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Lithiotid Bivalves in Slovenia and Their Mode of Life

Litiotidne školjke v Sloveniji in njihov način življenja

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Ključne besede: spodnjejurske školjke, pliensbachij, *Lithiotis, Cochlearites, Lithioperna* (syn. *Lithiopedalion),* morfološke adaptacije, blatni substrat, Dinarska karbonatna platforma, Slovenija

Abstract

Lithiotid bivalves are a characteristic faunal element of the shallow marine facies of Lower Jurassic beds in southern Slovenia. The horizon containing Middle Liassic bivalves, which is up to 75 m thick, is called the "lithiotid horizon" and is attributed to the Pliensbachian or Domerian.

In Slovenia the name lithiotid bivalves represents three morphologically similar genera or species of sessile monomyarian dysodont bivalves: *Lithiotis problematica, Cochlearites loppianus* and *Lithioperna scutata,* which are systematically examined in this paper. The term lithiotid bivalves does not have any taxonomic significance, since they are now classified in different families. The order is Pterioida.

Lithiotid bivalves lived in an upright position on soft lagoonal bottoms in a tight aggregate of individuals crowded together which mutually supported one another and simultaneously competed for living space and light. The sedimentation of calcareous mud was fairly rapid, thus throughout their lives they grew constantly in a subvertical direction so that the small soft body space at the ventral end remained above the level of the surrounding substratum. Lithiotid bivalves had peculiar, variable shells adapted to the specific environment. They are very large, flat and distinctly dorso-ventrally elongated. Their inner surface is tripartite; in the middle is the central area, and at the sides there are feather-like areas. The mechanism of opening and closing their valves has not yet been fully explained.

Kratka vsebina

Litiotidne školjke so značilen favnistični element plitvomorskega razvoja spodnjejurskih plasti južne Slovenije. Do 75 metrov debeli horizont s srednjeliasnimi

školjkami imenujemo "litiotidni horizont" in ga uvrščamo v pliensbachij oz. domerij.

Pod imenom litiotidne školjke v Sloveniji združujemo tri morfološko podobne rodove oziroma vrste sesilnih, monomiarnih, disodontnih školjk: *Lithiotis problematica, Cochlearites loppianus* in *Lithioperna scutata,* ki so sistematično obdelane v tem prispevku. Izraz litiotidne školjke nima taksonomskega pomena, saj jih danes uvrščamo v različne družine. Spadajo v red Pterioida.

Litiotidne školjke so v pokončnem položaju živele na mehkem lagunskem dnu, v tesni združbi skupaj nagnetenih osebkov, ki so se med seboj podpirali in hkrati tekmovali za življenjski prostor. Sedimentacija karbonatnega blata je bila precej hitra, zato so litiotidne školjke vse življenje enakomerno rastle v navpični smeri, tako da je njihov bivalni del na ventralnem koncu ostajal nad nivojem obdajajočega substrata. Litiotidne školjke so imele nenavadne, variabilne, specifičnemu okolju prilagojene lupine. So zelo velike, sploščene in izrazito razpotegnjene v višino. Njihova notranja površina je tridelna; v sredini je glavno oz. osrednje polje, ob straneh pa peresasti polji. Mehanizem odpiranja in zapiranja njihovih lupin še danes ni docela pojasnjen.

Introduction

In the Middle Liassic lithiotid bivalves inhabited the relatively calm muddy bottom of the restricted shelf on the Dinaric Carbonate Platform. The horizon with the bivalves barely wedges out in the Lower Jurassic beds of southern Slovenia; its thickness at some localities reaches 75 m. It is named the "lithiotid horizon" after these characteristic bivalves. B u s e r (1965, 44-46) attributed it to the Pliensbachian, or its upper section: to the Domerian. The most important localities of Lower Jurassic bivalves in Slovenia, which extend for over one hundred kilometres in length and several tens of kilometres in width, were presented in the 37th issue of Geologija. The palaeoecological conditions that enabled the characteristic bivalve fauna to flourish for a relatively short period have also been examined (B u s e r & D e b e l j a k, 1996).

This paper gives a systematic description of lithiotid bivalves and their mode of life. The term lithiotid bivalves is still used in Slovenia although it no longer has any taxonomic meaning. It comprises three frequent and characteristic, and at first sight similar genera: *Lithioperna* (syn. *Lithiopedalion), Cochlearites* and *Lithiotis.* All three genera were widespread in the shallow marine regions of the western and southern margins of the Tethys and even the Eastern Pacific (genus *Lithiotis).* Lithiotid bivalves therefore have great palaeogeographical, biostratigraphical and palaeoecological significance. They became well-known mainly because of their unusual shapes, which still challenge palaeontologists to offer various explanations.

The remaining species of Lower Jurassic bivalves from southern Slovenia will be presented on another occasion.

Previous Research into Lithiotid Bivalves in Slovenia

Between 1959 and 1965 B u s e r (1965) geologically mapped the territory of Southern Slovenia. He subdivided Jurassic beds and collected rich fossil material, mainly hundreds of specimens of unusually shaped large-shelled bivalves. Among them he determined the species *Lithiotis problematica* and *Cochlearites loppianus,* which were previously known from classic localities in northern Italy. He established that the majority of the specimens in southern Slovenia belong to a new genus of bivalves

with the multivincular type of ligament. In his doctoral dissertation he named it *Lithiopedalion*. Together with the genera *Lithiotis* and *Cochlearites* he classified it into the family Lithiotidae because of their obvious similarities. B u s e r (1972) presented his work at the international meeting of palaeontologists in Graz, but unfortunately failed to publish it in the manner required by the International Code of Zoological Nomenclature. The genus *Lithiopedalion* was later described under the name *Lithioperna* (A c c o r s i B e n i n i, 1979).

Systematic Descriptions of Lithiotid Bivalves

Subclassis PTERIOMORPHIA Beurlen, 1944
Ordo **Pterioida** Newell, 1965
? Subordo **Lithiotina** A c c o r s i B e n i n i & B r o g l i o L o r i g a, 1977
? Superfamilia L i t h i o t a c e a A c c o r s i B e n i n i & B r o g l i o L o r i g a, 1977

Familia L i t h i o t i d a e R e i s, 1903
Genus *Lithiotis* Gümbel, 1871

Lithiotis problematica Gümbel, 1871
Pl. 1, figs. 1-3; Pl. 2, figs. 1-3

1871 *Lithiotis problematica* - G ü m b e l, 48; Pl. 2, figs. 13, 14.
1890 *Lithiotis problematica (= Lithiotis ostreacina, Ostrea lithiotis)* - G ü m b e l, 64-67, Textfigs. 1-4.
1892 *Ostrea problematica* Gümbel - B ö h m, 71-73; Pl. 3, figs. 1-3.
1903 *Lithiotis problematica* Gümbel - R e i s, 9-13, Textfig. 4; Pl. 6, figs. 5-16; Pl. 7, figs. 1-10.
1923 *Lithiotis timorensis* sp. nov. - K r u m b e c k, 80-81; Pl. 5, fig. 9.
1923 *Lithiotis* sp. (?) aff. *problematicae* (Gümb.) - K r u m b e c k, 81-82; Pl. 5, figs. 10a, b.
1923 Lithiotis problematica Gümbel - R e i s; Pl. 6, figs. 17-22.
1930 *Plicatostylus gregarius* new species, new genus - L u p h e r & P a c k a r d, 204-207; Pl. 1-3, Pl. 4, fig. 1.
1962 *Lithiotis problematica* Gümbel - D e C a s t r o, 13-14; Pl. 10, figs. 1-6.
1965 *Lithiotis problematica* Gümbel - B u s e r, 17-18; Pl. 8, figs. 1, 2; Pl. 9, figs. 1, 2; Pl. 10, figs. 1-4; Pl. 11, figs. 1-4.
1969 *Plicatostylus gregarius* Lupher & Packard - C o x (M o o r e ed.), N866, Textfigs. H2,4a-c.
1971 *Lithiotis problematica* Gümbel - S t e n z e l (M o o r e & T e i c h e r t eds.), N1200, Textfigs. J150,1a-c (kop. Reis, 1903).
1971 *Lithiotis problematica* Gümbel - B e r t i C a v i c c h i, B o s e l l i n i & B r o g l i o L o r i g a, 43-47, Textfigs. 1, 3; Pl. 1, figs. 1-5.
1977 *Lithiotis problematica* Gümbel - A c c o r s i B e n i n i & B r o g l i o L o r i g a, 42-50, Textfigs. 1-9, 16-18; Pl. 1, figs. 1-4; Pl. 2, figs. 1-3; Pl. 3, fig. 2; Pl. 8, fig. 1; Pl. 9, figs. 1, 2.
1977 *Plicatostylus gregarius* Lupher & Packard - A c c o r s i B e n i n i & B r o g l i o L o r i g a, Pl. 3, figs. 1, 3, 4.

1982 *Lithiotis problematica* Gümbel - C h i n z e i, 179-196, Textfigs. 2, 4, 6, 7, 10.
1988 *Lithiotis* Gümbel - N a u s s & S m i t h, 258-259, Textfigs. 6-8.
1989 *Lithiotis problematica* Gümbel - B u s e r I., 20-24, Textfigs. 13-15; Pl. 1, figs. 1, 2; Pl. 2, fig. 1; Pl. 10, fig. 1.
1995 *Lithiotis problematica* Gümbel - S a v a z z i, 281-289, Textfigs. 1-5.

M a t e r i a l: Over one hundred specimens. Mainly they consist of shell fragments several centimetres high, with clearly recognisable characteristics. In six cases the apex was preserved. Only five specimens have part of the body space preserved.

D e s c r i p t i o n: It is characteristic that in all cases only one of the valves was preserved: that with which the bivalve was attached to the solid base. According to C h i n z e i (1982) this was the right valve. The opposite valve was so thin that only fragments have been preserved. Evidence for this are fragments of a 1 to 2 mm thick limestone "crust", which can be found anywhere on the inner surface of the thicker valve. *Lithiotis problematica* is ribbon shaped; narrow and distinctively dorso-ventrally elongated. It is thought that adult specimens measured 20 to 50 cm in height (or even more in some cases) and were about 4 to 7 cm wide. The apex is pointed. From the side the shell is flat, consequently its cross section is elliptical. Generally the valve is 1 to 2 cm thick. The apex is vertical or bent in any direction. The shell is sometimes straight, but sometimes fairly curved (Pl. 2, figs. 1, 2). The outer surface of the attached valve is irregularly undulating, as with oysters. Only rarely can small concentric growth lines (increments) be seen.

Figure 1 shows the shape of the attached valve and the characteristics of its interior. The pear-shaped body space was exceptionally small in adult specimens when compared to the total size of the shell. It was limited to the ventral end. The soft body extended several centimetres into the hollow part of the shell, called the umbonal notch or cavity. The internal buttress divided it into smaller and larger cavity. Along the sides of the inner surface are two feather-like areas. They are composed of increments which are at times linked into sheaves (Pl. 1, fig. 2). Between the feather-like areas is a vertical, 2 to 4 cm wide furrowed plate, which is somewhat elevated above the lateral feather-like areas. Parallel grooves with intermediate ridges, which split into shallower grooves and ridges which again split into even shallower ones, run throughout its height. Thus, depending on how well the specimen is preserved, the number of grooves can range from less than 8 to over 50.

The microstructure of the shell is described in the following works: A c c o r s i B e n i n i and B r o g l i o L o r i g a (1977) and C h i n z e i (1982), summarized in B u s e r I. (1989).

C o m p a r i s o n: Despite their very pronounced variability, specimens of *Lithiotis problematica* extracted from rock have such specific characteristics that they cannot be mistaken for any other species. The uniqueness of this bivalve is also seen in that it is today the sole species of the family Lithiotidae, and together with the species *Cochlearites loppianus* it is classified as an independent suborder Lithiotina (according to A c c o r s i B e n i n i & B r o g l i o L o r i g a, 1977). A possible relation with oysters (B ö h m, 1892) was rejected by the aforementioned Italian palaeontologists on the basis of proof that the shells were originally made of aragonite, while oysters have calcitic shells. Systematic classification of the genera *Lithiotis* and *Cochlearites* has not yet been fully resolved. C h i n z e i (1982) is of the opinion that they are taxonomically close to the Pteriacea superfamily, and especially to the Isognomonidae family.

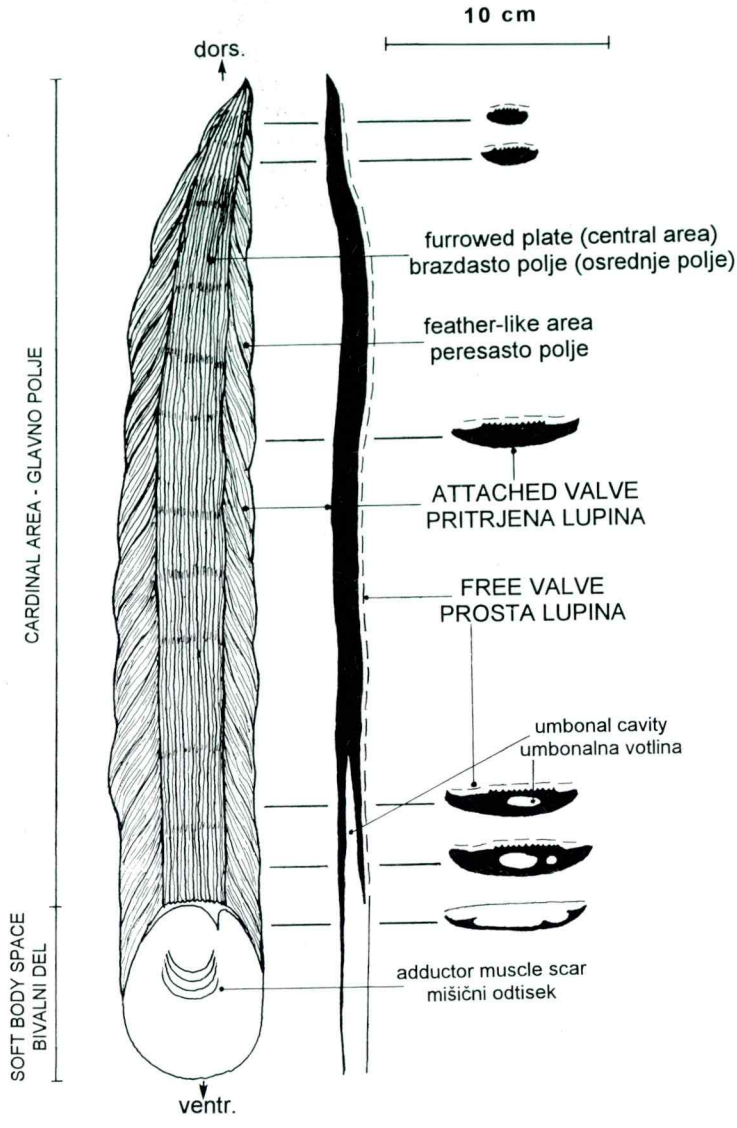

Fig. 1. *Lithiotis problematica* Gümbel. Left: interior side of the thicker, attached (probably right) valve. Centre: longitudinal section. Right: cross sections at various heights. The thin, free valve is marked by the dashed line. The growth position was subvertical, with the ventral end turned upwards

Sl. 1. *Lithiotis problematica* Gümbel. Levo: notranja stran debelejše (verjetno desne) lupine, s katero se je školjka pritrdila na trdno podlago. Sredina: vzdolžni prerez. Desno: prečni prerezi na različnih višinah. Tanko, prosto lupino označuje prekinjena črta. Življenjski položaj je bil pokončen; ventralni konec je bil pri tem obrnjen navzgor

The possibility that *Lithiotis* and *Plicatostylus* (later described from Oregon) are identical genera was raised by G r u b i ć (1959; 1961). B u s e r (1965) confirmed this assumption with a study of the original specimens which the American authors Lupher and Packard sent to Professor Kühn in Vienna.

Lithiotis problematica can also be distinguished from the other lithiotid bivalves by cross-sections in solid rock. These are always monovalve and of an elliptical shape in the cross-section (see B u s e r & D e b e l j a k, 1996, 36, figs. 9, 10). Especially characteristic are the "ear-like" sections with an opening in the central part, after which *Lithiotis* was named.

L o c a l i t i e s: *Lithiotis problematica* is the rarest species of lithiotid bivalves in Slovenia. B u s e r (1965) found it in a deserted quarry on the right bank of the river Sušica, west of Dolenjske Toplice. Unfortunately this quarry is now filled in. Buser found some specimens on the northern slope of Mokrec during the construction of a new road. Today these outcrops are overgrown. A large number of specimens can still be found east of the village Zafara near Žužemberk. Relatively well preserved shells of *L. problematica* can be extracted from limestone in the vicinity of the Glijun spring and on the Poljanica hill west of Bovec. Characteristic sections can be observed in the ornamental Podpeč limestone (B u s e r & D e b e l j a k, 1996), but the shells of *L. problematica* in Podpeč cannot be extracted from solid rock.

During the Pliensbachian and Toarcian *Lithiotis* heavily populated the extensive and interconnected shallow marine areas of the western and southern margins of the Tethys and the Eastern Pacific. Various authors have reported finds of the species in southern Spain (?) and western France (?), northern Italy, the south-central Apennines, Croatia (?), Herzegovina, Montenegro, Albania (?), Greece, Turkey (?), Marocco (?), Somalia (?), Oman (?), Iran (?), Iraq (?), the Himalayas (?), the island of Timor in Indonesia, the USA (Oregon, Nevada, California), Chile and Peru. A question mark denotes that the locality is not reliably confirmed. The above data are collected from: B r o g l i o L o r i g a and N e r i, 1976; A c c o r s i B e n i n i and B r o g l i o L o r i g a, 1977; G e y e r, 1997; N a u s s and S m i t h, 1988; B u s e r and D e b e l j a k, 1996.

Familia C o c h l e a r i t i d a e Accorsi Benini & Broglio Loriga, 1977
Genus *Cochlearites* Reis, 1903

Cochlearites loppianus (Tausch, 1890)
Pl. 3, figs. 1-3

1890 *Trichites Loppianus* n. f. - T a u s c h v o n G l o e c k e l s t h u r n, 18-19; Pl. 5, figs. 5-7.
1892 *Ostrea Loppiana* Tausch - B ö h m, 67-71; Pl. 2, figs. 1-4.
1892 *Ostrea problematica* Gümbel var. *lithiotis* - B ö h m, 74; Pl. 4, fig. 1.
1903 *Cochlearites Loppianus*, nov. gen. - R e i s, 2-8, Textfigs. 1-3; Pl. 1, figs. 1-8; Pl. 2, figs. 1-10; Pl. 3, figs. 1-11; Pl. 4, figs. 1-11; Pl. 5, figs. 1-9; Pl. 6, figs. 1-4.
1965 *Cochlearites loppianus* (Tausch) - B u s e r, 19-20; Pl. 12, figs. 1, 2; Pl. 13, figs. 1-4.
1971 *Cochlearites loppianus* (Tausch) - C o x (M o o r e ed.), N1200, Textfigs. J150,2a,b (kop. Reis, 1903).
1971 *Cochlearites gr. loppianus* (Tausch) - B e r t i C a v i c c h i, B o s e l l i n i & B r o g l i o L o r i g a, 43-47, Textfigs. 2, 4; Pl. 2, figs. 1-4.

1977 *Cochlearites loppianus* (Tausch) - Accorsi Benini & Broglio Loriga, 52-57, Textfigs. 12, 19; Pl. 4, figs. 1-5; Pl. 5, figs. 1-3; Pl. 6, figs. 1-3.
1977 *Cochlearites loppianus* f. A - Accorsi Benini & Broglio Loriga, 56, Textfigs. 14, 20; Pl. 6, fig. 4; Pl. 7, figs. 1-4; Pl. 8, fig. 2.
1982 *Cochlearites loppianus* (Tausch) - Chinzei, 179-196, Textfigs. 3, 5, 8, 11c, 13.
1989 *Cochlearites loppianus* (Tausch) - Buser I., 25-28, Textfigs. 16, 17; Pl. 2, figs. 2, 3a,b; Pl. 10, fig. 2.

Material: Approximately 80 specimens. Mostly fragments of left valves up to 10 cm large; fewer right valves. Ten of the specimens have both valves partially preserved. The apex of the shell and the body space are not preserved in any of the specimens. The ligament groove is visible in six shells.

Description of Species: The shell is narrow, and strongly dorso-ventrally elongated with a tapered apex. Adult specimens measure from about 20 to more than 50 cm in height; their average width is 5 to 8 cm. The animal attached itself to the solid base with its left valve, which is approximately 1 to 2 cm thick. The right valve was free and thinner than the left; at its centre it measure approximately 0.5 to 1 cm. The shell is usually straight, but may be bent to the side (Pl. 3, fig. 2). Concentric growth lines can sometimes be seen on the rough and irregular outer surface.

The shape and interior of the shell is shown in fig. 2. The inner side of the shell is tripartite, which is characteristic of lithiotid bivalves. The central area is about 2 to 4 cm wide, and bordered by two feather-like areas. The feather-like appearance is created by growth lines, which can be joined into sheaves. The valves usually gaped at the edges of the feather-like areas. The soft body space of the shell was very small compared to the total size of the shell. The central area where the valves were tightly joined has a relief form. A more or less wide depression bordered by two ridges runs down the centre of the left valve and the central crest of the right valve fits tightly into it. Semicircular traces are often found on the central area; these are growth lines which the edge of the mantle left behind as it moved in the ventral direction.

At the apical end approximately down the middle of the cardinal area of both valves runs a deep and narrow groove (resilifer) in which the fibrous ligament was attached. The lamellar part of the ligament was attached at both sides of the groove. The height of the ligament groove varies with the specimens. Usually it measures 3 to 6 cm.

Slovenian specimens usually have recrystallised shells, but during fossilisation the parts with a different original microstructure were selectively coloured so that the characteristic features of the basic structure can often be observed in the sections (Buser I., 1989, Pl. 10; cf. Chinzei, 1982).

Comparison: The specimens of *Cochlearites* extracted from rock cannot be mistaken for any other bivalve. Confusion can arise when an attempt is made to determine the species from sections in the rock alone. They can be very similar to sections of *Lithioperna scutata*. However, in specimens of *Cochlearites* the left valve is thicker than the right, whereas in *Lithioperna* the two shells are equally thick. Normally in Lithioperna both valves fit tightly around the edges; one valve follows the other like a mirror image. In *Cochlearites* the valves often gape in the feather-like areas. The easiest to identify are cross-sections with a characteristic central ridge on the right valve and a corresponding depression on the left valve (Buser & Debeljak, 1996, p. 32 - fig. 4, p. 41 - fig. 15).

Individual specimens of *Cochlearites loppianus* can differ considerably from one another in the shape and size of the shell. Such variations have arisen owing to con-

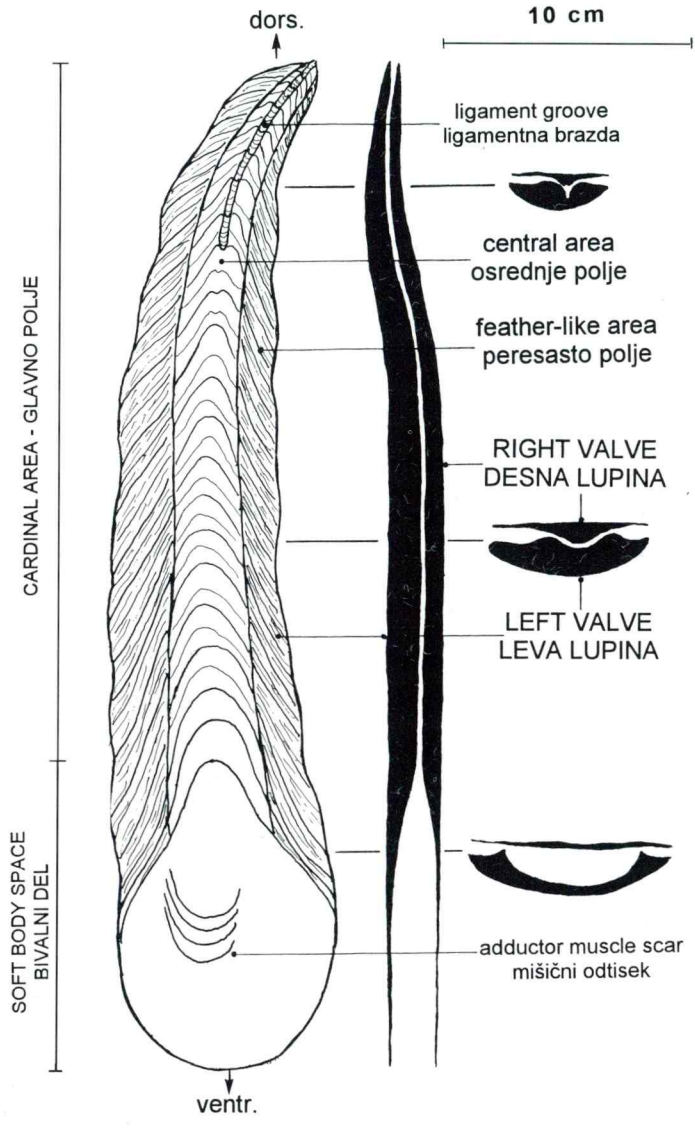

Fig. 2. *Cochlearites loppianus* (Tausch). Left: interior side of the right, fixed valve. Centre: longitudinal section of both valves. Right: cross sections at various heights. The growth position was subvertical, with the ventral end turned upwards

Sl. 2. *Cochlearites loppianus* (Tausch). Levo: notranja stran desne, proste lupine. Sredina: vzdolžni prerez čez obe lupini. Desno: prečni prerezi na različnih višinah. Življenjski položaj je bil pokončen; ventralni konec je bil pri tem obrnjen navzgor

stant adaptations to the environment and growth in tight communities or aggregates. Practically no two specimens have identical central areas. According to the ligament groove Reis (1903) identified three types of *Cochlearites*. Accorsi Benini and Broglio Loriga (1977) admitted only two types: the normal type, in which the ligament was connected to the mantle, and the abnormal type (forma A), in which a short, stunted fibrous ligament no longer had any connection with the living part of the bivalve, which can be ascertained by shifted mantle growth lines. Chinzei (1982, 193) showed that practically all adult specimens belong to the abnormal type or form A, which results from the ligament becoming stunted sooner or later during the growth of the bivalve. This finding makes irrelevant considerations of different types or even subspecies with regard to the appearance of the ligament area.

The systematic position of the *Lithiotis* and *Cochlearites* genera has not been finally determined, and their possible relationship is similarly not yet clear.

Localities: Buser (1965) found the finest specimens south-west of Lož and in the northern and southern parts of Mokrec. Today those localities are overgrown. Individual specimens can still be obtained at the Globočec spring west of Zagradec, and on the Stražišče hill east of Gorenje Jezero near Cerknica. *Cochlearites loppianus* also occurs in the Podpeč quarry, in the surroundings of Grčarevec near Logatec, at Borovec in the Kočevje region, and on Travna gora, as in these localities characteristic sections have been observed in limestone or dolomite.

Elsewhere in the world *C. loppianus* was found in northern Italy, the south-central Apennines, Montenegro, Greece and Morocco. It may possibly occur in western France, Somalia and on the island of Timor in Indonesia. (After: Broglio Loriga & Neri, 1976; Accorsi Benini & Broglio Loriga, 1977; Geyer, 1977; Buser & Debeljak, 1996).

Subordo **Pteriina** Newell, 1965
Superfamilia Pteriacea Gray, 1847

Familia Isognomonidae Woodring, 1925
Genus *Lithioperna* Accorsi Benini, 1979 - syn. *Lithiopedalion* Buser, 1965

Lithioperna scutata (Dubar, 1948)
Pl. 4, fig. 1; Pl. 5, figs. 1a, b; Pl. 6, fig. 1; Pl. 7, figs. 1-3; Pl. 8, fig. 1; Pl. 9, figs 1a, b

? 1948 *Perna scutata* n. sp. - Dubar, 158-159; Pl. 11, figs. 1-3.
? 1948 *Perna* sp. nov. - Dubar, 159-161, Textfig. 51; Pl. 13, figs. 10a,b.
1965 *Lithiopedalion kuehni* n. sp., n. gen. - Buser, 21-22; Pl. 14, fig. 1.
1965 *Lithiopedalion* sp. - Buser, 20-21; Pl. 15, figs. 1-5; Pl. 16, figs. 1-3; Pl. 17, figs. 1, 2; Pl. 18, figs. 1-3.
1971 *"Perna"* - Berti Cavicchi, Bosellini & Broglio Loriga, 47-48, Textfigs. 5a,b; Pl. 3, figs. 1-3.
1976 *Lithiopedalion kuehni* Buser - Broglio Loriga & Neri, 656-657; Pl. 85, figs. 1, 2.
1979 *Lithioperna scutata* (Dubar), n. gen. - Accorsi Benini, 251-253, Textfigs. 1-12, 15; Pl. 1, figs. 1, 2; Pl. 2, figs. 1, 2; Pl. 3, figs. 1-4; Pl. 5, figs. 1, 2; Pl. 6, figs. 1, 2.
? 1979 *Lithioperna scutata* (Dubar) - Accorsi Benini, 251, Textfig. 14.

1989 *Lithioperna scutata* (Dubar) - B u s e r I., 30-34, Textfigs. 18, 19, 25; Pl. 4, fig. 1; Pl. 5, figs. 1-3; Pl. 11, fig. 1.
1996 *Lithiopedalion scutatus* (Dubar) - B u s e r & D e b e l j a k, 25, Textfigs. 4, 8.

M a t e r i a l: About 80 specimens, most with both valves preserved. Fragments of the apical parts of the central plate with ligament grooves are predominant in the collection. The marginal parts are generally missing.

D e s c r i p t i o n o f G e n u s a n d S p e c i e s: The shell is linguiform and often very large. Sections in the limestone reveal that some specimens reached a height of three-quarters of a metre. The marginal parts of the shell are very thin, and for this reason we have so far not succeeded in finding an undamaged intact specimen. Therefore, in citing size we have to rely on sections in the limestone. On average, the shells are 30 to 70 cm high. The height is usually about twice the length. From the side the shell is distinctly compressed. The two valves have the same shape, size and thickness, and fit closely. Together they are 1 to 4 cm thick. The longitudinal section often has an undulating appearance. The external surface of the valve is normally rough and irregular, and in some rare specimens concentric growth lines can be seen on it.

Characteristics of the shell interior are shown in Figure 3. Flat feather-like areas are well-formed at both sides with clearly visible increments. (These indicate the former lateral outline of the body cavity which shifted in the ventral direction with the growth of the bivalve.) The anterior feather-like area is generally larger and often bent into a knee shape. A byssal notch runs along its interior edge. Under the apex it is shaped like a byssal groove, and towards the body space it is bordered by two folds or edge lines. Between the two there is a ridge of greater or lesser width in the right valve, and a corresponding depression in the left valve that can be shallow (Pl. 5) or quite deep (Pl. 6).

Between the lateral feather-like areas is an even, fairly flat central area or plate, which covers the largest part of the interior of the shell. The bivalve's mantle was spread over this surface, and here both valves were tightly joined. Under the apex a characteristic ligament area is formed, with a straight or occasionally a semicircular upper edge. The ligament was multivincular. The fibrous ligament was placed in several ligament grooves or resilifers, while the lamellar ligament was attached in spaces between them. As the bivalve grew the ligament shifted in the ventral direction and left behind thin growth lines, which in the grooves are curved in a convex manner with respect to the apex, but between the grooves they are concave. The ligament grooves are generally sub-parallel. In several specimens the position and centre of gravity of the shell was changed during growth, and the ligament later progressed in a different direction to the original one. Sometimes the ligament grooves run so distinctly towards the anterior part that they reach the anterior feather-like area (Pl. 7, figs. 2, 3).

Even if the byssal notch on the anterior side is not preserved, it can be determined whether the specimen is the left or the right valve. First, a vertical boundary is traced between the central plate and the feather-like area, and then a straight line is imagined running through the ends of the ligament grooves. The angle made by the two lines is less than 90° on the anterior side and more than 90° on the posterior. The left and right valves can thus be distinguished.

The density of the ligament grooves can vary. With regard to the width of the lamellar part of the ligament, that is of the intervals between individual ligament grooves, two groups can be determined. In both groups the grooves are 2 to 3 mm wide.

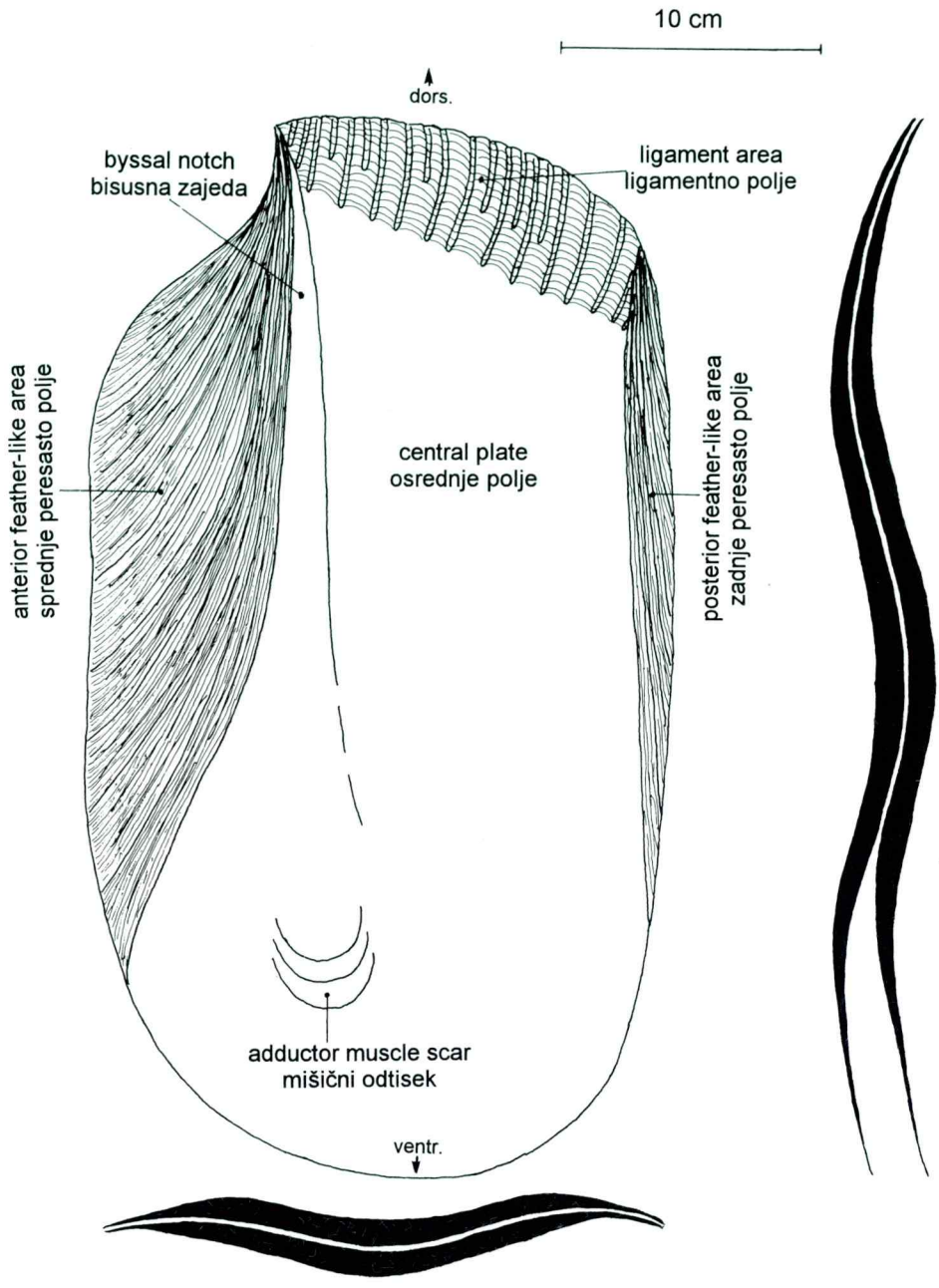

Fig. 3. *Lithioperna scutata* (Dubar). Left: inner surface of the right valve. Right: characteristic undulating longitudinal section of both valves. Bottom: cross sections through both valves

Sl. 3. *Lithioperna scutata* (Dubar). Levo: notranja površina desne lupine. Desno: značilen, valovit vzdolžni prerez obeh lupin. Spodaj: prečni prerez čez obe lupini

The intermediate sections are 2 to 3 mm wide in the first group, and 8 to 10 mm wide in the second. In the first group there are about 16 grooves on 10 cm of the hinge axis, in the second about 8. In some specimens it is clear that some ligament grooves have lagged behind while others have continued to develop at the normal rate (Pl. 7, fig. 2; Pl. 9). It can be concluded that in the second group approximately every other ligament groove with a fibrous ligament became stunted, and the lamellar part of the ligament was attached in its place. The ligament grooves can range from just a few millimetres in height to 8 cm. The amount of ligament area preserved depends on the thickness of the valve beneath the apex: the thicker the valve, the longer the grooves. In any case, the majority of specimens are very thin beneath the apex.

The body space of the bivalve with a single muscle scar is small in comparison to the overall size of the shell. It occupies only the ventral section of the shell and part of the space between the anterior border folds or lines. The depression for the soft body is very shallow.

An analysis of extremely well-preserved specimens from around Verona has shown that *Lithioperna* shells were composed of aragonite (Accorsi Benini, 1979, 228). In many specimens from Slovenia the characteristic structure of the shell can be seen with the naked eye, i.e. an alternation of lighter and darker laminae or layers parallel to each other and to the external surface of the valve (Buser I., 1989, Pl. 11, fig. 1). The light, glittering layers once had a prismatic microstructure, and the darker, opaque layers had a nacreous microstructure (Accorsi Benini, 1979).

Comparison: The *Lithioperna* genus is now classified with the Isognomonidae. In these bivalves the hinge teeth are absent, but a large multivincular ligament compensates for them. The classification among the Isognomonidae is still somewhat uncertain because the shell structure of *L. scutata* is uniquely developed (Accorsi Benini, 1979). Among the Isognomonidae *Lithioperna* could be compared with Isognomon Solander in Lightfoot, 1786 (syn. *Perna* Bruguiére, 1789), in which the shells were attached to the firm base by a byssus as well. However there is no large central plate in *Isognomon*. The feather-like areas on the sides are not present, the valve is biconvex, and there is no alternation of two types of laminae.

Lithioperna can also be recognised from sections in rock (Buser & Debeljak, 1996, 32, fig. 4). Typical sections are very long and thin, and usually undulate gently. The two valves are of equal thickness and fit closely on all edges. In general only the very thin soft body space gapes (fig. 3).

At present the genus contains only the species *L. scutata,* although individual specimens differ considerably. Variations in shell size proportions and shape are very common, and the appearance of the ligament area also differs. No two specimens are the same. However, only one specimen, described below, is essentially different, which is not sufficient to describe a new species.

Remarks: The name *Lithiopedalion* was given to the genus by Buser (1965) in his doctoral thesis according to the common characteristics of *Lithiotis* and *Pedalion* Dillwyn, 1817 (an old synonym for *Isognomon).* The new genus and species was presented at the 42nd annual meeting of the Palaeontological Society in Graz (Buser, 1972). Unfortunately this work was not published in the way required by international rules, but the name *Lithiopedalion* was nevertheless used in Slovenia and in the literature elsewhere (cf. Bosellini, 1972; Broglio Loriga & Neri, 1976). After many years of collaboration he was overtaken in publication by the Italian palaeontologist Accorsi Benini (1979), who described the genus under the name: *Lithioperna.*

Together with the genus Buser (1965) described a new species *Lithiopedalion kuehni,* but Accorsi Benini (1979) equated it with the species *Perna scutata* from Morocco as already described by Dubar (1948), and included it in *Lithioperna.* Given that Benini studied original material from Dubar's collection, for the time being her classification of these as the same species must be trusted. However, despite this we think that three modest figures showing poorly preserved specimens do not exhibit all the characteristics typical of specimens from Slovenia and northern Italy. According to their shape they are considerably reminiscent of *Gervilleioperna* Krumbeck, 1923; this applies in particular to Dubar's specimen that Accorsi Benini (1979, 251, fig. 14) presented as a paralectotype in describing the new genus. Judging by the description and pictures the anterior feather-like area is formed as a lunule, while the byssal notch is very deep and just under the apex spreads and deepens into the body cavity. The Slovenian and Italian specimens have a significantly more dorso-ventrally elongated shell, a higher ligament area, a shallower byssal notch in most cases, and, above all, a larger central plate where the valves were tightly joined. In the future it would certainly be recommendable to make a revision of the *Lithioperna scutata* species using the Dubar material, which is kept in France (Lille).

Localities: In the lithiotid horizon of Middle Liassic beds in Slovenia (Trnovski gozd, Hrušica, Nanos, Logaška planota, Krim-Mokrec hills, Dolenjska) *Lithioperna scutata* is the most common species, found in almost all localities (Buser & Debeljak, 1996, 28, fig. 2; presented in this article as *Lithiopedalion scutatus*). Specimens that can be extracted from marly layers between limestone can now be found at Špik, north of Col in Trnovski gozd, in the Podpeč quarry, and along the railway between the stations Preserje and Verd. Buser (1965) found numerous specimens on the Krim-Mokrec hills; the outcrops are now almost entirely overgrown. The locality on Javornik and those north of Cerknica and south of Lož are also overgrown. The quarry on the right bank of the Sušica west of Dolenjske Toplice is now filled in.

Elsewhere in the world *Lithioperna* can be found in Liassic beds of northern Italy (Berti Cavicchi et al., 1971; Broglio Loriga & Neri, 1976), the central Apennines, Albania, Greece, France and Morocco (after Accorsi Benini, 1979). Rey (1990; 1997) reports it from southeastern Spain. We estimate that the *Lithioperna* is present elsewhere, but different authors have designated it under the name *Perna* or *Isognomon,* or in some places have perhaps classified it with the oysters (e.g. *Pernostrea* Munier-Chalmas, 1864 with the multivincular type of ligament).

? *Lithioperna* sp.
Pl. 9, fig. 1

Material and Site: One poorly preserved specimen with both valves. Only the ligament area, part of the central plate, and the upper part of the byssal notch are preserved. The specimen was found by a forest road north of Mokrec.

Description and Comparison: Extremely narrow ligament grooves are present on the ligament area, approximately 1 mm wide. On the hinge axis (in so far as it has been preserved), which is 11 cm long there are 36 ligament grooves. That is at least twice as many as is common for *Lithioperna scutata.* The height (more than 4 cm) and density of the ligament grooves could fit the *Isognomon* genus or the *Hippochaeta* Philippi, 1844 subgenus, which is known only from Tertiary strata. Howe-

ver in *Isognomon* the body cavity begins under the ligament, but in the specimen described, as in *Lithioperna scutata,* the ligament grooves end in the flat central plate, where the valves were tightly joined.

The specimen is too poorly preserved for a more detailed determination, or for the description of a new species.

Mode of Life of Lithiotid Bivalves

In southern Slovenia during the Middle Liassic lithiotid bivalves flourished in the mainly quiet environment of a more or less restricted shelf on the Dinaric Carbonate Platform. Individual species created monocolonies in the form of sea-bottom mats or biostromes with several lens-like accumulations. The moderate influence of the pelagic sea could be felt from the north. Sedimentation in the lagoon was rapid, and the substratum on the sea bed was principally composed of mud, which was determined with regard to the properties of the matrix in bivalve lumachelles. Biodiversity in such lumachelles is very low. Bivalves were able to build shells of three-quarters of a metre in length only under tropical or sub-tropical conditions. The palaeogeographical and palaeoecological conditions that enabled the existence of the characteristic bivalve fauna and the distribution of various species have already been described (B u s e r & D e b e l j a k, 1996).

A description of the living habits and special adaptations of individual genera is given below.

Lithiotis

Although the first investigators in Italy discovered *Lithiotis* 250 years ago, it still presents a puzzle to palaeontologists today. The specimens extracted from rock do not really resemble present-day bivalves, and it is not surprising that they were first described as plant remains (G ü m b e l, 1871; cf. 1890). It is supposed that the life of such bivalves developed as described below.

The larvae first swam or floated in water until they found a suitable attachment point. On the muddy sea floor the firmest substratum was presented by the shells of other bivalves, usually adult *Lithiotis* individuals. Juveniles fixed themselves to these with a sp cial adhesive substance, oriented in such a way that they could grow vertically u> vards. Numerous *Lithiotis* specimens testify to this, having identically oriented you nger individuals fixed to their surfaces (B u s e r, 1965, Pl. 8, 9). It can also be seen from sections in the limestone that certain adults were literally cemented to each other (E u s e r & D e b e l j a k, 1996, fig. 9). C h i n z e i (1982) suggested that the attachn ent area was small, and that cementation was possible only in juveniles. On the ba sis of our own observations we have concluded that these bivalves retained the capacity for cementation throughout their lives, thus the construction of their aggregates was very firm, and after death they often remained in their life position.

In any case *Lithiotis* bivalves lived in large groups, giving one another support and spreading out in bunches (fig. 4). Sedimentation of carbonate mud took place quite rapidly, so that the shell was permanently anchored in it. The body space increased only in young individuals, afterwards the shell grew only in height, in a subvertical

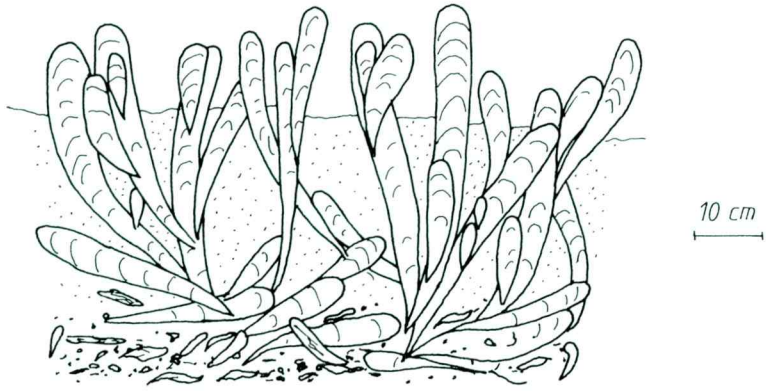

Fig. 4. Aggregate of *Lithiotis* shells; characteristic branching in subvertical direction

Sl. 4. Združba školjk rodu *Lithiotis;* značilno razraščanje v subvertikalni smeri

direction (cf. G ö h n e r, 1980; C h i n z e i, 1982; C h i n z e i et al., 1982; S e i l a c h e r, 1984). Much can be learned about the growth from the incremental lines on the exterior surface and on the feather-like areas. They are combined into sheaves that on well-preserved specimens repeat approximately every centimetre. C h i n z e i (1982, 189-192) concluded that periods of faster and slower growth alternated, resulting in the appearance of annual rings. By counting the growth lines and measuring the size of the shell he reached the conclusion that it took about forty years for the shell to attain a height of 50 cm. During all this time mud gathered around it. Individuals that did not grow quickly enough became buried in mud. This often happened to juveniles, which owing to the crowd did not succeed in gaining living space. Whenever an individual became dangerously tilted, it was still able to correct its position during further growth. Such specimens with "bent knee" shells are very common (Pl. 2, fig. 1).

It is interesting that in *Lithiotis* it was only the thicker valve that was preserved, i.e. the valve cemented to the base. The opposite, free valve must have been extremely thin. Only pieces of thin crust on the thicker valve remained of it. In limestone too only single-valve *Lithiotis* specimens can be observed. Sometimes thin traces that could be fragments of the thinner valve are scattered among them (B u s e r & D e b e l j a k, 1996, 36). Today it is still not known whether this valve was as big as the thicker, attached valve (R e i s, 1903, 11; C h i n z e i, 1982, 181; S a v a z z i, 1996, 287), or whether it covered the bivalve's soft body only in the form of an operculum (L u p h e r & P a c k a r d, 1930; A c c o r s i B e n i n i & B r o g l i o L o r i g a, 1977, 21). The thicker attached valve was hollow under the lowermost part of the furrowed plate. Here the soft body found support, so that its weight did not burden the thin, free valve.

The mechanism of opening and closing the shell has not yet been fully explained. Usually in bivalves the valves are opened by a ligament functioning in the opposite way to the adductor muscle. C h i n z e i (1982, 193) suggested that there was no functional ligament in *Lithiotis,* and that the valves were able to open and close

due to the elasticity of the thin valve. This would have been bent over the ventral edge of the furrowed plate (in this case it would be the hinge axis) whenever the adductor muscle was contracted. When the muscle was relaxed, the thin valve stretched out and the valves gaped open. The question with this hypothesis is what (apart from mud) held both valves together at the dorsal end if there was no ligament or hinge teeth. The valves themselves were very large but the body space with the adductor muscle was small. If the valves were really the same height, then during opening they might become displaced and irruption of mud might occur. In this case it is indeed more likely that the thin valve was merely some sort of operculum over the body space of the thick valve. This supposition is somewhat contradicted by the fact that remnants of the thin valve are found at all heights on the thick shell. It is possible that the thin shell gradually broke up and fragmented in the dorsal area while the shell grew in height and the body space shifted in the ventral direction.

Also unsolved is the question of what function the central furrowed plate served. It can not be that this was just a frick of nature. There are no traces on it left behind by the mantle. The soft part of the bivalve did not extend to this area. B ö h m (1892) even thought that the characteristic grooves arose secondarily, owing to weathering. G ü m b e l (1890, 65) and B u s e r (1965, 18) described the furrowed area as the place for the ligament. R e i s (1903, 43) asserted that the ligament was stunted and that the indentation of the furrowed area acted as a sort of hinge. A c c o r s i B e n i n i and B r o g l i o L o r i g a (1977, 21-24) suggested that the furrowed area was just a superstructure that covered special internal tubes in the shell where thin mantle appendages, the centres of calcification, were located. The grooves would have originated as these internal tubes opened outwards. Recently S a v a z z i (1996) found evidence for the presence of the ligament on the furrowed plate, and suggested that in *Lithiotis* the ligament was active throughout the height of the furrowed area and not only on the ventral end or hinge axis, as is normal for bivalves with the multivincular ligament. In *Lithiotis* the ligament structure would have developed in a highly original way. S a v a z z i found that the ligament fibres were oriented and inserted in such a manner that they allowed small changes in the reciprocal distance of the valves. This increased the length over which the free valve flexed when the bivalve closed. Stress was thus more evenly distributed; tension was reduced, as was the possibility that the thin shell would break up or become damaged. Thus according to S a v a z z i the free valve was able to close by flexing, as established by C h i n z e i (1982), but not by articulating over the hinge axis.

C h i n z e i (1982; 1986) compared the shell shape and mode of growth of *Lithiotis* and *Cochlearites* with certain oysters that are also strongly elongated and live or used to live in a vertical position on soft, muddy ground: *Saccostrea* Dollfus & Dautzenberg, 1920, which live along the coast of east Africa and whose shape is reminiscent of rudists - the thin free valve is shaped like an operculum (S t e n z e l, 1971); and *Konbostrea* Chinzei, 1986, an Upper Cretaceous oyster from northern Japan, which is most similar to *Lithiotis* in its shape and growth pattern.

We assume that *Lithiotis problematica* was very selective in its choice of habitat. Data from Slovenian localities indicate that it formed monocolonies; it required its own living space which was not shared with other lithiotid bivalves and excluded the majority of other organisms as well (B u s e r & D e b e l j a k, 1996). The *Lithiotis* genus is the rarest among lithiotid bivalves in Slovenia.

Cochlearites

Cochlearites is very common in the lithiotid horizon in Slovenia, particularly in those places where restricted parts of shelf were spread.

The *Cochlearites* shell grew similarly to *Lithiotis* shells (see previous section). Owing to its narrow and compressed shape many individuals of the same species were able to crowd together. Their living position was vertical, as seen today in *Pinna* Linné, 1758. Its shells are also very elongated in height, but during growth the soft body part increases in size. Using its foot *Pinna* can bury itself in sandy or muddy sediment, after which it uses a bunch of byssal threads to fix itself to any solid base, for example a buried stone (C o x, 1969, N8-N10). *Cochlearites* and *Lithiotis* were unable to bury themselves, as the small soft body occupied only the ventral end of the bivalve; in addition, one valve was immobile, always cemented to a fixed base. We think that the shell cementation capability in *Cochlearites* was much more limited than that of *Lithiotis,* and so the construction of their aggregates was not as firm. The sedimentation of calcareous mud in which the bivalve was anchored took place quite rapidly, thus the valve in any case had sufficient support. A considerable amount of fecal mud accumulated around the bivalves (suspension-feeders) themselves, because they continuously filtered large quantities of water in which small particles of nutritives floated. It can be imagined that the sedimentation environment must have been fairly calm. Strong waves and currents would have washed away the mud which supported the bivalves, and scattered them around the sea floor, where they would have perished.

C h i n z e i (1982, 193) considered that in *Cochlearites* the ligament was active only in very young individuals, but then became stunted and no longer had any connection with the mantle, that is with the living part of the body. The majority of bivalves need the ligament as like a spring it opposes the action of the adductor muscle, thus opening the valves whilst also connecting them. In *Cochlearites* the relief structure of the cardinal area assumed the role of the hinge teeth (which lithiotid bivalves do not have), so that the valves did not become displaced. Most of the shell was stuck in the mud. Therefore along its entire height the shell should not open, because mud would irrupt. In the cardinal area the valves were in close contact all the time, but in the body space they gaped somewhat, and thus remained flat and parallel during growth. The solid valves may have been elongated into the conchiolin-rich lamellae (C h i n z e i, 1982, 194). With the help of these elastic lamellae the bivalve was able to close hermetically like some of today's bivalves. When the adductor muscle relaxed, the lamellae flattened and left a narrow slit at the end. According to C h i n z e i the elasticity of the ventral parts of the valves replaced the ligament.

As in *Lithiotis,* the soft body was very small, and always remained above the level of the surrounding mud. The bivalve probably extended its mantle through the narrow slit at the ventral end, intercepting and absorbing the substances it needed to build a large shell.

Lithioperna

Of all the lithiotid bivalves in Slovenia *Lithioperna* was the most common. Its shells usually lie in limestone parallel to the bedding plane. Only rarely are layers with numerous subvertically oriented sections found, which tell us much about their original life position.

Originally *Lithioperna* shells were fixed to a firm object with the byssus, like other isognomonids. The byssal gland secreted a special sticky fluid that solidified in water into byssal threads. The byssus emerged from the anterior side of the valve. The anterior feather-like area is usually more strongly developed than that on the posterior. The anterior side of the shell was turned towards the weak currents that brought nutrients to the bivalve (fig. 5). In most specimens the ligament grooves run somewhat obliquely towards the anterior margin. The hinge axis runs through their lower ends. The obliqueness of the hinge axis can be explained on the assumption that the posterior side of the valve was more sunk in the soft sediment than the anterior. The hinge axis had to stay parallel to the surface of the substratum, otherwise mud would irrupt into the posterior during opening (fig. 5).

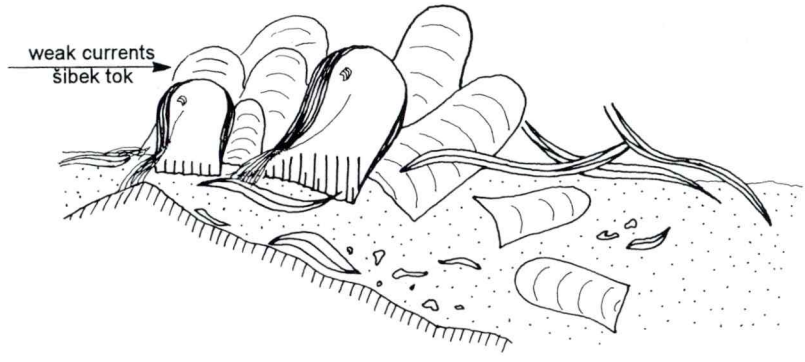

Fig. 5. Growth position in *Lithioperna* (syn. *Lithiopedalion*). Mostly younger individuals grew vertically (left), providing mutual support, and branched radially. Some gradually tilted towards the soft sea floor, or even fell over (right). The right valve is not shown in two specimens so that the inner surface with ligament area can be seen

Sl. 5. Naravni položaj pri rodu *Lithioperna* (syn. *Lithiopedalion*). Predvsem mlajši osebki so rastli navpično (levo) in se medsebojno podpirali ter razraščali. Nekateri so se sčasoma nagnili ali pa celo prevrnili na mehko morsko dno (desno). Desna lupina pri dveh primerkih ni narisana, zato da se vidi notranja površina z ligamentnim poljem

Like all lithiotid bivalves, *Lithioperna* grew rapidly in height. The effectiveness of the byssus was gradually diminished, and it became more difficult for it to hold the shell in an upright position. Adjacent individuals provided one another with support, like books on a book shelf. In addition they were anchored in the mud. Those individuals whose support was not solid enough eventually overturned, and spent the remainder of their life lying flat on the sea floor. According to A c c o r s i B e n i n i (1979, 245-246) the shell was able to adapt its growth so that the ventral end of the valve with the soft body always remained above the level of the mud. The changes in the direction of growth gave the specimen a characteristic wave-like appearance. This undulation also helped maintain effective mutual contact between the two valves. The large, flat shell was stable on the sea floor and did not sink into the soft sediment. From time to time weak tidal currents washed mud away from it. *Lithioper-*

na bivalves were probably also capable of cleaning themselves, as certain oysters do: by rapidly contracting the adductor muscle they can squirt a strong jet of water out of the mantle cavity to clean their surface (S t e n z e l, 1971, N1001).

Lithioperna bivalves lived in such shallow water that occasionally they may have found themselves on dry ground. In such cases the valves sealed hermetically. They also closed in such a manner when the decay of organic matter caused oxygen-depleted conditions on the sea floor. In such periods the bivalve was forced to breath anaerobically. According to A c c o r s i B e n i n i (1979, 228-242) this is reflected in the shell microstructure: During growth, when the valves gaped open the mantle absorbed Ca^{2+} ions and secreted nacre on its external surface. During periods of anaerobic respiration acidic products accumulated in the extrapallial liquid between the mantle lobe and the shell wall and reacted with the shell. To neutralise the acidity, calcium ions were released. During this process the shell's internal layer, which previously had a nacreous microstructure, took on a new pseudoprismatic appearance. This happened repeatedly, and the shell consequently has two types of alternating laminae or layers with a different microstructure.

Owing to the size and undulating shape of the shell the ligament was under considerable stress during opening. The fibrous part of the ligament was located in several ligament grooves (i.e. resilifers). When the adductor muscle contracted, the fibres were compressed, and when it relaxed, the fibres stretched out like a spring. During this process the valves opened somewhat. The lamellar part of the ligament, which was attached between the grooves, connected the two valves. Owing to the mechanical load the ligament was permanently cracked and decayed at the dorsal end. As it was composed of organic matter, it was also destroyed by bacteria. Therefore only the ventral part of the ligament, continuously excreted by the mantle isthmus, was active. This occurs in many bivalves that have a similar type of ligament, i.e. multivincular (S t e n z e l, 1979, N971-974). The hinge axis also shifted in the ventral direction together with the ligament. In certain specimens the ligament grooves ceased growing and the lamellar ligament attached itself in their place. This probably occurred because effective contact between the two valves was essential. The fibrous ligament, used for opening, was not so important. Moreover, at the ventral end the solid valves gaped open by a few millimetres for most of the time, and thus during growth remained flat and parallel; they did not become curved as in most other bivalves. *Lithioperna* bivalves may have secreted poisonous mucus from the ventral slit as a defence measure. It is supposed that the opening was sealed when necessary by thin elastic scales or lamellae that fringed the greatly thinned ventral edge of the two valves, as in *Lithiotis* and *Cochlearites*. Such lamellae have not been preserved as fossils, because they were poorly calcificated and rich in organic matter (cf. S t e n z e l, 1971, N977). In numerous present-day oysters such conchiolin lamellae are semi-translucent and dark brown to olive in colour, with a horny appearance. Even during the lifetime, they are prone to split and decay in the old parts.

The largest part of the shell interior in *Lithioperna* is occupied by the central plate. The bivalve's mantle spread over its entire surface. The mantle was also a respiratory organ, relieving the gills. From the water it absorbed oxygen and the calcium ions needed to build the shell (S t e n z e l, 1971, N967). The larger mantle surface in *Lithioperna* provided a larger respiratory capacity, which was needed to enable the bivalve to thrive and build an immense shell.

Conclusion

The period in which lithiotid bivalves flourished was relatively short. They mostly disappeared in the transition from the Pliensbachian to the Toarcian. Their extinction was hastened by extensive tectonic movements, changes in the sea level causing fundamental changes in habitat and the environment which highly specialised organisms could not successfully respond to (B u s e r & D e b e l j a k, 1996).

The similarity of the sessile mode of life in a specific environment (muddy substratum, rapid sedimentation) and in dense aggregates, and the associated morphological properties and adaptations characteristic of the convergent and contemporary genera *Lithiotis, Cochlearites* and *Lithioperna,* justify the use of a common name, although the name lithiotid bivalves does not have any taxonomic significance.

All three genera are distinguished by their very large, unusually shaped and remarkably variable shells. Their principal characteristic is their flatness and height elongation, i.e. in the direction of growth, which made more or less constant progress during their entire lifetime. The body space of lithiotid bivalves was unusually small: it occupied only the far ventral end of an otherwise very large shell. The valves were tightly joined over almost the entire surface. All three genera have a tripartite internal construction in common, with feather-like areas on the sides and a central area with a very different shape in the middle. Lithiotid bivalves had a considerable capacity for twisting as they grew.

The great variability of lithiotid bivalves can be attributed to the constant adaptation of the growth of the shell to changes in the environment and in the close community in which hundreds of individuals of the same species crowded together, thus providing mutual support and spreading out in bunches, similarly to plants in their search for sunlight.

Lithiotid bivalves are undoubtedly one of the most interesting and distinctive fossil groups in Slovenia. Since their first discovery (B u s e r, 1965) a systematic description has long been delayed. This paper also presents their mode of life, which was reconstructed using the authors' own observations and the findings of numerous researchers from around the world. Many questions remain unanswered, and new findings on these unusual bivalves can be expected in the future.

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Litiotidne školjke v Sloveniji in njihov način življenja

Uvod

V srednjem liasu so školjke množično poseljevale pretežno mirno, blatno dno zaprtega šelfa na Dinarski karbonatni platformi. Horizont s školjkami se v spodnjejurskih plasteh južne Slovenije skorajda ne izklinja; njegova debelina na nekaterih mestih doseže kar 75 metrov. Po značilnih školjkah ga imenujemo "litiotidni horizont". B u s e r (1965, 44-46) ga je uvrstil v pliensbachij oziroma njegov zgornji del - domerij. V predzadnji številki Geologije so bila predstavljena najpomembnejša nahajališča spodnjejurskih školjk v Sloveniji, ki se sicer razprostirajo v dolžini več kot sto in v širini več deset kilometrov. Podane so bile paleoekološke razmere, ki so omogočile razcvet značilne školjčne favne (B u s e r & D e b e l j a k, 1996).

V tokratnem prispevku so sistematično opisane litiotidne školjke in njihov način življenja. Izraz litiotidne školjke je pri nas še vedno v veljavi, čeprav nima več taksonomskega pomena. Združuje tri zelo pogostne in značilne, na prvi pogled podobne rodove *Lithioperna* (syn. *Lithiopedalion*), *Cochlearites* in *Lithiotis*. Vsi trije rodovi so bili široko razširjeni po obrobnih plitvomorskih predelih zahodnega in južnega obrobja Tetide in celo vzhodnega Pacifika (rod *Lithiotis*). Litiotidne školjke so zato paleogeografsko, biostratigrafsko in paleoekološko zelo pomembne. Zaslovele pa so predvsem po zaslugi svoje nenavadne oblike, ki paleontologe še danes izziva k različnim znanstvenim razlagam.

Preostale vrste spodnjejurskih školjk iz južne Slovenije bodo predstavljene ob drugi priložnosti.

Dosedanje raziskave litiotidnih školjk v Sloveniji

V letih 1959-65 je B u s e r (1965) geološko kartiral ozemlje južne Slovenije. Pri tem je razčlenil jurske plasti in nabral bogat fosilni material, predvsem na stotine primerkov nenavadno oblikovanih velikolupinskih školjk. Med njimi je določil vrsti *Lithiotis problematica* in *Cochlearites loppianus*, ki so ju prej poznali s klasičnih nahajališč severne Italije. Ugotovil je, da večina primerkov v južni Sloveniji pripada novemu rodu školjk z večveznim ligamentom. V svoji doktorski disertaciji ga je poimenoval *Lithiopedalion*. Skupaj z rodovoma *Lithiotis* in *Cochlearites* ga je zaradi očitne podobnosti uvrstil v družino Lithiotidae. B u s e r (1972) je svoje delo predstavil na mednarodnem srečanju paleontologov v Gradcu, vendar ga žal ni objavil na način, kot zahteva Kodeks zoološke nomenklature. Rod *Lithiopedalion* je bil kasneje opisan pod novim imenom *Lithioperna* (A c c o r s i B e n i n i, 1979).

Sistematski opisi litiotidnih školjk

Subclassis PTERIOMORPHIA Beurlen, 1944
Ordo **Pterioida** Newell, 1965
? Subordo **Lithiotina** Accorsi Benini & Broglio Loriga, 1977
? Superfamilia L i t h i o t a c e a Accorsi Benini & Broglio Loriga, 1977

Familia L i t h i o t i d a e Reis, 1903
Genus *Lithiotis* Gümbel, 1871

Lithiotis problematica Gümbel, 1871
Tab. 1, sl. 1-3; tab. 2, sl. 1-3

M a t e r i a l: Več kot sto primerkov. Večinoma so to nekaj centimetrov visoki deli lupin z lepo razpoznavnimi značilnostmi. Pri šestih je ohranjen vrh. Le pet primerkov ima ohranjen del bivalne votline.

O p i s: Značilno je, da je vedno ohranjena le ena lupina, tj. tista, s katero se je školjka pritrdila na trdno podlago. Po C h i n z e i-ju (1982) je to desna lupina. Druga lupina je bila tako tanka, da se je ohranila le fragmentarno. O njej pričajo koščki 1-2 mm debele apnenčeve "skorje", ki jih najdemo kjerkoli na notranji površini debelejše lupine. Vrsta *Lithiotis problematica* je trakaste oblike, ozka in izrazito dorzo-ventralno razpotegnjena. Sklepamo, da so odrasli primerki merili v višino 20-50 cm (najbrž pa tudi več) in so bili široki okoli 4-7 cm. Vrh je koničasto priostren. Od strani je lupina sploščena, zato je prečni presek eliptičen. Pri večini primerkov je lupina debela 1-2 cm. Vrh je pokončen ali pa nagnjen v katerokoli stran. Lupina je včasih ravna, včasih pa precej upognjena (tab. 2, sl. 1, 2). Zunanja površina pritrjene lupine je nepravilno valovita; takšna, kakršno imajo ostrige. Zelo redko opazimo na njej drobne koncentrične prirastnice.

Slika 1 shematično ponazarja obliko pritrjene lupine in značilnosti njene notranjosti. Hruškasto oblikovani bivalni del je bil pri odraslih osebkih v primerjavi s celotno velikostjo lupine izredno majhen; omejen je bil le na njen ventralni konec. Mehko telo školjke je za nekaj centimetrov segalo tudi v izvotljeni del lupine, ki ga imenujemo umbonalna votlina. Notranji opornik jo deli na manjši in večji del. Ob straneh notranje površine debelejše lupine sta peresasti polji. Sestavljajo ju prirastnice, ki se včasih združujejo v snope (tab. 1, sl. 2). Med peresastima poljema je navpično, okoli 2-4 cm široko brazdasto polje, ki je nekoliko dvignjeno nad stranski peresasti polji. Po vsej njegovi višini potekajo vzporedne brazde z vmesnimi grebeni, ki se cepijo v plitvejše brazde in grebenčke in ti v še plitvejše. Tako v osrednjem delu razločimo, odvisno od ohranjenosti, od manj kot 8 do več kot 50 brazd.

Struktura oziroma mikrostruktura lupine je opisana v naslednjih delih: A c c o r s i B e n i n i in B r o g l i o L o r i g a (1977) in C h i n z e i (1982) ter povzeta v: B u s e r I. (1989).

P r i m e r j a v a: Iz kamnine izluščeni primerki vrste *Lithiotis problematica* imajo kljub zelo izraženi variabilnosti tako svojstvene značilnosti, da jih ne moremo zamenjati z nobeno drugo vrsto. O enkratnosti te školjke priča tudi dejstvo, da jo danes kot edino vrsto uvrščamo v družino Lithiotidae in skupaj z vrsto *Cochlearites loppianus* v samostojen podred Lithiotina (po A c c o r s i B e n i n i & B r o g l i o L o r i g a, 1977). Možno povezavo z ostrigami (B ö h m, 1892) sta omenjeni italijanski paleontologinji ovrgli na podlagi dokazov, da so bile lupine prvotno aragonitne, medtem ko imajo ostrige kalcitne lupine. Sistematska uvrstitev rodov *Lithiotis* in *Cochlearites* še ni dokončno rešena. C h i n z e i (1982) meni, da sta taksonomsko blizu naddružini Pteriacea, še posebno družini Isognomonidae.

Na možno istovetnost rodov *Lithiotis* in *Plicatostylus,* slednji je bil kasneje opisan iz Oregona, je opozoril že G r u b i ć (1959 oz. 1961). B u s e r (1965) je to domnevo potrdil s študijem originalnih primerkov, ki sta jih ameriška avtorja Lupher in Packard poslala profesorju Kühnu na Dunaj.

Od drugih litiotidnih školjk lahko vrsto *Lithiotis problematica* ločimo tudi po presekih v trdni kamnini. Ti so vedno enolupinski in imajo v prečnem prerezu eliptično obliko (glej B u s e r & D e b e l j a k, 1996, 36, sl. 9, 10). Posebno značilni so "ušesasti" preseki z odprtino v sredini, po katerih je rod *Lithiotis* dobil svoje ime.

N a h a j a l i š č a: Vrsta *Lithiotis problematica* je med vsemi litiotidnimi školjkami v Sloveniji najredkejša. B u s e r (1965) jo je našel v opuščenem kamnolomu na desnem bregu Sušice zahodno od Dolenjskih Toplic. Na žalost je danes ta kamnolom zasut. Nekaj primerkov je Buser našel tudi na severnem pobočju Mokrca, ko so tam gradili novo cesto. Danes so ti useki preraščeni. Zelo številne primerke še vedno najdemo vzhodno od vasi Zafara pri Žužemberku. Razmeroma dobro ohranjene lupine *L. problematica* je mogoče izluščiti iz apnenca nedaleč od izvira Glijun in na hribu Poljanica zahodno od Bovca. V okrasnem podpeškem kamnu lahko opazujemo značilne preseke te vrste (B u s e r & D e b e l j a k, 1996), vendar školjk *L. problematica* v Podpeči ne moremo izluščiti iz trdnega apnenca.

Lithiotis je v pliensbachiju in toarciju množično poselil obsežne, med seboj povezane plitvomorske predele zahodnega in južnega obrobja Tetide ter vzhodnega Pacifika. Različni avtorji poročajo, da so ga našli v južni Španiji (?), zahodni Franciji (?), severni Italiji, na Apeninih, Hrvaškem (?), v Hercegovini, Črni gori, Albaniji (?), Grčiji, Turčiji (?), Maroku (?), Somaliji (?), Omanu (?), Iranu (?), Iraku (?), na Himalaji (?), na otoku Timor v Indoneziji, v ZDA (Oregon, Nevada, Kalifornija), Čilu in Peruju. Nahajališča, ob katerih je postavljen vprašaj, niso zanesljivo potrjena. Podatki so povzeti po: B r o g l i o L o r i g a in N e r i, 1976; A c c o r s i B e n i n i in B r o g l i o L o r i g a, 1977; G e y e r, 1977; N a u s s in S m i t h, 1988; B u s e r in D e b e l j a k, 1996.

Familia C o c h l e a r i t i d a e Accorsi Benini & Broglio Loriga, 1977
Genus *Cochlearites* Reis, 1903

Cochlearites loppianus (Tausch, 1890)
Tab. 3, sl. 1-3

M a t e r i a l: Okoli 80 primerkov. Večidel so to do 10 cm veliki kosi levih lupin; desnih lupin je manj. Deset primerkov ima delno ohranjeni obe lupini. Vrh lupine in bivalna votlina nista ohranjeni pri nobenem primerku. Na šestih lupinah je vidna ligamentna brazda.

O p i s v r s t e: Lupina je ozka, močno dorzo-ventralno razpotegnjena in ima koničast vrh. Odrasli primerki merijo v višino od približno 20 do več kot 50 cm; široki so povprečno 5 do 8 cm. Z levo lupino se je žival pritrdila na stabilno podlago; debela je približno 1 do 2 cm. Desna lupina, ki je bila prosta, je tanjša od leve; v sredini meri okoli 0.5 do 1 cm. Školjka je ponavadi ravna, lahko pa je tudi upognjena vstran (tab. 3, sl. 2). Na grobi, nepravilni zunanji površini včasih opazimo koncentrične prirastnice.

Obliko in notranjost lupine ponazarja slika 2. Notranja stran lupine ima za litiotidne školjke značilno tridelno zgradbo. Osrednje polje je široko okoli 2 do 4 cm, omejujeta pa ga peresasti polji. Peresast videz ustvarjajo prirastnice, ki se lahko združujejo v snope. Na obrobju peresastih polj sta lupini običajno zevali. Bivalni del školjke je bil v primerjavi s celotno velikostjo lupine zelo majhen. Osrednje oz. glavno polje, kjer se lupini tesno stikata, je reliefno oblikovano. Po sredini leve lupine poteka bolj ali manj široka globel, ki jo omejujeta dva grebena. Vanjo se prilega osrednji

greben desne lupine. Vsi omenjeni reliefi blizu telesne votline poplitvijo in niso več tako izraziti. Na osrednjem polju pogosto opazimo polkrožne sledi; to so prirastnice, ki jih je plaščni rob puščal za seboj, ko se je pomikal v ventralni smeri.

Pod vrhom, približno po sredini glavnega polja obeh lupin, poteka globoka, ozka brazda (resilifer), v kateri je imel sedež vlaknati oziroma fibrozni del ligamenta. Lamelarni del ligamenta se je pritrjal ob straneh te brazde. Ligamentna brazda je pri različnih osebkih različno visoka. Ponavadi meri od 3 do 6 cm.

Slovenski primerki imajo večinoma prekristaljene lupine, med fosilizacijo pa so se deli s prvotno različno mikrostrukturo selektivno obarvali, tako da se v presekih pogosto razločijo značilne poteze osnovne zgradbe lupine (B u s e r I., 1989, tab. 10; cf. C h i n z e i, 1982).

P r i m e r j a v a: Iz kamnine izluščeni primerki rodu *Cochlearites* so tako značilni, da jih ne moremo zamenjati z nobeno drugo školjko. Do zamenjave lahko pride, če skušamo ugotoviti vrsto le po presekih v kamnini. Ti so lahko precej podobni presekom vrste *Lithioperna scutata*. A pri rodu *Cochlearites* je leva lupina debelejša od desne, medtem ko ima *Lithioperna* obe lupini enako debeli. Običajno se lupini rodu Lithioperna ob vseh robovih tesno prilegata; ena lupina kot negativ sledi drugi. Pri rodu *Cochlearites* lupini na obrobju peresastih polj večinoma zevata. Najbolj značilni in nedvoumni pa so prečni preseki z značilnim osrednjim grebenom v desni in z ustrezno vboklino v levi lupini (B u s e r & D e b e l j a k, 1996, 32- sl. 4, 41- sl. 15).

Posamezni primerki vrste *Cochlearites loppianus* se lahko med seboj precej razlikujejo tako po obliki kakor po velikosti lupine. Takšne variacije so nastale zaradi stalnega prilagajanja okolju in zaradi rasti v tesnih združbah. Praktično niti dva primerka nimata enakega osrednjega polja. Glede na videz ligamentne brazde je R e i s (1903) ločil tri tipe rodu *Cochlearites*. A c c o r s i B e n i n i in B r o g l i o L o r i g a (1977) sta priznali le dva tipa. Normalni tip naj bi bil tisti, pri katerem je ligament imel zvezo s plaščem, nenormalni tip (forma A) pa naj bi imel kratek, zakrnel vlaknati ligament, ki ni imel več povezave z živim delom školjke, kar lahko ugotovimo po odmaknjenih plaščevih prirastnicah. C h i n z e i (1982, 193) je dokazal, da praktično vsi odrasli osebki pripadajo nenormalnemu tipu oziroma formi A, kar je posledica tega, da je ligament pri rasti školjke prej ko slej zakrnel. S to ugotovitvijo odpadejo razmišljanja o različnih tipih ali celo podvrstah glede na videz ligamentnega polja.

Sistematska uvrstitev rodov *Lithiotis* in *Cochlearites* še ni dokončno rešena, prav tako ni pojasnjena njuna morebitna sorodnost.

N a h a j a l i š č a: B u s e r (1965) je najlepše primerke našel jugozahodno od Loža in na severnem in južnem pobočju Mokrca. Danes so ta nahajališča zaraščena. Posamezne primerke še vedno dobimo pri izviru Globočec zahodno od Zagradca in na hribu Stražišče vzhodno od Gorenjega Jezera pri Cerknici. Vrsta *Cochlearites loppianus* zagotovo nastopa tudi v podpeškem kamnolomu, v okolici Grčarevca pri Logatcu, pri Borovcu na Kočevskem in na Travni gori, kajti v teh nahajališčih smo opazili značilne preseke v apnencu oziroma dolomitu.

Drugod v svetu so vrsto *C. loppianus* našli v severni Italiji, Apeninih, Črni gori, Grčiji in Maroku. Morda nastopa tudi v zahodni Franciji, Somaliji in na otoku Timor v Indoneziji. (Po: B r o g l i o L o r i g a & N e r i, 1976; A c c o r s i B e n i n i & B r o g l i o L o r i g a, 1977; G e y e r, 1977; B u s e r & D e b e l j a k, 1996.)

Subordo **Pteriina** Newell, 1965
Superfamilia P t e r i a c e a Gray, 1847

Familia I s o g n o m o n i d a e Woodring, 1925
Genus *Lithioperna* Accorsi Benini, 1979 - syn. *Lithiopedalion* Buser, 1965

Lithioperna scutata (Dubar, 1948)
Tab. 4, sl. 1; tab. 5, sl. 1a, b; tab. 6, sl. 1; tab. 7, sl. 1-3; tab. 8, sl. 1; Tab. 9, sl. 1a, b

M a t e r i a l: Približno 80 primerkov; večina med njimi ima ohranjeni obe lupini. V zbirki prevladujejo fragmenti vrhnjih delov glavnega polja z ligamentnimi brazdami. Obrobni deli v splošnem niso ohranjeni.

O p i s r o d u i n v r s t e: Lupina ima jezičasto obliko in je pogosto izrazito velika. Preseki v apnencu pričajo, da so nekateri osebki dosegli v višino kar 3/4 metra. Obrobni deli lupine so zelo stanjšani, zato nam doslej še ni uspelo najti nepoškodovanega, v celoti ohranjenega primerka. Pri navajanju velikosti smo se zato prisiljeni opirati na preseke v apnencu. V povprečju merijo lupine v višino 30 do 70 cm. Višina je ponavadi približno dvakrat večja od dolžine. Od strani je školjka izrazito sploščena. Obe lupini sta po obliki, velikosti in debelini enaki ter se tesno prilegata. Skupaj sta debeli 1 do 4 cm. Vzdolžni presek ima pogostokrat valovit videz. Zunanja površina lupine je ponavadi vegasta in nepravilna. Pri redkih primerkih pa se na njej vidijo koncentrične prirastnice.

Značilnosti notranjosti lupine ponazarja slika 3. Ob straneh sta razviti ploski peresasti polji z razločno vidnimi prirastnicami. (Prirastnice kažejo nekdanji stranski obris telesne votline, ki se je z rastjo školjke pomikala v ventralni smeri). Sprednje peresasto polje je praviloma večje in velikokrat kolenasto upognjeno. Ob njegovem notranjem robu poteka bisusna zajeda. Pod vrhom je oblikovana kot bisusna brazda, proti bivalnemu delu lupine pa jo omejujeta sprednji obrobni gubi oziroma obrobni liniji. Med njima je v desni lupini bolj ali manj izrazit širok greben, v levi lupini pa ustrezna poglobitev, ki je lahko plitva (tab. 5) ali precej globoka (tab. 6).

Med stranskima peresastima poljema je gladko, bolj ali manj ravno osrednje polje, ki zavzema največji del notranjosti lupine. Po tej površini se je raztezal školjkin plašč in tu sta se lupini tesno stikali. Pod vrhom je razvito značilno ligamentno polje z ravnim oziroma redkeje polkrožnim zgornjim robom. Ligament je bil večvezen. Vlaknati ali fibrozni del ligamenta se je pritrjal v več ligamentnih brazdah, med katerimi je imel sedež lamelarni del ligamenta. Z rastjo školjke se je ligament selil v ventralni smeri in puščal za sabo drobne prirastnice, ki so v brazdah upognjene konveksno glede na vrh, med brazdami pa so konkavne. Ligamentne brazde so običajno približno vzporedne. Pri nekaterih primerkih pa je med rastjo prišlo do spremembe v legi oziroma težišču lupine in ligament je poslej napredoval v drugi smeri kakor na začetku. Ligamentne brazde včasih potekajo tako izrazito proti sprednjemu delu, da lahko dosežejo sprednje peresasto polje (tab. 7, sl. 2, 3).

Tudi če bisusna zajeda na sprednji strani nekega primerka ni ohranjena, lahko ugotovimo, ali gre za desno ali levo lupino. Mejo med osrednjim in peresastim poljem postavimo navpično. Skoz konce ligamentnih brazd si zamislimo premico. Kot, ki ga oklepa z navpičnico, je na sprednji strani manjši od 90 stopinj, na zadnji pa večji. S tem sta določeni leva in desna lupina.

Gostota ligamentnih brazd je lahko različna. Glede na širino lamelarnega dela ligamenta, to je presledkov med posameznimi ligamentnimi brazdami, ločimo dve

osnovni skupini. Brazde so v obeh skupinah široke 2-3 mm. Razmiki med njimi so v prvi skupini široki 2-3 mm, v drugi pa 8-10 mm. V prvi skupini naštejemo približno 16 brazd na 10 cm sklepnega roba, v drugi pa jih je približno 8. Pri nekaj primerkih je razvidno, da so posamezne ligamentne brazde zaostale v rasti, medtem ko so druge rastle naprej (tab. 7, sl. 2; tab. 9). Sklepamo lahko, da je v drugi skupini približno vsaka druga brazda z vlaknatim ligamentom zakrnela in se je na njeno mesto pritrjal lamelarni del ligamenta. Ligamentne brazde so lahko visoke le nekaj mm pa tja do 8 cm. Od debeline lupine pod vrhom je odvisno, koliko ligamentnega polja se je ohranilo. Debelejša je lupina, daljše so brazde. Večina primerkov pa je pod vrhom močno stanjšana.

Bivalni del školjke z enim mišičnim odtiskom je v primerjavi s celotno velikostjo lupine majhen. Zavzema le ventralni del lupine in deloma prostor med sprednjima obrobnima gubama. Depresija za mehko telo je zelo plitva.

Analiza izredno dobro ohranjenih primerkov iz okolice Verone je pokazala, da so bile lupine rodu *Lithioperna* prvotno aragonitne (Accorsi Benini, 1979, 228). Pri mnogih primerkih iz Slovenije že s prostim očesom opazimo značilno zgradbo lupine, to je menjavanje svetlejših in temnejših lamin oziroma plasti, ki so vzporedne med seboj in z zunanjo površino lupine (Buser I., 1989, tab. 11, sl. 1). Svetle, bleščeče lamine so imele nekoč prizmatsko mikrostrukturo, temnejše, motne plasti pa mikrostrukturo biserne matice (Accorsi Benini, 1979).

Primerjava: Rod *Lithioperna* danes uvrščamo med Isognomonidae. Sklepne zobce pri teh školjkah nadomešča velik večvezni ligament. Accorsi Beninijeva (1979) je pred uvrstitvijo med izognomonide postavila vprašaj, ker je struktura lupine pri vrsti *L. scutata* razvita zelo samosvoje. Med izognomonidami bi lahko z rodom *Lithioperna* primerjali rod *Isognomon* Solander in Lightfoot, 1786 (syn. *Perna* Bruguiére, 1789), pri katerem so se lupine pritrjale na podlago prav tako z bisusom. Vendar, pri rodu *Isognomon* ni velikega osrednjega stičnega polja. Peresasti polji ob straneh nista razviti, lupina je bikonveksna in v strukturi lupine se ne menjavata dve vrsti lamin.

Rod *Lithioperna* lahko spoznamo tudi po presekih v kamnini (Buser & Debeljak, 1996, 32, sl. 4). Značilni preseki so zelo dolgi, tanki in ponavadi rahlo valoviti. Obe lupini sta enako debeli in se na vseh robovih tesno prilegata. Običajno zeva le močno stanjšani bivalni del lupine (slika 3).

Rod *Lithioperna* zaenkrat obsega le vrsto *L. scutata,* čeprav se posamezni primerki med seboj precej razlikujejo. Variacije v razmerjih dimenzij in obliki lupin so izredno številne. Različno je tudi ligamentno polje. Niti dva primerka nista enaka. Vendar, bistveno odstopa le primerek, opisan v nadaljevanju, ki pa ne zadošča za opis nove vrste.

Pripomba: Ime rodu *Lithiopedalion* je postavil Buser (1965) v svoji doktorski disertaciji, in sicer po skupnih značilnostih rodu *Lithiotis* in *Pedalion* Dillwyn, 1817 (star sinonim za rod *Isognomon).* Novi rod in vrsto je predstavil na 42. letnem srečanju Paleontološkega društva v Gradcu (Buser, 1972). Tega dela žal ni objavil na način, kakor to zahtevajo mednarodna pravila, vendar se je ime *Lithiopedalion* vseeno uveljavilo v Sloveniji in se uporabljalo tudi v tuji strokovni literaturi (cf. Bosellini, 1972; Broglio Loriga & Neri, 1976). Z objavo ga je po dolgoletnem sodelovanju prehitela italijanska paleontologinja Accorsi Benini (1979) in opisala rod pod drugim imenom: *Lithioperna.*

Buser (1965) je hkrati z rodom opisal tudi novo vrsto *Lithiopedalion kuehni,* vendar jo je Accorsi Benini (1979) poistovetila z vrsto *Perna scutata,* ki jo je

opisal D u b a r (1948) iz Maroka, ter jo vključila v rod *Lithioperna*. Glede na to, da je Beninijeva preučila originalni material iz Dubarjeve zbirke, moramo zaenkrat verjeti njenim ugotovitvam, da gre za isto vrsto. Vendar avtorja kljub temu meniva, da tri skromne upodobitve slabo ohranjenih primerkov ne kažejo vseh značilnosti tipičnih primerkov iz Slovenije ali severne Italije. Po obliki precej spominjajo na rod *Gervilleioperna* Krumbeck, 1923; predvsem velja to za Dubarjev primerek, ki ga je pri opisu novega rodu kot paralektotip upodobila A c c o r s i B e n i n i (1979, 251, sl. 14). Po opisu in slikah sodeč je sprednje peresasto polje razvito kot lunula, bisusna zajeda je zelo globoka in se kmalu pod vrhom razširi in poglobi v telesno votlino. Naši in italijanski primerki imajo precej bolj dorzoventralno razpotegnjeno lupino, višje ligamentno polje, večinoma plitvejšo bisusno zajedo in predvsem večje osrednje polje, kjer sta se lupini tesno stikali. V bodočnosti bi bilo vsekakor dobro opraviti revizijo vrste *Lithioperna scutata* na originalnem Dubarjevem materialu, ki je sedaj v Franciji (Lille).

N a h a j a l i š č a: V litiotidnem horizontu srednjeliasnih plasti v Sloveniji (Trnovski gozd, Hrušica, Nanos, Logaška planota, Krimsko-Mokrško hribovje, Dolenjska) je *Lithioperna scutata* najpogostnejša vrsta, prisotna skorajda na vseh nahajališčih (B u s e r & D e b e l j a k, 1996, 28, sl. 2, v tem članku predstavljena kot *Lithiopedalion scutatus)*. Primerke, ki se dajo izluščiti iz lapornatih plasti med apnencem, danes najdemo na Špiku severno od Cola na Trnovskem gozdu, v kamnolomu v Podpeči ter ob železnici med postajama Preserje in Verd. B u s e r (1965) je našel številne primerke na Krimsko-Mokrškem hribovju; useki takrat narejenih cest pa so danes skoraj docela zaraščeni. Zaraščena so tudi nahajališče na Javorniku in nahajališči severno od Cerknice in južno od Loža. Kamnolom na desnem bregu Sušice zahodno od Dolenjskih Toplic pa je danes zasut.

Drugod po svetu so rod *Lithioperna* našli v liasnih plasteh severne Italije (B e r t i C a v i c c h i et al., 1971; B r o g l i o L o r i g a & N e r i, 1976), na Apeninih, v Albaniji, Grčiji, Franciji in Maroku (po A c c o r s i B e n i n i, 1979). R e y (1990; 1997) jo navaja tudi iz jugovzhodne Španije. Ocenjujemo, da je rod *Lithioperna* prisoten še marsikje na obrobju nekdanje Tetide, le da so ga avtorji označili z imenom *Perna* ali *Isognomon*, ponekod pa so ga morda pripisali ostrigam (npr. rodu *Pernostrea* Munier-Chalmas, 1864 z večveznim ligamentom).

? *Lithioperna* sp.
Tab. 10, sl. 1

M a t e r i a l , n a j d i š č e: En sam, slabo ohranjeni primerek z obema lupinama; ohranjeni so le ligamentno polje, del osrednjega stičnega polja in zgornji del bisusne zajede. Primerek je bil najden ob gozdni cesti severno od vrha Mokrec.

O p i s i n p r i m e r j a v a: Na ligamentnem polju so razvite izredno tanke ligamentne brazde, široke okoli en mm. Na 11 cm dolgem sklepnem robu (toliko ga je ohranjenega) lahko naštejemo kar 36 ligamentnih brazd. To je vsaj enkrat več, kakor je običajno za vrsto *Lithioperna scutata*. Gostota in višina ligamentnih brazd (več kot 4 cm) bi lahko ustrezala rodu *Isognomon* oz. podrodu *Hippochaeta* Philippi, 1844, ki pa ga poznamo le iz terciarnih plasti. Toda pri rodu *Isognomon* se pod ligamentom začne bivalna votlina školjke, pri opisanem primerku pa se podobno kot pri vrsti *Lithioperna scutata* ligamentne brazde končujejo na osrednjem, ravnem stičnem polju, kjer sta se lupini tesno prilegali.

Za natančnejšo določitev oziroma za opis nove vrste je primerek preslabo ohranjen.

Način življenja litiotidnih školjk

Na področju sedanje južne Slovenije so v srednjem liasu litiotidne školjke množično uspevale v pretežno mirnem okolju bolj ali manj zaprtega šelfa na Dinarski karbonatni platformi. Posamezne vrste so sestavljale monokolonije v obliki podmorskih trat (biostrome) s posameznimi lečastimi odebelitvami. S severa je bilo čutiti zmeren vpliv pelagiala. Sedimentacija v laguni je bila hitra, substrat na morskem dnu pa je sestavljalo predvsem blato, kar smo ugotovili glede na lastnosti prikamnine v školjčnih lumakelah. Biodiversiteta v takšnih lumakelah je zelo nizka. Do 3/4 metra visoke lupine so školjke lahko gradile le v tropskih ali subtropskih pogojih. Paleogeografske in paleoekološke razmere, ki so pogojevale obstoj značilne školjčne favne, so bile že opisane; prav tako sta bili že opisani razširjenost in razporeditev različnih vrst (B u s e r & D e b e l j a k, 1996).

Sledi opis načina življenja in posebnih prilagoditev pri posameznih rodovih.

Rod *Lithiotis*

Čeprav so ga prvi raziskovalci v Italiji poznali že pred več kot 250 leti, je za paleontologe še danes velika uganka. Iz kamnine izluščeni primerki res ne spominjajo na današnje školjke in prav nič čudno ni, da so jih sprva opisali kot rastlinske ostanke (G ü m b e l, 1871; cf. 1890). Domnevamo, da se je življenje teh školjk razvijalo takole:

Ličinke so sprva plavale oziroma lebdele v vodi, dokler niso našle za pritrditev primernega mesta. Na blatnem morskem dnu so najtrdnejšo podlago predstavljale lupine drugih školjk; ponavadi odrasli osebki rodu *Lithiotis*. Juvenilne školjke so se nanje pritrdile s posebno, lepljivo snovjo, obrnjene tako, da so lahko rastle navpično navzgor. O tem pričajo številni primerki rodu *Lithiotis*, ki imajo na svoji površini pritrjene enako orientirane mlajše osebke (B u s e r, 1965, tab. 8, 9). Tudi po presekih v apnencu lahko opazimo, da so posamezni odrasli primerki dobesedno cementirani eden ob drugega (B u s e r & D e b e l j a k, 1996, sl. 9). C h i n z e i (1982) je menil, da je bilo mesto pritrditve majhno, oziroma da je bila cementacija možna le pri juvenilnih osebkih. Avtorja pa sva na podlagi svojih opazovanj prišla do sklepa, da so te školjke obdržale sposobnost cementiranja vse življenje, tako da je bila konstrukcija njihovih agregatov zelo trdna in so tudi po odmrtju pogosto ostale v življenjskem položaju.

Školjke rodu *Lithiotis* so vsekakor živele v velikih skupinah, si med seboj dajale oporo in se šopasto razraščale (sl. 4). Sedimentacija karbonatnega blata je bila precej hitra, tako da je bila lupina vseskozi zasidrana v njem. Bivalni del se je povečeval le pri mladih osebkih, potem pa je lupina rastla le še v višino, v subvertikalni smeri (cf. G ö h n e r, 1980; C h i n z e i, 1982; C h i n z e i et al., 1982; S e i l a c h e r, 1984). O rastnem vzorcu nam mnogo povedo prirastnice na zunanji površini in peresastih poljih. Združujejo se v snope, ki si pri dobro ohranjenih primerkih sledijo približno na centimeter. C h i n z e i (1982, 189-192) je sklepal, da je šlo za menjavanje obdobij hitrejše in počasnejše rasti; nekakšne letnice torej. S štetjem prirastnic in merjenjem velikosti lupine je prišel do sklepa, da je v približno štiridesetih letih lupina dosegla

višino 50 cm. V vsem tem času se je okoli nje nabiralo blato. Osebke, ki niso dovolj hitro rastli, je blato zasulo. To se je večkrat zgodilo z juvenilnimi primerki, ki si zaradi gneče niso uspeli izboriti življenjskega prostora. Ko se je kak osebek nevarno nagnil, je z nadaljnjo rastjo še vedno lahko popravil svoj položaj. Takšni primerki s kolenasto upognjenimi lupinami so zelo pogosti (tab. 2, sl. 1).

Zanimivo je, da se je pri rodu *Lithiotis* vedno ohranila le debelejša, verjetno desna lupina, to je tista, s katero se je školjka cementirala na podlago. Druga, prosta lupina je morala biti izredno tanka. O njej pričajo le koščki tanke skorje na debelejši lupini. Tudi v trdni kamnini lahko opazimo le enolupinske preseke rodu *Lithiotis*. Med njimi so včasih "razmetane" tanke sledi, ki bi lahko predstavljale polomljene ostanke druge, tanke lupine (B u s e r & D e b e l j a k, 1996, 36). Še danes ne vemo, ali je bila ta lupina enako velika kot debela, tj. pritrjena lupina (R e i s, 1903, 11; C h i n z e i, 1982, 181; S a v a z z i, 1996, 287) ali pa je pokrivala mehko telo školjke le v obliki pokrovčka (L u p h e r & P a c k a r d, 1930; A c c o r s i B e n i n i & B r o g l i o L o r i g a, 1977, 21). Debela, pritrjena lupina je bila pod spodnjim delom brazdastega polja izvotljena. Tu je mehko telo našlo oporo, tako da s svojo težo ni obremenjevalo tanke, proste lupine.

Mehanizem odpiranja in zapiranja lupin še ni docela pojasnjen. Navadno pri školjkah odpira lupini ligament, s tem da deluje kot nasprotje zapiralni mišici. C h i n z e i (1982, 193) je menil, da funkcionalnega ligamenta pri rodu *Lithiotis* sploh ni bilo in da sta se lupini lahko odpirali in zapirali zaradi prožnosti tanjše lupine. Ta naj bi bila upognjena prek spodnjega roba brazdastega polja (v tem primeru bi bil to sklepni rob), kadar je bila zapiralna mišica skrčena. Ko je mišica popustila, se je tanka lupina zravnala in školjka je zazevala. Pri tej hipotezi se lahko vprašamo, kaj (razen blata) je lupini na dorzalnem koncu držalo skupaj, če ligamenta in sklepnih zobcev ni bilo. Velikost školjke je bila zelo velika, bivalni del z zapiralno mišico pa majhen. Če sta bili lupini res enako visoki, bi pri odpiranju zlahka prišlo do zamika lupin in vdora blata. Pri tem je torej res bolj verjetno, da je tanjša lupina oblikovala le nekakšen pokrovček nad bivalnim delom debelejše lupine. Tej domnevi pa nasprotuje dejstvo, da najdemo ostanke tanke lupine po vsej višini druge lupine. Morda je tanjša lupina na dorzalnem delu postopoma razpadala in se lomila, medtem ko je školjka rastla v višino in se je bivalni del vse bolj odmikal.

Nerešeno je tudi vprašanje, čemu je služilo osrednje brazdasto polje. Težko je verjeti, da je šlo le za igro narave. Na njem ni nobenih sledi, ki bi jih za sabo pustil plašč. Mehki del školjke na to polje torej ni segal. B ö h m (1892) je celo menil, da so značilne brazde nastale sekundarno, zaradi preperevanja. G ü m b e l (1890, 65) in B u s e r (1965, 18) sta brazdasto polje opisala kot sedež ligamenta. R e i s (1903, 43) je trdil, da je ligament zakrnel in da je nazobčanost brazdastega polja delovala kot nekakšen sklep. Italijanski paleontologinji A c c o r s i B e n i n i in B r o g l i o L o r i g a (1977, 21-24) sta domnevali, da je brazdasto polje le nadgradnja, ki prekriva posebne kanalčke v lupini, kjer so se nahajali tanki priveski plašča - centri kalcifikacije. Brazde naj bi nastale tako, da so se ti kanalčki odpirali navzven. Pred kratkim je S a v a z z i (1996) našel dokaze o prisotnosti ligamenta na osrednjem polju. Menil je, da je bil ligament pri rodu *Lithiotis* aktiven po vsej višini brazdastega polja in ne le na ventralnem oziroma sklepnem robu, kot je to običajno pri školjkah z večveznim ligamentom. Ligamentna struktura naj bi bila pri rodu *Lithiotis* zelo samosvoje razvita. S a v a z z i je ugotovil, da so bila vlakna ligamenta oblikovana in pritrjena tako, da so dopuščala majhne razlike v medsebojni razdalji obeh lupin. S tem se je povečala površina, prek katere se je upognila tanjša prosta lupina, kadar se je školjka zapr-

la. Obremenitev se je tako enakomerneje porazdelila; zmanjšala se je napetost in hkrati možnost, da bi se tanka lupina polomila ali poškodovala. Prosta lupina se je torej po mnenju S a v a z z i j a zapirala z upogibanjem, kakor je ugotovil že C h i n z e i (1982), vendar ne z artikulacijo prek sklepne osi.

C h i n z e i (1982; 1986) je primerjal obliko lupine in način rasti rodov *Lithiotis* in *Cochlearites* z nekaterimi ostrigami, ki so prav tako močno razpotegnjene v višino in živijo, oziroma so živele v vertikalnem položaju na mehkih, blatnih tleh. Rod *Saccostrea* Dollfus & Dautzenberg, 1920, ki živi ob obali vzhodne Afrike, po obliki spominja na rudiste; tanko prosto lupino ima oblikovano kot pokrovček (S t e n z e l, 1971). *Konbostrea* Chinzei, 1986, zgornjekredna ostriga iz severne Japonske, po obliki in razrasti še najbolj spominja na rod *Lithiotis*.

Domnevamo, da je bila vrsta *Lithiotis problematica* pri izbiri habitata zelo izbirčna. Podatki s slovenskih nahajališč kažejo, da je sestavljala monokolonije; zahtevala je samostojen življenjski prostor, ki ga ni delila z drugimi litiotidnimi školjkami in je izključeval tudi večino drugih organizmov (B u s e r & D e b e l j a k, 1996). Rod *Lithiotis* je med litiotidnimi školjkami v Sloveniji najredkejši.

Rod *Cochlearites*

Cochlearites je v litiotidnem horizontu Slovenije zelo pogost, predvsem tam, kjer so se nekoč razprostrirali zatišni deli šelfa.

Lupina rodu *Cochlearites* je rastla podobno kot pri rodu *Lithiotis* (glej prejšnje poglavje). Zaradi ozke in sploščene oblike se je skupaj lahko nagnetla množica istovrstnih primerkov. Življenjski položaj posameznih osebkov je bil navpičen, takšen, kot ga danes na morskem dnu zavzema rod *Pinna* ali leščur. Tudi ta ima lupino zelo podaljšano v višino, vendar se z rastjo veča tudi bivalni del školjke z mehkim telesom. Leščur se lahko z mišičasto nogo sam zakoplje v peščeni ali blatni sediment, nakar se s šopom bisusovih vlaken pritrdi na kakršnokoli trdno podlago, na primer na pokopani kamen (C o x, 1969, N8-N10). Rodova *Cochlearites* in *Lithiotis* se nista mogla sama vkopati, saj je majhno mehko telo zavzemalo le ventralni konec školjke; poleg tega je bila ena lupina nemobilna, vseskozi cementirana na trdno podlago. Pri tem avtorja meniva, da je bila sposobnost cementiranja lupine pri rodu *Cochlearites* mnogo bolj omejena kakor pri rodu *Lithiotis*, zato konstrukcija njihovih združb ni bila tako trdna. Sedimentacija karbonatnega blata, v katerem je bila školjka zasidrana, je bila precej hitra, tako da je imela lupina vseeno dovolj opore. Precej blata so okoli sebe akumulirale tudi školjke same, saj so neprestano filtrirale velike količine kalne vode, v kateri so lebdeli drobci hranilnih snovi. Lahko si predstavljamo, da je moralo biti sedimentacijsko okolje kolikor toliko mirno. Močni valovi in tokovi bi lahko izprali blato, ki je dajalo školjkam oporo, in jih razmetali po morskem dnu, kjer bi bile obsojene na propad.

C h i n z e i (1982, 193) je ugotovil, da je bil ligament rodu *Cochlearites* aktiven le pri zelo mladih osebkih, potem pa je zakrnel in ni imel več povezave s plaščem oziroma z živim delom telesa. Večina školjk ligament potrebuje, ker kot nekakšna vzmet nasprotuje delovanju zapiralne mišice in tako odpira lupini, hkrati pa ju tudi povezuje. Pri rodu *Cochlearites* je reliefno oblikovano glavno polje prevzelo vlogo sklepnih zobcev (ki jih litiotidne školjke nimajo), tako da ni prihajalo do zamika lupin. Večji del lupine je tičal v blatu. Po vsej višini se torej lupina ni smela odpirati, ker bi vanjo vdrlo blato. Na osrednjem polju sta se lupini ves čas tesno stikali, v bivalnem

delu pa nekoliko zevali, zato sta pri rasti ostajali sploščeni in vzporedni. Trdni lupini sta se morda podaljševali v dolge konhiolinske lamele (C h i n z e i, 1982, 194). S pomočjo teh prožnih lamel se je školjka lahko neprodušno zaprla, podobno kot nekatere današnje školjke (cf. S t e n z e l, 1971, N977-978). Ko je zapiralna mišica popustila, so se lamele zravnale in na koncu je zazevala ozka reža. Prožnost ventralnih delov lupin je tako po mnenju C h i n z e i a nadomestila ligament.

Podobno kot pri rodu *Lithiotis* je bilo mehko telo zelo majhno in je vseskozi ostajalo nad ravnijo obdajajočega blata. Skozi ozko režo na ventralnem koncu je školjka verjetno iztegovala plašč. Z njim je lovila in absorbirala snovi, potrebne za gradnjo velike lupine.

Rod *Lithioperna*

Med vsemi litiotidnimi školjkami v Sloveniji je rod *Lithioperna* najpogostejši. Njegove lupine leže v apnencu večidel vzporedno s plastnatostjo. Le redko najdemo plasti s številnimi, navpično orientiranimi preseki, ki nam zgovorno kažejo, kakšna je bila njihova življenjska lega.

Lupine rodu *Lithioperna* so bile prvotno z bisusom pritrjene na podlago, podobno kot pri drugih izognomonidah. Bisusna žleza je izločala posebno snov, ki se je v vodi strdila v bisusne nitke. Bisus je izhajal iz sprednje strani lupine. Sprednje peresasto polje je običajno močneje razvito od zadnjega. Sprednja stran lupine je bila obrnjena proti šibkim tokovom, ki so školjki prinašali hranljive snovi (sl. 5). Pri večini primerkov potekajo ligamentne brazde nekoliko poševno proti sprednjemu robu. Skozi njihove spodnje konce poteka sklepna os. Poševnost sklepnega robu si lahko razložimo tako, da se je zadnja stran lupine bolj pogreznila v mehak sediment kakor sprednja. Sklepni rob je pri tem moral ostati vzporeden s površino substrata, sicer bi pri odpiranju lupine v zadnji del vdrlo blato (sl. 5).

Tako kot vse litiotidne školjke, je tudi rod *Lithioperna* zelo hitro rastel v višino. Učinkovitost bisusa je bila vse manjša in vse težje je držal veliko lupino v navpični legi. Posamezni osebki so se med seboj podpirali, podobno kot knjige na knjižni polici. Poleg tega so bili zasidrani v blatu. Tisti primerki, ki niso imeli dovolj trdne opore, pa so se prej ko slej zvrnili. Ostanek življenja so potem preživeli tako, da so plosko ležali na morskem dnu. A c c o r s i B e n i n i (1979, 245-246) je sklepala, da je lupina lahko prilagajala svojo rast, tako da je ventralni konec lupine z mehkimi deli školjke vedno ostajal nad nivojem blata. Zaradi sprememb v smeri rasti ima školjka značilen valovit videz. Takšna valovitost je dodatno pomagala ohranjati učinkovit medsebojni stik obeh lupin. Velika, ploska lupina je bila na morskem dnu stabilna in ni potonila v mehak sediment. Šibki plimski tokovi so z nje od časa do časa sprali blato. Najbrž so se bile škojke rodu *Lithioperna* sposobne tudi same očistiti, podobno kot to počnejo nekatere ostrige. Z naglim skrčenjem zapiralne mišice iz plaščeve votline izbrizgajo močan curek vode, ki očisti njihovo površino (S t e n z e l, 1971, N1001).

Školjke rodu *Lithioperna* so živele v tako plitvi vodi, da so se od časa do časa morda celo znašle na suhem. V tem primeru se je lupina hermetično zaprla. Prav tako se je zaprla, kadar so na morskem dnu zaradi razpada organske snovi zavladali redukcijski pogoji. V takšnih obdobjih je bila školjka prisiljena dihati anaerobno. To se po mnenju paleontologinje A c c o r s i B e n i n i (1979, 228-242) odraža tudi v mikrostrukturi lupine. V času rasti, ko je lupina zevala, je plašč iz vode absorbiral Ca^{2+} ione in na svoji zunanji površini izločal biserno matico. V obdobjih anaerobnega diha-

nja pa so se v ekstrapalialni tekočini med zunanjo površino plašča in lupino nakopičili kisli produkti, ki so reagirali z lupino. Da bi se nevtralizirala kislost, so se sproščali Ca^{2+} ioni. Pri tem dogajanju je notranja plast lupine, ki je imela prej strukturo biserne matice, prevzela nov psevdoprizmatski videz. To se je večkrat ponovilo, zato se v lupini menjavata dve vrsti lamin oz. plasti z različno mikrostrukturo.

Zaradi velikosti in nagubanosti lupin je bil ligament pri odpiranju školjke močno obremenjen. Vlaknati del ligamenta je bil nameščen v več ligamentnih brazdah. Kadar je bila zapiralna mišica skrčena, so bila vlakna stisnjena, ko pa je popustila, so se vlakna iztegnila kot vzmet. Pri tem sta lupini nekoliko zazevali. Lamelarni del ligamenta, ki se je pritrjal med brazdami, je spajal obe lupini. Zaradi mehanskih obremenitev se je ligament na dorzalnem koncu stalno lomil in uničeval. Ker je bil sestavljen iz organske snovi, so ga napadale tudi bakterije. Aktiven je bil torej le ventralni del ligamenta, ki ga je sproti izločal rob plašča. To se dogaja pri vseh školjkah, ki imajo podoben, to je večvezni tip ligamenta (S t e n z e l, 1979, N971-974). Skupaj z ligamentom se je v ventralni smeri selila tudi sklepna os. Pri nekaterih primerkih so posamezne ligamentne brazde nehale rasti in se je na njihovo mesto pritrjal lamelarni del ligamenta. Verjetno je prišlo do tega zato, ker je školjka nujno potrebovala učinkovit stik obeh lupin. Vlaknati del ligamenta, ki služi za odpiranje, ni bil tako zelo pomemben. Trdni lupini sta na ventralnem koncu tako ali tako večino časa za nekaj milimetrov zevali, zato sta pri rasti ostajali sploščeni in vzporedni ter se nista bočili tako kot pri večini drugih školjk. Iz ventralne reže je *Lithioperna* morda izločala strupeno sluz, da se je ubranila pred morebitnimi sovražniki. Če je bilo potrebno, so odprtino domnevno zaprle tanke prožne luske ali lamele, ki so resasto obrobljale močno stanjšani ventralni rob obeh lupin, podobno kot pri rodovih *Lithiotis* in *Cochlearites*. Morebitne takšne lamele se fosilno niso ohranile, ker so bile slabo kalcificirane in bogate z organsko snovjo (cf. S t e n z e l, 1971, N977). Pri številnih današnjih ostrigah so konhiolinske lamele prosojne, temno rjave do olivne barve, na videz podobne roževini in se že za življenja na starejših delih sproti cepijo in propadajo.

Največji del notranjosti lupine pri rodu *Lithioperna* zavzema osrednje polje. Po vsej tej površini se je razprostiral školjkin plašč. Plašč je tudi dihalni organ, ki razbremenjuje škrge. Iz vode absorbira kisik in kalcijeve ione, potrebne za gradnjo lupine (S t e n z e l, 1971, N999). Povečana površina plašča je rodu Lithioperna povečala dihalno kapaciteto, ki je bila potrebna, da so te školjke tako dobro uspevale in gradile izjemno velike lupine.

Sklep

Cvetoča doba litiotidnih školjk je bila razmeroma kratka. Večidel so izginile na meji med pliensbachijem in toarcijem. Njihovo izumrtje so pospešila obsežna tektonska dogajanja, spremembe v višini vodne gladine ter s tem povezane bistvene spremembe življenjskega prostora in okolja, na kar se visoko specializirani organizmi niso mogli uspešno odzvati (B u s e r & D e b e l j a k, 1996).

Podoben način sesilnega življenja v specifičnem okolju (blatni substrat, hitra sedimentacija) in v gostih združbah ter s tem povezane morfološke posebnosti oziroma prilagoditve, ki so značilne za konvergentne in istodobne rodove *Lithiotis, Cochlearites* in *Lithioperna,* opravičujejo uporabo skupnega imena, čeprav izraz litiotidne školjke nima taksonomskega pomena.

Vsi trije rodovi: *Lithiotis, Cochlearites* in *Lithioperna* se odlikujejo po zelo velikih, nenavadno oblikovanih in močno variabilnih lupinah. Njihova bistvena značilnost je, da so izrazito sploščene in razpotegnjene v višino, to je v smeri rasti, ki je bolj ali manj konstantno napredovala vse življenje. Bivalni del litiotidnih školjk je bil nenavadno majhen; zavzemal je le skrajni ventralni konec sicer zelo velike lupine. Lupini sta se tesno stikali skorajda po vsej površini. Vsem trem rodovom je skupna tridelna notranja zgradba s peresastima poljema ob straneh in z različno oblikovanim osrednjim poljem. Litiotidne školjke so imele med rastjo precejšno sposobnost upogibanja in zvijanja.

Veliko variabilnost litiotidnih školjk lahko pripišemo temu, da se je rast lupine stalno prilagajala spremembam v okolju in tesni skupnosti, v kateri se je nagnetlo na stotine primerkov iste vrste, ki so se med seboj podpirali in se šopasto razraščali - podobno kot rastline v potrebi za sončno svetlobo.

Litiotidne školjke so nedvomno ena najbolj zanimivih in markantnih fosilnih skupin v Sloveniji. Od prvih odkritij (B u s e r, 1965) smo kar predolgo odlašali z njihovo sistematično obdelavo. V pričujočem prispevku je predstavljen tudi njihov način življenja, ki smo ga rekonstruirali s svojimi opažanji in ugotovitvami številnih raziskovalcev z različnih koncev sveta. Odprtih pa je ostalo še veliko vprašanj in v bodočnosti lahko o teh nenavadnih školjkah pričakujemo nove izsledke.

Zahvala

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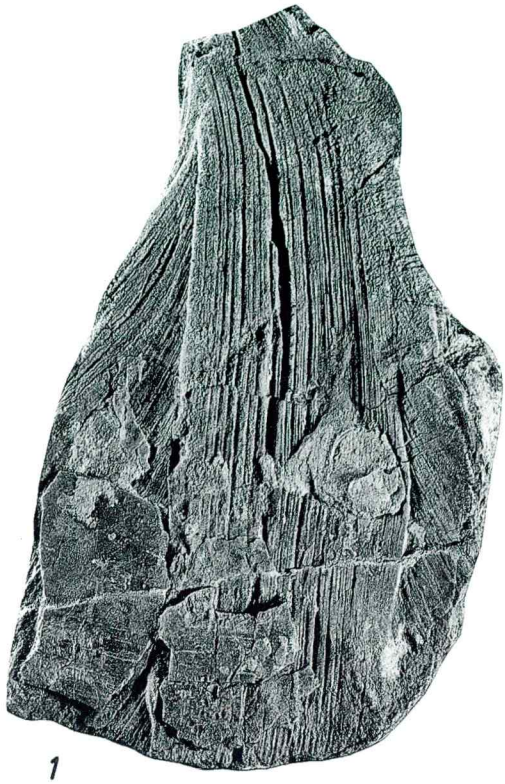
Plate 1

Lithiotis problematica Gümbel, 1871
Natural size
1 Part of the shell near the apex. Fragments of "crust" on the inner surface are remnants of the free, very thin valve. Zafara near Žužemberk
2 Central part of the shell with the long, flat furrowed plate. On some sections larger ridges split into smaller ones. Dolenjske Toplice
3 Fragment of the central part of the shell. Zafara near Žužemberk

Tabla 1

Lithiotis problematica Gümbel, 1871
Naravna velikost
1 Del lupine blizu vrha. Fragmenti "skorje" na notranji površini so ostanki proste, zelo tanke lupine. Zafara pri Žužemberku
2 Osrednji del lupine z dolgim, ravnim brazdastim poljem. Na nekaterih odsekih so večji grebenčki razcepljeni v manjše. Dolenjske Toplice
3 Fragment osrednjega dela lupine. Zafara pri Žužemberku



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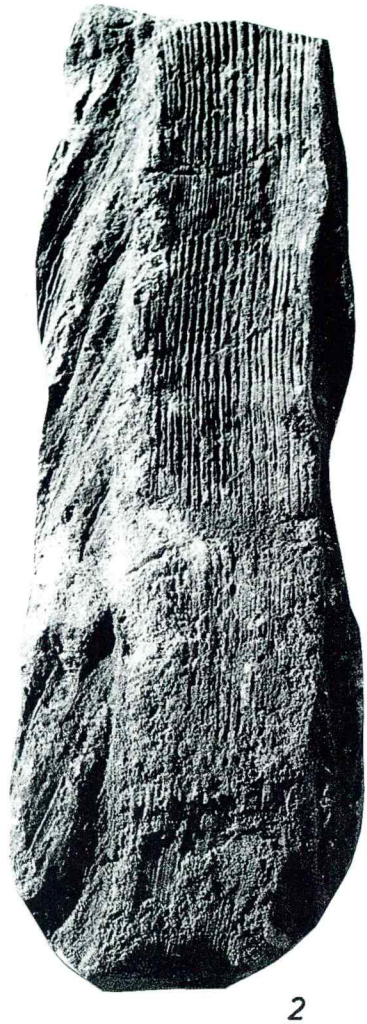

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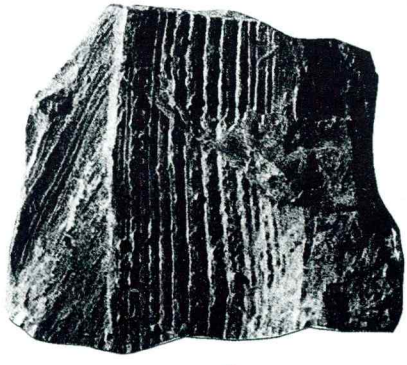

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Plate 2

Lithiotis problematica Gümbel, 1871
Natural size. Dolenjske Toplice
1 Central part of a knee-shaped specimen
2, 3 Two specimens with part of the umbonal cavity

Tabla 2

Lithiotis problematica Gümbel, 1871
Naravna velikost. Dolenjske Toplice
1 Osrednji del kolenasto upognjene lupine
2, 3 Dva primerka z delom telesne oz. umbonalne votline


1
2
3

Plate 3

Cochlearites loppianus (Tausch, 1890)
Natural size. Globočec near Zagradec
1a Fragment of the left valve; inner surface. In the middle is the depression in which the ridge of the right valve fits (fig. *1b*). Fragment of the right valve joins in the lower section
1b Piece of the right valve from the same individual. A prominent ridge runs along the middle of the inner surface
2 Upper part of the left valve; inner surface. The ligament groove is present under the apex. The posterior feather-like area in this specimen is more strongly developed than the anterior
3 Central part of the left valve. Mantle growth lines are visible on the cardinal area

Tabla 3

Cochlearites loppianus (Tausch, 1890)
Naravna velikost. Globočec pri Zagradcu
1a Fragment leve lupine; notranja stran. V sredini je globel, v katero se prilega greben desne lupine (s slike *1b*). V spodnjem delu se je drži fragment desne lupine
1b Košček desne lupine istega osebka. Po sredini notranje površine poteka izrazit greben
2 Zgornji del leve lupine; notranja stran. Pod vrhom poteka ligamentna brazda. Zadnje peresasto polje je pri tem primerku močneje razvito od sprednjega
3 Osrednji del leve lupine. Na glavnem polju se vidijo plaščeve prirastnice


1a
1b
3
2

Plate 4

Lithioperna scutata (Dubar, 1948)
Natural size. Podpeč quarry
1 Left valve; inner side

Tabla 4

Lithioperna scutata (Dubar, 1948)
Naravna velikost. Kamnolom v Podpeči
1 Leva lupina; notranja površina

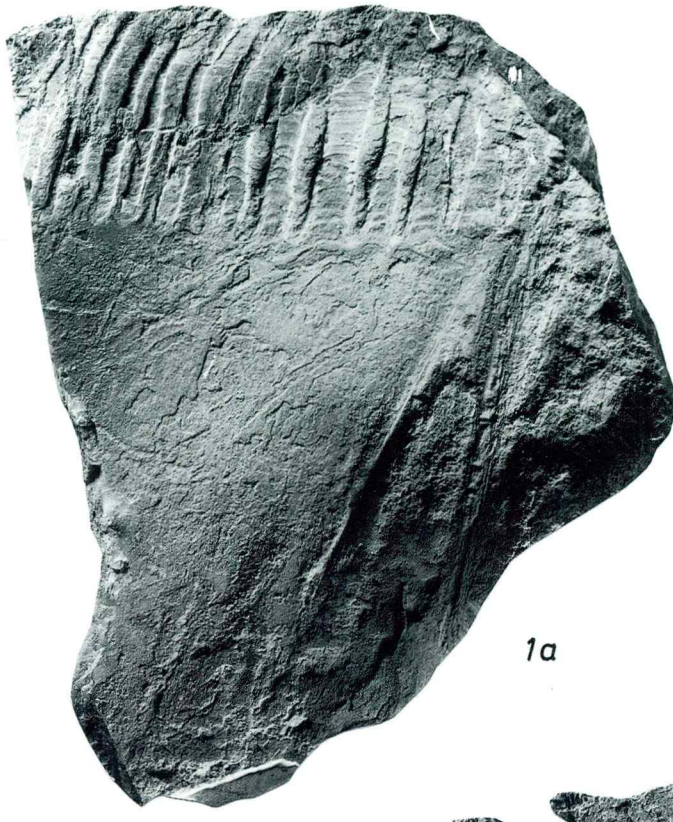

1

Plate 5

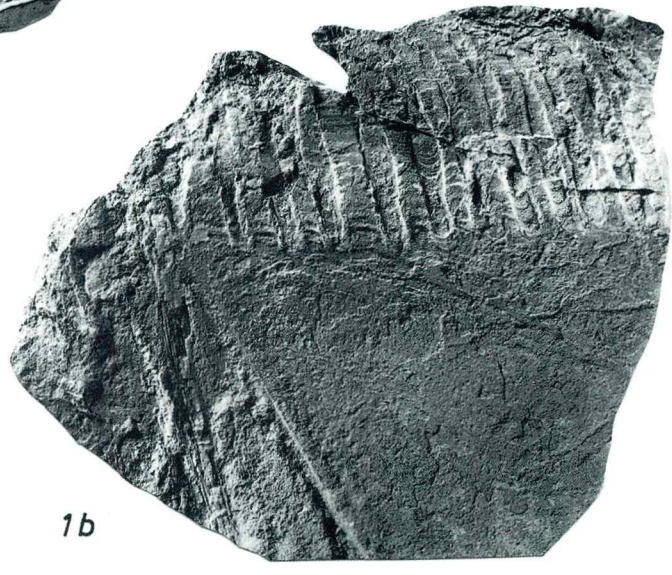
Lithioperna scutata (Dubar, 1948)
Natural size. Javornik
1a Fragment of the left valve; inner side with shallow byssal notch. Growth lines can be clearly seen on the ligament area
1b Corresponding part of the right valve of the same individual

Tabla 5

Lithioperna scutata (Dubar, 1948)
Naravna velikost. Javornik
1a Fragment leve lupine; notranja stran s plitvo bisusno zajedo. Na ligamentnem polju se lepo vidijo prirastnice
1b Ustrezen del desne lupine istega osebka



1a



1b

Plate 6

Lithioperna scutata (Dubar, 1948)
Natural size. Špik in Trnovski gozd
1 Inner surface of the left valve. The anterior feather-like area is knee-shaped. The byssal notch is very deep

Tabla 6

Lithioperna scutata (Dubar, 1948)
Naravna velikost. Špik v Trnovskem gozdu
1 Notranja površina leve lupine. Sprednje peresasto polje je kolenasto upognjeno. Bisusna zajeda je močno poglobljena


1

Plate 7

Lithioperna scutata (Dubar, 1948)
Natural size
1 Fragment of the left valve; inner surface with regularly spaced ligament grooves and a deep byssal notch. Špik in Trnovski gozd
2 Fragment of the right valve; inner surface with somewhat oblique ligament grooves, two of which have lagged during growth. At the side is part of the anterior feather-like area, on which the increments can be clearly seen. Podpeč
3a Fragment of the left valve; inner surface. The ligament grooves are angled towards the anterior feather-like area. Between Borovnica and Verd
3b Corresponding part of the right valve

Tabla 7

Lithioperna scutata (Dubar, 1948)
Naravna velikost
1 Fragment leve lupine; notranja površina z enakomernimi ligamentnimi brazdami in poglobljeno bisusno zajedo. Špik v Trnovskem gozdu
2 Fragment desne lupine; notranja površina z nekoliko poševnimi ligamentnimi brazdami. Dve od njih sta zaostali v rasti. Ob strani je del sprednjega peresastega polja, na katerem se lepo vidijo prirastnice. Podpeč
3a Fragment leve lupine; notranja površina. Ligamentne brazde so usmerjene poševno proti sprednjemu peresastemu polju. Ob železnici Borovnica-Verd
3b Ustrezen del desne lupine

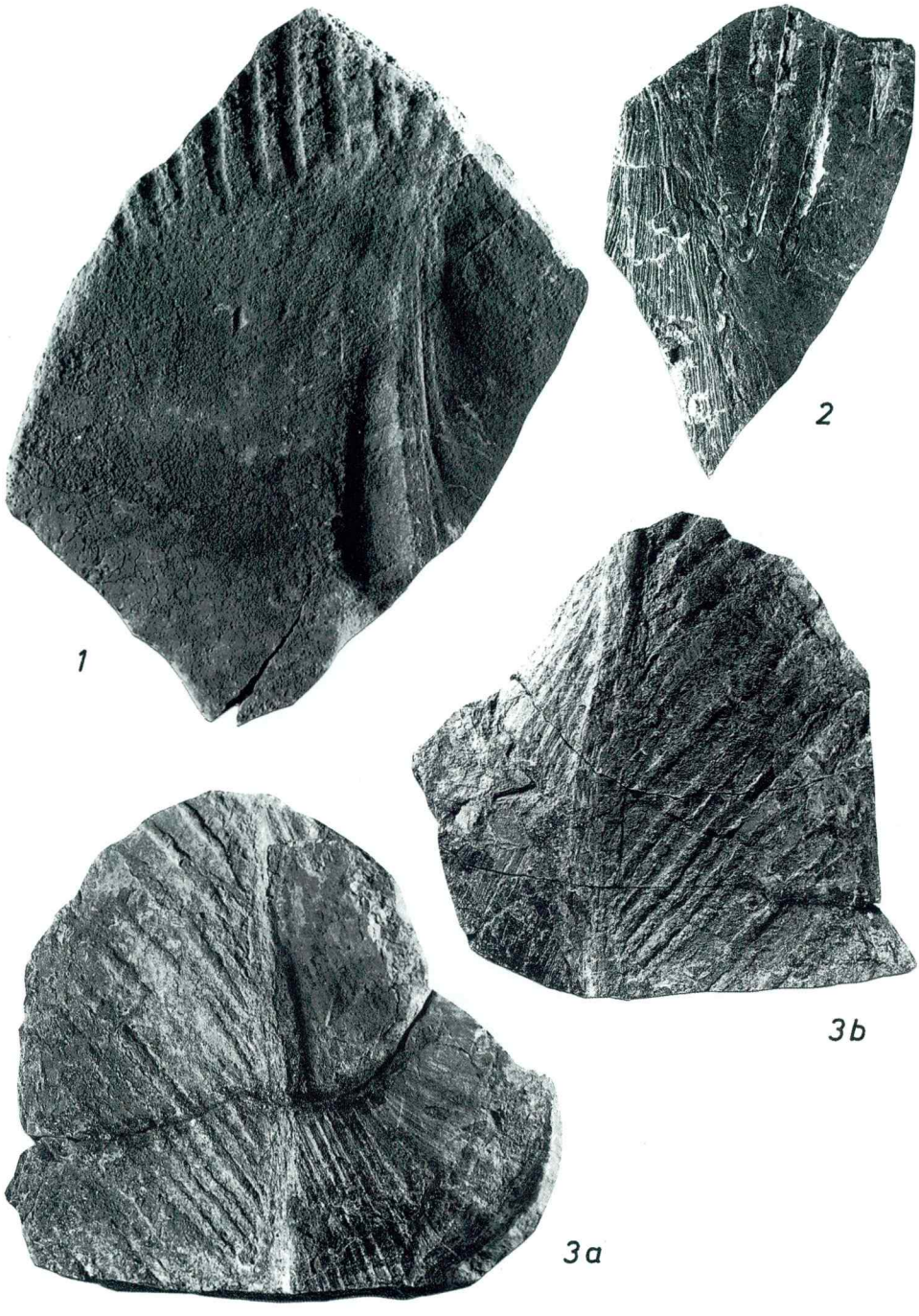

1
2
3b
3a

Plate 8

Lithioperna scutata (Dubar, 1948)
Reduced 0.75×. Podpeč quarry, Slovenia
1 Inner side of the right valve. Only the ventral i.e. body space is missing. Longitudinal traces run from the ligament grooves over the central plate. The anterior feather-like area is more strongly developed than the posterior. Along this is the byssal notch

Tabla 8

Lithioperna scutata (Dubar, 1948)
Pomanjšano 0,75×. Kamnolom v Podpeči
1 Notranja stran desne lupine. Manjka le ventralni, bivalni del. Od ligamentnih brazd po osrednjem polju potekajo vzdolžne sledi. Sprednje peresasto polje je močneje razvito od zadnjega. Ob njem je bisusna zajeda

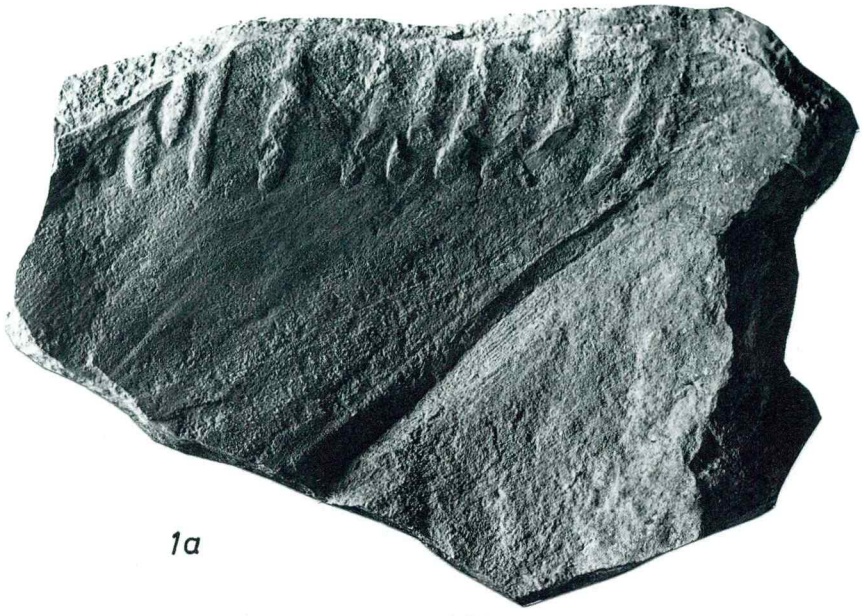

1

Plate 9

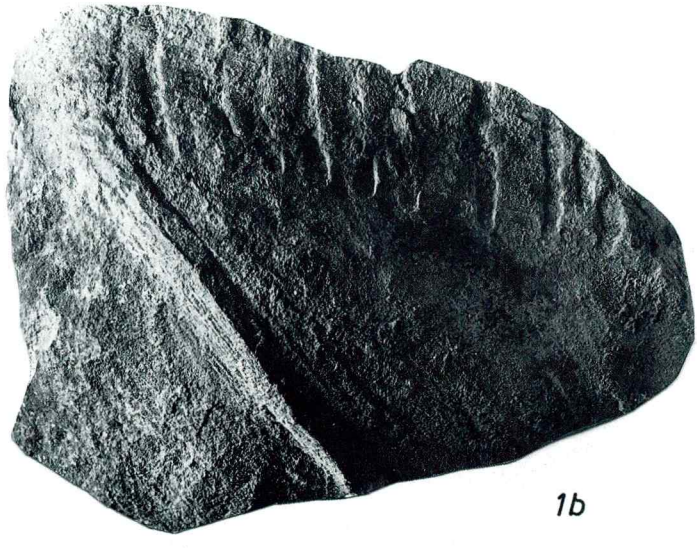
Lithioperna scutata (Dubar, 1948)
Natural size. Špik in Trnovski gozd
1a Fragment of the left valve; inner surface
1b Fragment of the right valve of the same specimen

Tabla 9

Lithioperna scutata (Dubar, 1948)
Naravna velikost. Špik v Trnovskem gozdu
1a Fragment leve lupine; notranja površina
1b Fragment desne lupine istega primerka

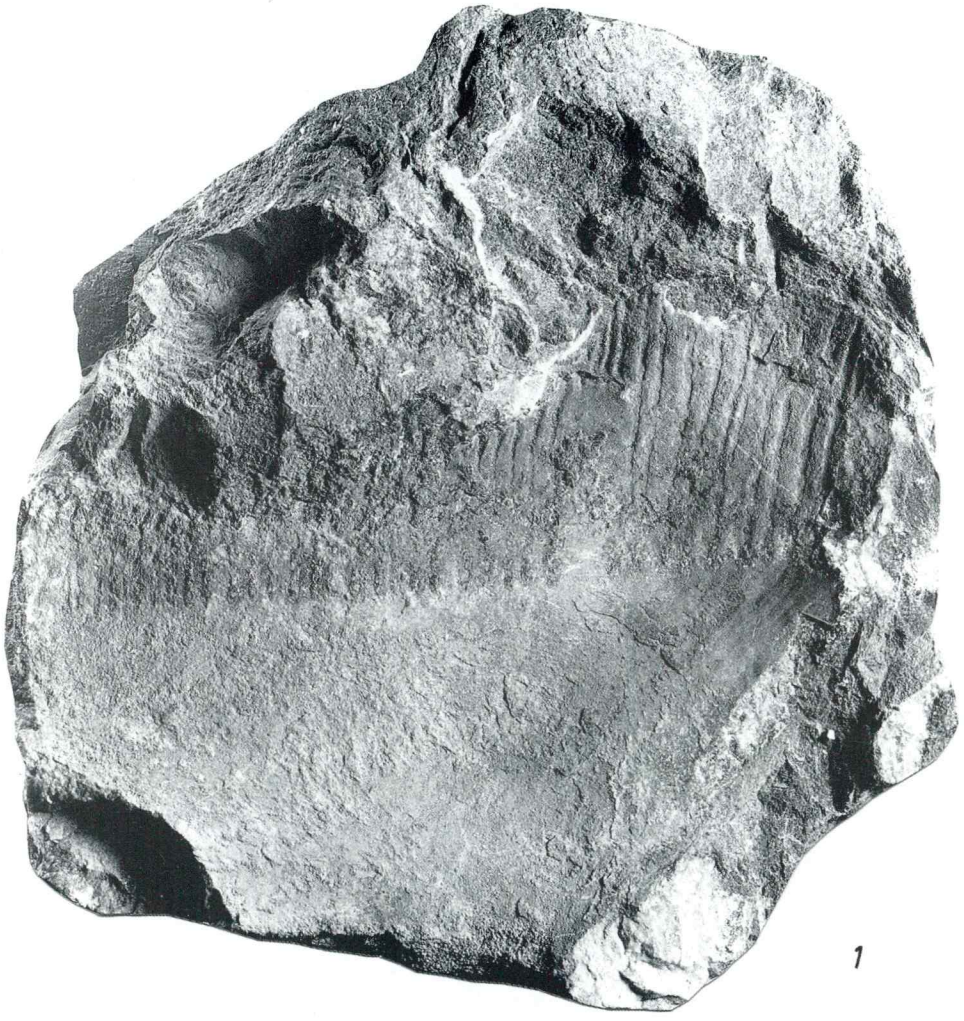


1a



1b

Plate 10 - Tabla 10



? *Lithioperna* sp.
Natural size. Mokrec
1 Left valve of the specimen with very dense ligament grooves

? *Lithioperna* sp.
Naravna velikost. Mokrec
1 Leva lupina primerka z zelo gostimi ligamentnimi brazdami