and feed on plant remains, and the presence of several different species in one sample, could indicate that they have limited dispersal abilities.

Most species living on sunken land plants are distributed along the tropical western and eastern coasts of the Pacific Ocean and extending into the Caribbean Sea, which was likewise once part of the ancient Pantalassian coast. All these species of chitons belong to the most basal lineages of chitons and their features are predominantly plesiomorphic. One can assume that the deep waters off the southern Japan, Philippines, Indonesia, New Caledonia, Vanuatu, and New Zealand from the western Pacific, off Baja California, and the Panama Basin from the eastern Pacific, and the adjacent Caribbean Sea are all the regions where species with

relatively conservative morphology have persisted. In the future, it is likely that additional living relicts will be found in the deep waters of these areas, which are the last remaining areas of Pantalassa still persisting to the present day, because the spreading of Plates have buried all the other old abyssal bottoms under continental plates. These deepwater portions of Pantalassa were exposed with less abiotic and biotic exchanges than in the other parts of the World Ocean.

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