Ann. Naturhist. Mus. Wien, Serie A	122	165–185	Wien, 31 Jan. 2022

First record of the echinoid genus *Orthopsis* Cotteau, 1864 from the Kössen Formation (Rhaetian, uppermost Triassic) of Vorarlberg (Austria), with description of a new species

Rico Stecher[1]

(with 11 figures and 2 tables)

Manuscript submitted on July 2nd 2019,
the revised manuscript on December 1st 2019.

Abstract

A new species of sea urchin is described from deposits assigned to the Kössen Formation (uppermost Triassic, Rhaetian) of Vorarlberg, Austria. A comparison with other fossil echinoids has shown that the available specimen can be assigned to the genus *Orthopsis*. Moreover, several distinctive features of the material allow it to be described here as a new species, *O. kiseljaki* sp. nov. The new species is the stratigraphically earliest representative of the genus and the first to be recorded from the Triassic, although a considerably higher family level diversity of Echinoidea does not occur until the beginning of the Jurassic Period. The new finding from the Kössen Formation implies that the Rhaetian might be an important time for the diversification of echinoids, particularly with regard to the echinacean *Orthopsis*.

Kewords: Late Triassic, Rhaetian, Echinoidea, Orthopsidae, Lorüns Quarry.

Zusammenfassung

Aus der Kössen-Formation (oberste Trias, Rhaetium) von Vorarlberg, Österreich wird ein neue Seeigel-Spezies beschrieben. Vergleiche mit anderen fossilen Echinoiden zeigen, dass es sich bei den Funden um Vertreter der Gattung *Orthopsis* handelt. Deutliche Unterschiede in den Merkmalen zu anderen *Orthopsis*-Arten legen außerdem nahe, dass hier eine neue Art vorliegt. Diese wird als *Orthopsis kiseljaki* sp. nov. eingeführt und beschrieben. Es handelt sich um den stratigraphisch frühesten Vertreter der Gattung und um den ersten Fund aus der Trias. Viele Seeigel-Familien erscheinen zu Beginn der Jurazeit. Der hier dokumentierte Vertreter lässt jedoch vermuten, dass bereits das Rhaetium ein wichtiger Zeitabschnitt für den Ursprung einiger Echinoiden, insbesondere für die Gattung *Orthopsis*, darstellt.

Schlüsselwörter: Obertrias, Rhaetium, Echinoidea, Orthopsidae, Steinbruch Lorüns.

---

[1] Schellenbergstrasse 13, 7000 Chur, Switzerland; e-mail: ricostecher@yahoo.com

ZooBank LSID: urn:lsid:zoobank.org:pub:645CF346-1360-4B4C-84EB-F7935F9339A7

Introduction

Echinoids are rare in Rhaetian (latest Triassic) fossil record. Until recently, and compared to younger strata, we know few echinoid fossils from this time interval. The following echinoid species have been reported from the Rhaetian and are preserved as complete or fragmentary tests (records of isolated spines, often unidentified, are more common, but not included in the list below).

Stefanini (1924) described *Pseudodiadema silbinense* based on two small tests from Rhaetian sediments named "calacari retici fossiliferi" from Selvena of the Tuscan Appennines mountains near Siena (Italy) with maximum test diameters and heights of 7 and 3.5 mm. The apical system is about 30 % of the test diameter. Unfortunately, the two specimens could neither be located in the collections of the Paleontological Museum of Florence, nor in the collection of the University of Pisa or in the geological collection of the University of Milan (Kier 1977).

Another Rhaetian echinoid is *Diademopsis* ? *desori* Stoppani, 1860–1865, found in the "couche à Avicula Contorta" from Lèzzeno near Como in Lombardy (Italy) of the Southern Alps. Kier (1977) remarked that this was probably a pedinoid, but this cannot be verified anymore as material was lost in 1943 during bombings of World War II (Kier 1977).

Other species, *Diademopsis michelini* Cotteau, 1882 and *Diademopsis micropora* Agassiz, 1841 were recorded from the Rhaetian "calcaires hydrauliques" at Poully in Département Nièvre in the region Bourgogne-Franche-Comté in France (Smith 1990).

Cidaroids of Rhaetian age include *Paracidaris toucasi* from France by Cotteau (1875). According to Kier (1977), this specimen is lost.

Lambert (1924) described a cidaroid echinoid from Rhaetian sediments of the Swiss Helvetian Alps as *Paracidaris jeanneti*. According to Kier (1977), the material could not be located in the former Toucas collection, now the collection of the University of Sorbonne. Other specimens of *Paracidaris jeanneti* were found in the Kössen Beds at Hindelang (Allgäu, Bavaria, Germany) (Smith 1990).

Paracidaris ? *florida* Merian, 1857 has been originally recorded from Rhaetian sediments of the Stockhorn near Thun (Swiss Alps). Other records are from Italy (*Rhaetavicula contorta* Beds of Azzarola and Black Calcarous Schists of Bonzanico) and Switzerland (Neunenenfall, also near Thun in the Swiss Alps) (Smith 1990).

Of the seven echinoid species mentioned above, the type material of three species could not be located, and is definitely destroyed for another species. Therefore, the original illustrations of these species represent the main source of information and were used for comparison with the new material reported herein. Some of these taxa are so poorly known or described that it would be impossible to assign future finds to them with confidence. As a consequence, some of these taxa are herein considered nomina dubia: *Pseudodiadema silbinense* Stefanini 1924, *Diademopsis* ? *desori* Stoppani, 1860–1865, *Paracidaris toucasi* Cotteau, 1875, and *Paracidaris* ? *florida* Merian, 1857.

From the Jurassic and Cretaceous, many different echinoids are known. Among them are representatives of the genus *Orthopsis* COTTEAU, 1864, which comprise about 30 species (FELL & PAWSON 1966). Here, I describe a new echinoid that has features similar to *Orthopsis* COTTEAU, 1864. According to KROH & SMITH (2010), *Orthopsis* is a stem group member of the Echinacea. KIER & LAWSON (1978) listed eight species of *Orthopsis* described between 1924 and 1970. KROH (2010) listed only one additional species described between 1971 and 2008. Additional valid species of *Orthopsis* described earlier are listed alphabetically and by stratigraphic position in Tab. 1. Nominal *Orthopsis* species not classified as *Orthopsis* at present are reported in Tab. 2.

Material and methods

In autumn 2018, Renato KISELJAK (Schruns, Austria) and the author of this paper recorded a number of very small fossil sea urchins in a red slate layer during a field trip at the Lorüns Quarry. During two additional field trips, it was possible to recover more than 100 echinoid tests in the same layer. Some of these are crushed by tectonical force. All sea urchins are more or less complete. Disarticulate plates were not found. Records of spines were very rare. Not all specimens are preserved well enough to show details necessary for study.

For preparation of the small sea urchins, the following techniques were used, sometimes in combination:

- Chemical preparation: potassium hydroxide (KOH).
- Manual preparation: needles under a binocular microscope with up to 32× magnification.
- Mechanical preparation: air chisels and sandblasting tool (calcareous powder) with low pressure about 1.5 bars at maximum.
- Fibreglass eraser (4 mm in diameter).

Tab. 1. Overview of valid species of *Orthopsis* listed alphabetically and by stratigraphic position.

Middle Jurassic:	*O. peroni* COTTEAU, 1885
	O. saemanni WRIGHT, 1855
	O. varusensis COTTEAU, 1885
Upper Jurassic:	*O. pomeraniae* KONGIEL, 1957
	O. willei VADET & WILLE, 2002
Lower Cretaceous:	*O. titicacana* COOKE, 1949
Upper Cretaceous:	*O. grossouvrei* LAMBERT, 1911
	O. haugi LAMBERT, 1922
	O. miliaris (D'ARCHIAC, 1837) [note: D'ARCHIAC (1837) spelt the name *Cidarites milliaris*]
	O. occidentalis CRAGIN, 1893
	O. ruppelli (DESOR, in AGASSIZ & DESOR, 1846)
	O. similis STOLICZKA, 1873

For better visibility of the plate boundaries, glycerine was used to wet the specimen. Sometimes the specimen had to be immersed in glycerine.

Photographs were made by the author with a pocket camera (Olympus Tough) that also provided a stacking function when necessary. SEM images were taken by Andreas KROH with a JEOL JSM-6610 LV scanning electron microscope at the NHMW.

All fossils were deposited in the collection of the Department of Geology & Palaeontology of the Natural History Museum Vienna (NHMW 2019/0187/0001 to 0008 [associated fauna], NHMW 2020/0182/0001 to 0111 [*Orthopsis kiseljaki* sp. nov.]).

Tab. 2. Overview of nominal *Orthopsis* species no more classified as *Orthopsis*.

O. amellagense (LAMBERT, 1937)	After the original description the primary tubercles are crenulated, therefore it is not an *Orthopsis*.
O. microgramma (WRIGHT, 1857)	belongs to *Miorthopsis* POMEL, 1883 [after POMEL (1883)]
O. aguilerai MALDONADO-KOERDELL, 1953	belongs to *Pseudodiadema* DESOR, 1855 [after SMITH & RADER (2009)]
O. bahiaensis BRITO, 1964	*Tetragramma malbosi* BRITO, 1964 [after SMITH & BENGTSON (1991)]
O. carteri (DUNCAN, 1865)	Synonym of *O. miliaris* D'ARCHIAC, 1837 [after JAGT *et al.* (2018)]
O. comalensis WHITNEY & KELLUM, 1966	Synonym of *Parorthopsis repellini* GRAS, 1848 [after SMITH & RADER (2009)]
O. repellini (GRAS, 1848)	belongs to *Parorthopsis* SMITH & RADER, 2009 [after FORNER I VALLS *et al.* (2015)]
O. royoi LAMBERT, 1935	*Parorthopsis royoi* LAMBERT, 1935 [after FORNER I VALLS *et al*. (2015)]
O. australis (WHITE, 1887)	Synonym of O. miliaris D'ARCHIAC, 1837 [after SMITH & BENGTSON (1991)]
O. casanovai COOKE, 1955	Synonym of *O. miliaris* D'ARCHIAC, 1837 [after SMITH & BENGTSON (1991)]
O. charltoni (CRAGIN, 1894)	Synonym of *O. miliaris* D'ARCHIAC, 1837 [after SMITH & BENGTSON (1991)]
O. flouesti COTTEAU, 1867	After POMEL (1883) primary tubercles are crenulated, therefore it is not an *Orthopsis*.
O. granularis (AGASSIZ, in AGASSIZ & DESOR, 1846)	Synonym of *O. miliaris* D'ARCHIAC, 1837 [after SMITH & BENGTSON (1991)]
O. indicus DUNCAN, 1887	Synonym of *O. miliaris* D'ARCHIAC, 1837 [after SMITH (2010)]
O. morgani COTTEAU & GAUTHIER, 1895	Synonym of. *O. miliaris* D'ARCHIAC, 1837 [after SMITH (1995); NÉRAUDEAU *et al.* (1995)]
O. ovata (COQUAND, 1863)	After the original description the primary tubercles are crenulated, therefore it is not an *Orthopsis*.
O. planulata CLARK & TWITCHELL, 1915	Synonym of *O. miliaris* D'ARCHIAC, 1837 [after SMITH & BENGTSON (1991)]
O. sanfilippoi CHECCHIA-RISPOLI, 1933	Synonym of *O. miliaris* D'ARCHIAC, 1837) [after SMITH (1995); NÉRAUDEAU *et al*. (1995)]

Abbreviations

L.C.	Lower Cretaceous
M.J.	Middle Jurassic
MNHN.F.	Muséum National d'Histoire Naturelle (Paris, France)
NHMW	Naturhistorisches Museum Wien (Vienna, Austria)
U.C.	Upper Cretaceous
U.J.	Upper Jurassic
U.T.	Upper Triassic
ZKK-M.	Zirmenkopfkalk Member

Geological Setting

The present echinoid material originates from the Kössen Formation, a unit which is – together with its equivalents – widely distributed across Switzerland, Austria, and Hungary. These well-bedded sediments (limestones, marls, slate) of this formation overlie the Hauptdolomite Formation, representing the uppermost part of the Triassic. According to FELBER *et al.* (2015) the Triassic–Jurassic boundary is positioned between the Schattwald Beds and the Lorüns Oolite, overlying the Kössen Formation. The Kössen Formation is Norian to Rhaetian in age and divided into different members (FURRER 1993): the Alplihorn Member, Schesaplana Member, Ramoz Member, and Zirmenkopfkalk Member (ZKK-M.).

The Lorüns Quarry is located in the western part of the Northern Calcareous Alps, east of Bludenz in the Vorarlberg Region (Fig. 1) and belongs to the Lechtal Nappe of the Bajuvaric Nappe Group (MANDL 2000). At the Lorüns Quarry, sediments of the Cretaceous, Jurassic, and Late Triassic age are exposed. The uppermost part of the Kössen Formation is Rhaetian in age (FURRER 1993). According to MCROBERTS *et al.* (1997), the Kössen Fm. represents a regressive carbonate succession from normal marine conditions in a muddy interplatform basin, separated from the open ocean. From the Kössen Fm., only the "upper" ZKK-M., Ramoz Mb. and the "lower" ZKK-M. are exposed at the Lorüns Quarry (Fig. 2). The ZKK-M. consists of massive limestone beds with corals of the genus *Retiophyllia* EMMRICH, 1853 and a rich bivalve fauna (*Rhaetavicula contorta* PORTLOCK, 1843, *Atreta intusstriata* EMMRICH, 1853, *Gervillaria inflata* SCHAFHÄUTL, 1851, species of *Modiolus* LAMARCK, 1799, *Palaeocardita austriaca* VON HAUER, 1853, *Pinna miliaria* STOPPANI, 1857, species of *Chlamys* RÖDING, 1798, *Neomegalodon triqueter* WULFEN, 1793, species of *Conchodon* STOPPANI, 1860–1865, *Dicerocardium* STOPPANI, 1860–1865) and brachiopods (*Rhaetina gregaria* SUESS, 1854, *Zugmayerella uncinata* SCHAFHÄUTL, 1851, *Zugmayerella koessenensis* ZUGMAYER, 1880, *Austrirhynchia cornigera* SCHAFHÄUTL, 1851). Fish fossils, such as isolated skeletal elements and/or teeth of the genera *Lissodus* BROUGH, 1935, *Sargodon* PLIENINGER, 1847, and *Birgeria*

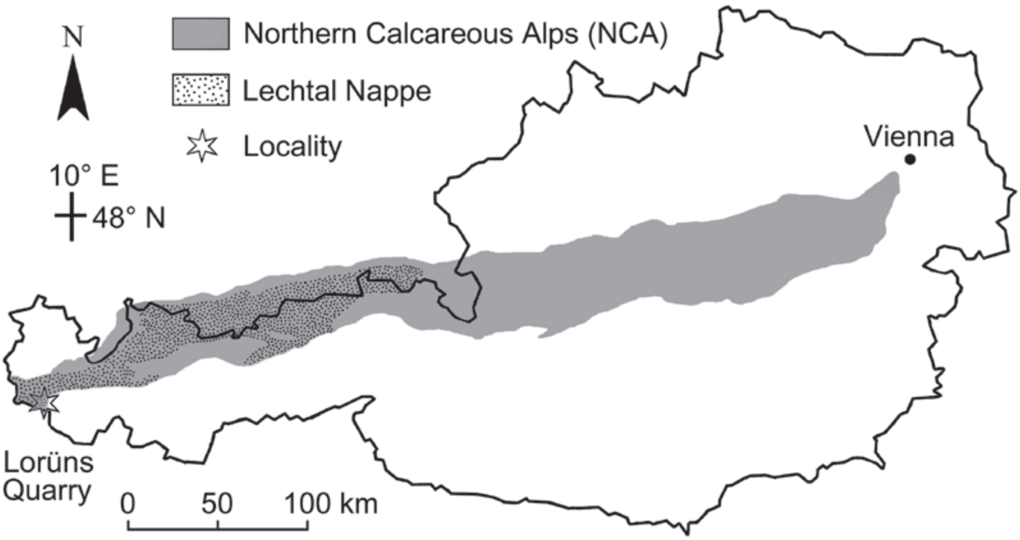


Fig. 1. Schematic map of Austria with tectonic data and the position of the Lorüns Quarry (Vorarlberg, Austria) (modified from STAUB 1923)

STENSIÖ, 1919, scales and teeth of *Paralepidotus* STOLLEY, 1920 and scales of *Gyrolepis* AGASSIZ in ALBERTI, 1834, are common. Reptilian remains, such as teeth of *Psephoderma alpinum* VON MEYER, 1858, are rare. A fish fauna with complete fish skeletons from the upper part of the Ramoz Mb. was described by BÜRGIN & FURRER (2004), comprising *Paralepidotus* STOLLEY, 1920, *Legnonotus* cf. *krambergeri* BARTRAM, 1977, *Pholidophorus* AGASSIZ, 1832, and probably *Caturus* AGASSIZ, 1834. (Fig. 2)

Only three horizons with echinoid tests are currently known. The first of these, a reddish marl with *Paracidaris jeanneti* LAMBERT, 1924, is located about four meters below the level with the fish fauna described by BÜRGIN & FURRER (2004). The two other levels are positioned about 8 meters above these fish-bearing beds.

Systematic palaeontology
(following KROH 2020)

Class Echinoidea LESKE, 1778

lnfraclass Carinacea KROH & SMITH, 2010

Family Orthopsidae DUNCAN, 1889

Genus *Orthopsis* COTTEAU, 1864

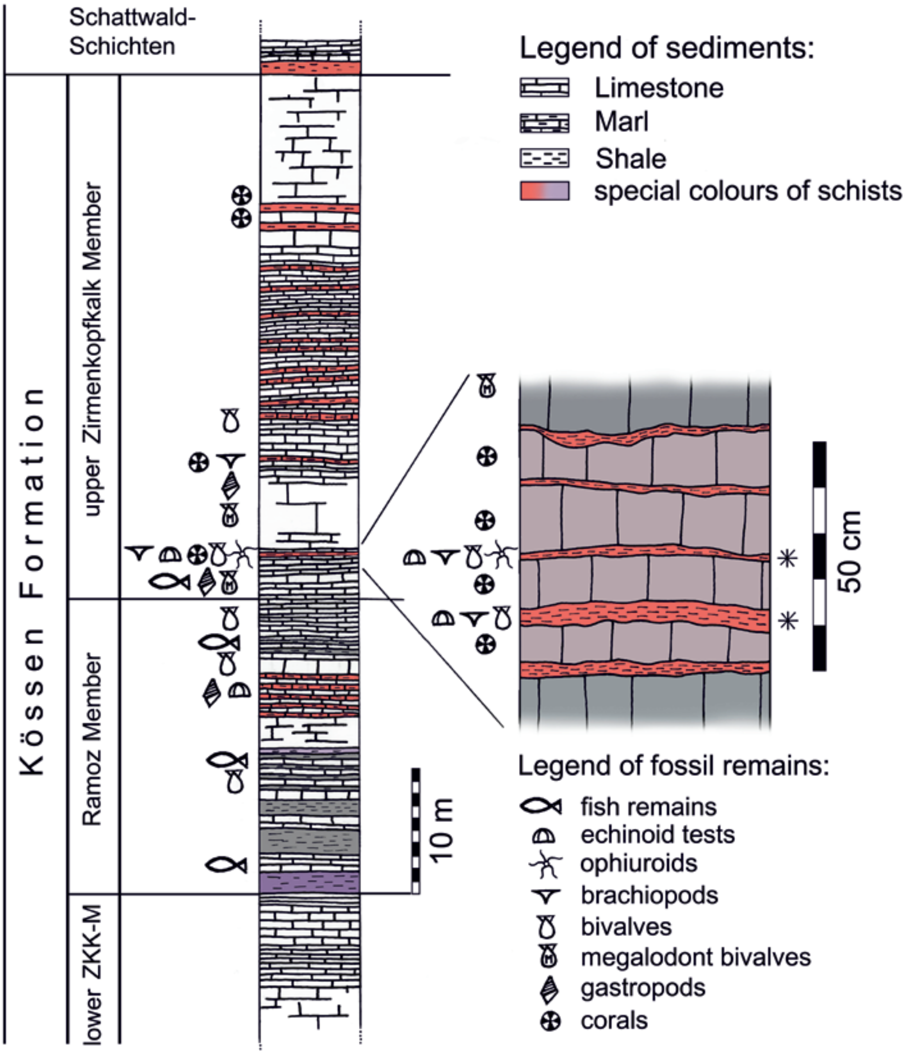


Fig. 2. Simplified stratigraphical log of the section of the Kössen Formation (uppermost Triassic, Rhaetian) at the Lorüns Quarry and detailed log of the echinoid-bearing levels (*).

Orthopsis kiseljaki sp. nov.
(Figs 3, 4, 5, 6, 7, 8, 9, 10)

Etymology – Named after Renato KISELJAK (Schruns, Vorarlberg, Austria) in honour of his collecting at the Lorüns Quarry over recent years.

Diagnosis – A small species of *Orthopsis* typically not exceeding 12.2 mm in test diameter, average test diameter about 6.4 mm. Test shapes range from hemispherical to slightly depressed, the lower side nearly flat. Dicyclic apical disc diameter about 35 % of

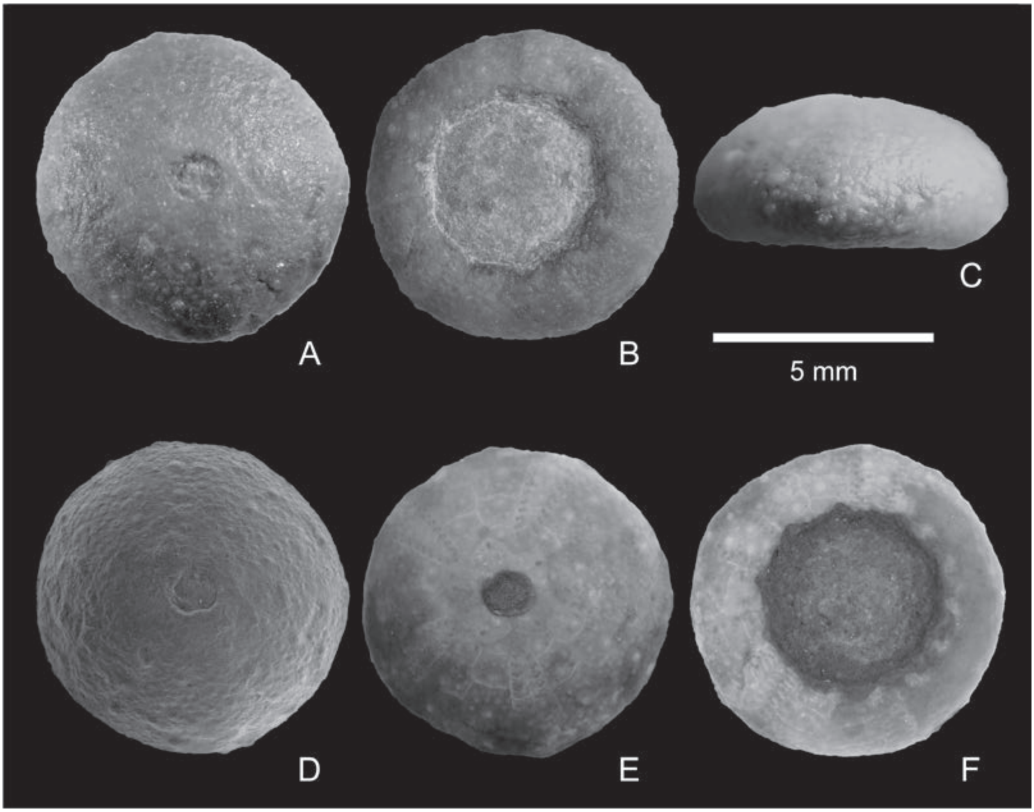


Fig. 3. *Orthopsis kiseljaki* sp. nov. (Holotype, NHMW 2020/0182/0008) in adapical (A, D, E), adoral (B, F) and lateral (C) views. In dry condition (A–C). SEM image (D). Photographed in glycerin bath (E, F).

the test diameter, small circular to subcircular periproct between 14 and 16 % of the test diameter. Simple plated ambulacra with primary tubercles on each third plate, uniserial pore-pairs. Primary tubercles placed in lower half of interambulacral element near edge. Perforated and non-crenulate primary tubercles flanked more or less irregularly by secondary tubercles and granules. Large peristome, about 60 % of test diameter with well developed buccal notches.

Type material – as holotype (NHMW 2020/0182/0008), the author designates a large sea urchin with characteristic features. Paratypes: (NHMW 2020/0182/0003, …/0009, …/0013, …/0111) helped to further ascertain details of the new species.

Additional material – In addition to the type material, the other 106 specimens were used to make a statement about their size (NHMW 2020/0182/0001, …/0002, …/0004 to …/0006, …/0007, …/0010 to …/0012, …/0014 to …/0110).

Locality – Austria, Vorarlberg, Lorüns, HOLCIM Quarry (coordinates: N 47°08.274′ / E 009°50.975′ at 618 (±5) metres above sea level)

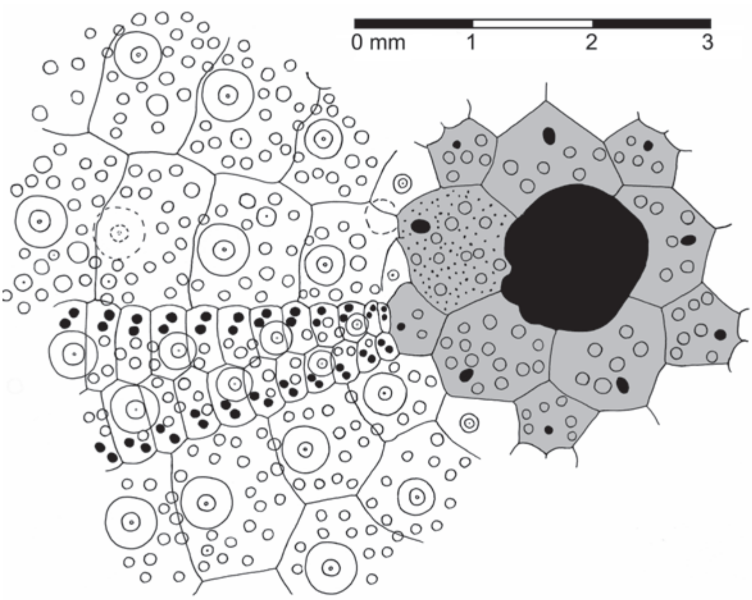


Fig. 4: Line drawing of the apical system and the aboral portion of ambulacrum III, and interambulacra 2 and 3 of holotype of *Orthopsis kiseljaki* sp. nov. (NHMW 2020/0182/0008).

S t r a t i g r a p h i c o c c u r r e n c e – Kössen Formation (uppermost Triassic, Rhaetian), Zirmenkopfkalk Member.

D e s c r i p t i o n o f t h e h o l o t y p e NHMW 2020/0182/0008: Test: Diameter 7.4 mm. Ambitus circular to weakly sub-pentagonal; shape regularly hemispherical with a rounded margin; the lower side nearly flat; height 48 % of test diameter, maximum height at central part of test.

Apical disc dicyclic, more or less firmly bound to corona, diameter about 34 % test diameter, approximately circular in outline; all five genital plates almost equal in size; each genital plate with single gonopore; all genital plates bear secondary tubercles. Periproct small, 16 % of test diameter.

Ambulacra simple; 24 ambulacral plates in each column; primary tubercle spanning two or three elements; primary tubercles perforate and non-crenulate; areoles never sunken; ambulacral primary tubercles similar in size to those of interambulacral plates; primary ambulacral tubercles on every third plate; central part of primary ambulacral tubercles not placed centrally on element, rather in upper half of element near edge. Pore-pairs with narrow interporal partition, arranged adapically in uniserial column forming a single dense contiguous band, pore-pairs are arranged in arcs of three.

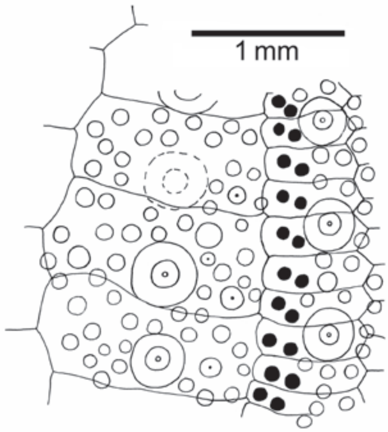


Fig. 5: Ambital ambulacral and interambulacral plates of paratype of *Orthopsis kiseljaki* sp. nov. (NHMW 2020/0182/0008).

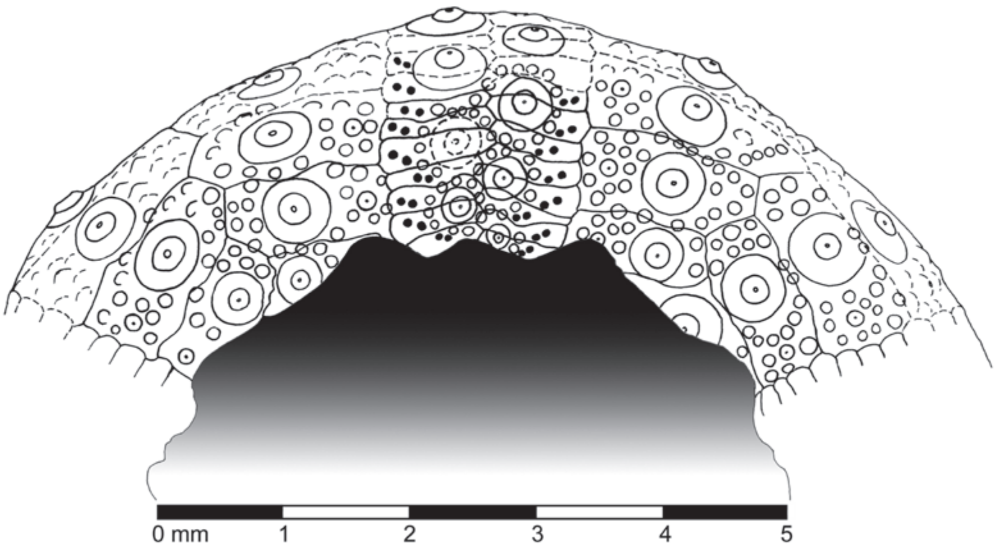
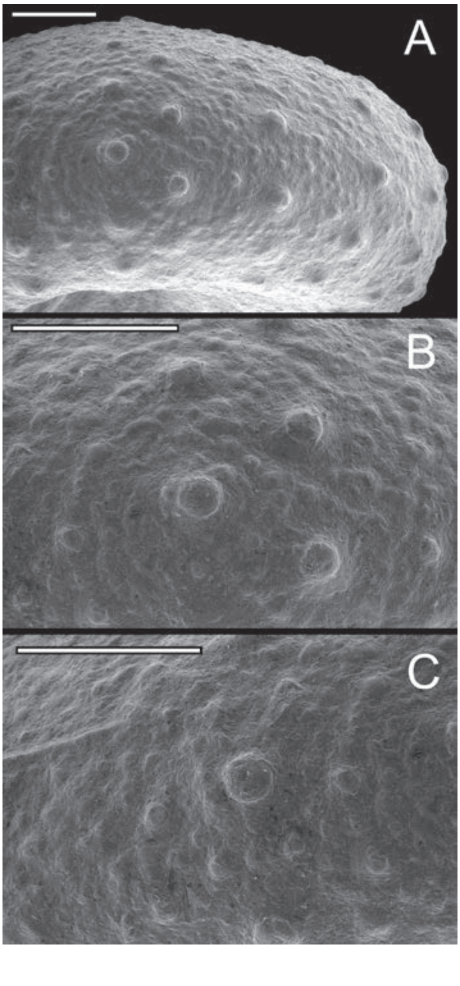


Fig. 6: Adoral view of paratype of *Orthopsis kiseljaki* sp. nov. (NHMW 2020/0182/0111).



Interambulacra: eight interambulacral plates in each vertical column; pair of interambulacral plates bordering peristome; primary interambulacral tubercle flanked more or less irregularly by secondary tubercles and granules; remainder of plate covered by sparse granules; interambulacral primary tubercles perforate, smooth, non-crenulate; primary tubercles not centrally placed on element, but rather in lower half of element near edge.

Peristome large, circular; diameter 60 % of the test diameter; buccal notches present and well developed, giving the peristome a jagged appearance.

Fig. 7: Tuberculation of paratype of *Orthopsis kiseljaki* sp. nov. (NHMW 2020/0182/0003). A: Lateral view of the ambulacral zone (left side) and interambulacral zone (right side). B: Detail of the ambulacral zone with primary tubercles. C: Detail of the interambulacral zone with central primary tubercle, secondary tubercles, and granules. Scale bars of SEM images equal 1 mm.

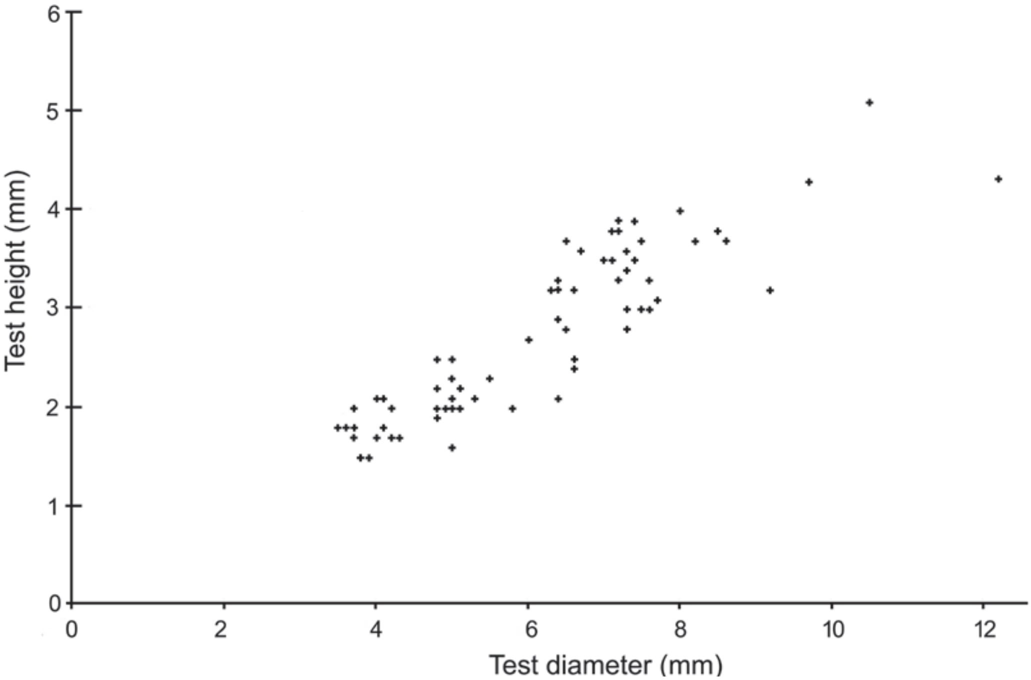


Fig. 8: Relationship between test diameter and height of *Orthopsis kiseljaki* sp. nov. For biometric data, only uncrushed and complete specimens were used.

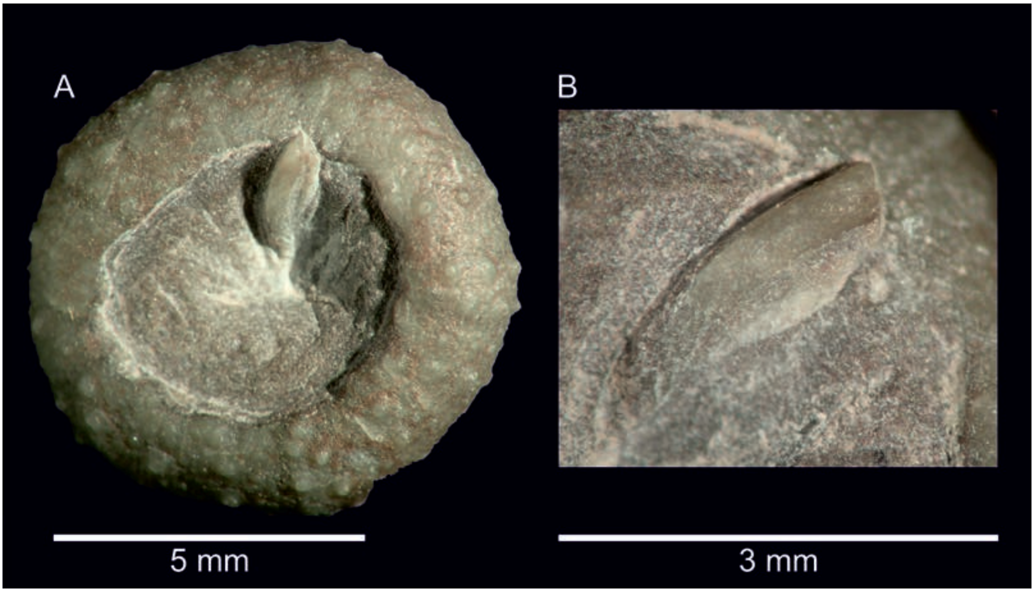


Fig. 9: Paratype of *Orthopsis kiseljaki* sp. nov. (NHMW 2020/0182/0003) in adoral view (A) and detailed view of a part of a hemipyramid (B).

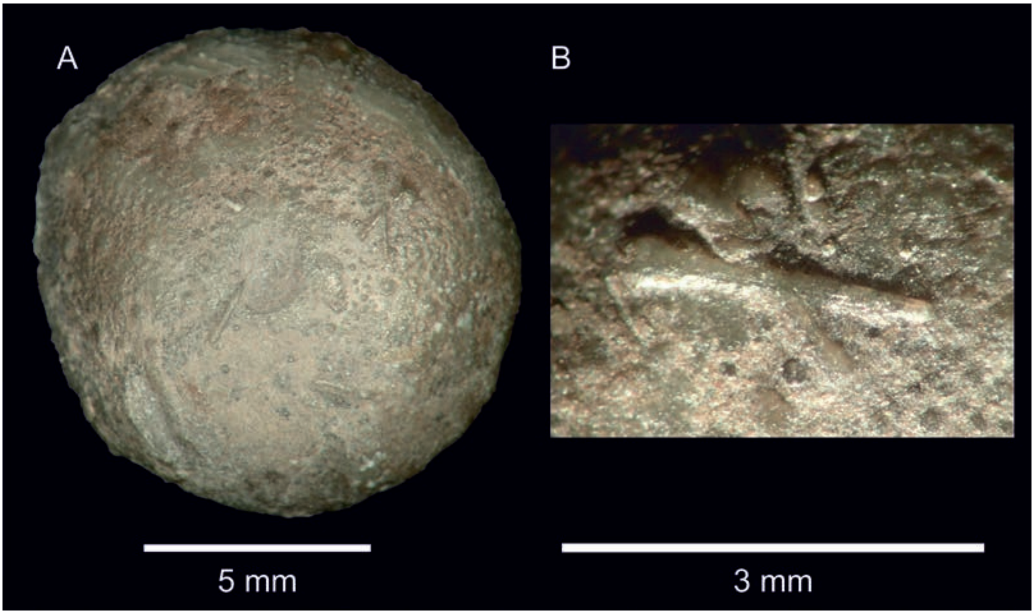


Fig. 10: Spines on the test surface of paratype NHMW 2020/0182/0009 in adapical view (A) and detail of two spines (B).

Lantern and spines not preserved.

Complementary description based on the paratypes:

- Test diameters between 3.7 mm (smallest specimen NHMW 2020/0182/0013) and 12.2 mm (largest specimen NHMW 2020/0182/0009). Average test diameter is about 6.2 mm.
- Average height/test diameter ratio of all uncrushed and complete specimens is about 46 % (NHMW 2020/0182/0111 with 43 %, NHMW 2020/0182/0013 with 49 %).
- Paratype NHMW 2020/0182/0003 shows part of a hemipyramid and peristome with a diameter of 60 % of the test diameter.
- Spines rarely preserved; specimen NHMW 2020/0182/0009 shows five small, fine, simple, cylindrical spines. Kroh & Smith (2010) called this spine type "smooth".

Discussion

Complete echinoid tests are rare in the Rhaetian fossil record. The analysis of the material demonstrates that the new echinoid is a member of the genus *Orthopsis* Cotteau, 1864. Kroh & Smith (2010) listed the following characteristics in the data matrix (Appendix 2) of this genus:

- small and dicyclic apical disc
- plating of the apical disc firmly bound to corona
- ambulacra narrow in acrosaleniid (KROH & SMITH 2010) or trigeminate style (FELL & PAWSON 1966)
- primary tubercles overlap two or three of three elements of the ambulacral plates
- pore-pairs uniserial or with every third pore-pair insert
- large primary tubercle on the interambulacral element flanked by secondary tubercles
- remainder of plate covered in sparse granules
- primary tubercles perforate and non-crenulate
- areole never sunken
- primary tubercles on interambulacral and ambulacral plates similar in size
- large peristome with buccal notches
- spines simple and cylindrical

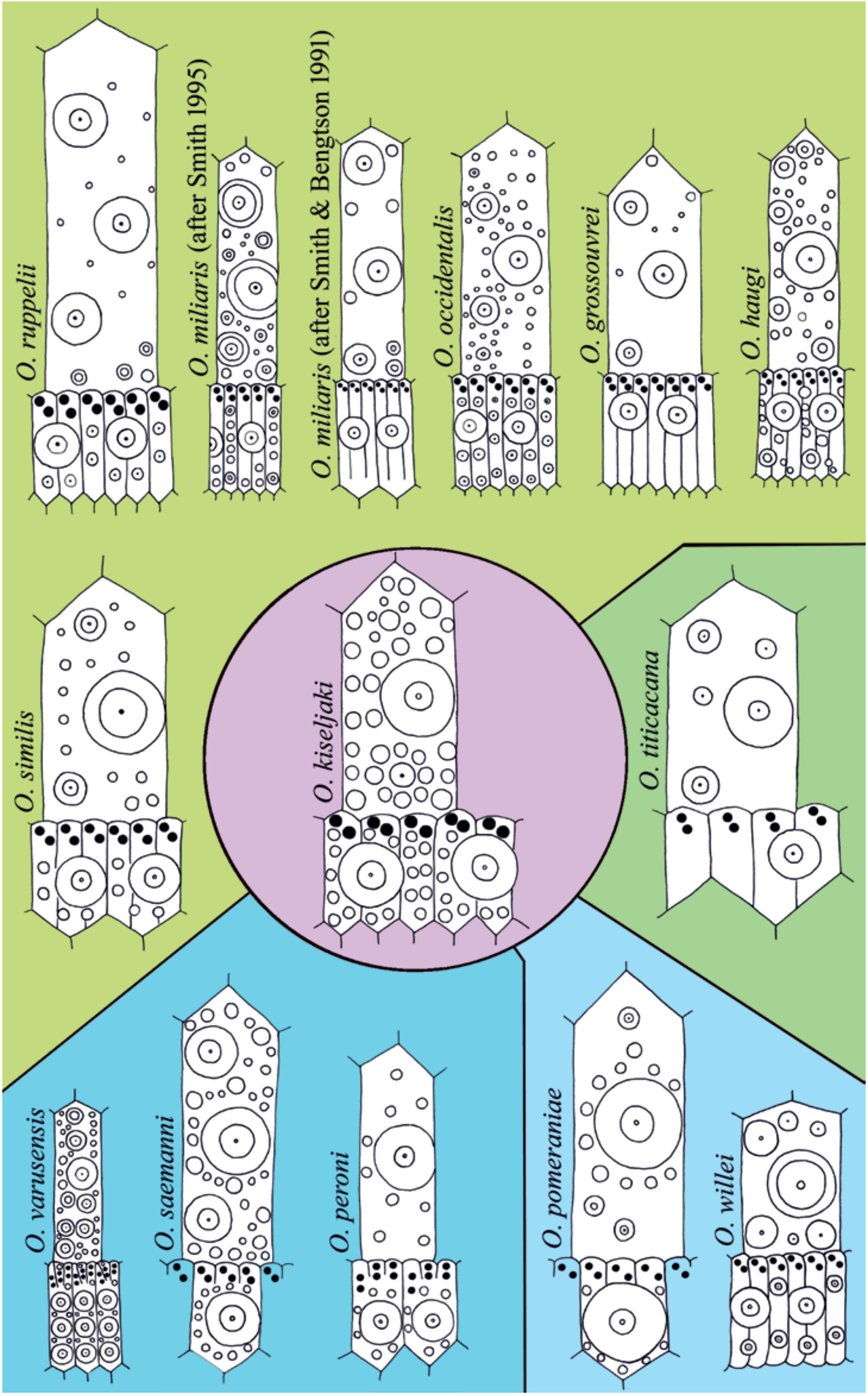
Orthopsis kiseljaki sp. nov. reveals clear differences from other known species of the genus *Orthopsis* in test diameter, shape, and tuberculation (number, size, arrangement, and distribution of primary and secondary tubercles, and granules). There are also significant differences among the species in relation to the ambulacral plate patterns. In view of the fact that this paper is not intended to be a revision of the genus *Orthopsis*, the author lists a faunal composition by interval (Fig. 11) for all *Orthopsis* species that differ from the new taxon.

Two diagnostic test features have been studied in more detail: firstly, the ambulacral plate compounding and secondly the ratio of the number of pore-pairs to one interambulacral plate. The following list shows the kind of ambulacral plate compounding in two groups in general:

- Trigeminate echinoid plating (three ambulacral elements are united to one ambulacral plate with three pore-pairs): *O. varusensis*, *O. saemanni*, *O. peroni*, *O. pomeraniae*, *O. titicacana*, *O. similis*, and *O. miliaris* (compare SMITH & BENGTSON 1991)
- Simple ambulacral plating (each ambulacral element is a single ambulacral plate with one pore-pair): *O. willei*, *O. ruppelli*, *O. occidentalis*, *O. grossouvrei*, *O. haugi*, *O. miliaris* (compare SMITH 1995), and *O. kiseljaki* sp. nov.

Another character is the relation between ambulacral and interambulacral plates, as follows:

- Each interambulacral plate in contact with seven ambulacral elements (seven pore-pairs): *O. varusensis* and *O. grossouvrei*.
- Each interambulacral plate in contact with six ambulacral elements (six pore-pairs): *O. miliaris* (following SMITH & BENGTSON 1991), *O. ruppelli*, *O. similis,* and *O. willei*.
- Each interambulacral plate in contact with five ambulacral elements (five pore-pairs): *O. haugi*, *O. miliaris* (after SMITH 1995), *O. occidentalis, O. peroni*, *O. pomeraniae*, and *O. saemanni*.


O. ruppelii
O. miliaris (after Smith 1995)
O. miliaris (after Smith & Bengtson 1991)
O. occidentalis
O. grossouvrei
O. haugi
O. similis
O. kiseljaki
O. titicacana
O. varusensis
O. saemanni
O. peroni
O. pomeraniae
O. willei

- Each interambulacral plate in contact with four ambulacral elements (four pore-pairs): *O. titicacana* and *O. kiseljaki* sp. nov.

Orthopsis titicacana and *O. kiseljaki* sp. nov. are broadly similar in this feature, but the combination of test features listed above, particularly the trigeminate ambulacral plates (simple in *O. titicacana*), shows that the new species can be differentiated from *O. titicacana* (Fig. 11).

Here follows a comparison of further features of *O. kiseljaki* sp. nov. and other species with simple ambulacral plating of the genus *Orthopsis*:

O. kiseljaki sp. nov. differs from *O. haugi* by the significantly smaller size of the test (12.2 mm test diameter *vs.* 46 mm in *O. haugi*), a significantly larger peristome (60 % of the test diameter *vs.* 40 % in *O. haugi*), and a larger periproct (16 % of the test diameter *vs.* 9 % in *O. haugi*). In addition, *O. haugi* shows no granules (LAMBERT 1922).

O. kiseljaki sp. nov. differs from *O. grossouvrei* in the significantly smaller size of the test (12.2 mm test diameter *vs.* 30 mm in *O. grossouvrei*). By comparison, *O. grossouvrei* has larger, well developed primary tubercles. *O. kiseljaki* is further distinguished from *O. grossouvrei* by its significantly larger peristome (60 % of the test diameter *vs.* 44 % in *O. grossouvrei*) and a larger periproct (16 % of the test diameter *vs.* 9.4–13.5 % in *O. grossouvrei*). (LAMBERT 1911 and after MNHN.F.J00860)

Orthopsis miliaris is after the first description a trigeminate ambulacral plated species. Nevertheless, there are specimens in literature, which are named *O. miliaris*, but show apparently simple ambital ambulacral plating (*e.g.* SMITH 1995: p. 137, fig. 13b). *O. kiseljaki* differs from *O. miliaris* by the significantly smaller size of the test (12.2 mm test diameter *vs.* 48 mm in *O. miliaris*) and by the slightly inflated test. *O. kiseljaki* is distinguished from *O. miliaris* by its significantly larger peristome (60 % of the test diameter *vs.* 36–40 % in *O. miliaris*) and its larger periproct (16 % of the test diameter vs. estimated 10–14 % in *O. miliaris*) (SMITH 1995; D'ARCHIAC 1837).

O. kiseljaki sp. nov. differs from *O. occidentalis* by the significantly smaller size of the test (12.2 mm test diameter *vs.* 57 mm in *O. occidentalis*), by a more inflated test, by a significantly larger peristome (60 % of the test diameter *vs.* 33 % in *O. occidentalis*), and a larger periproct (16 % of the test diameter *vs.* 9.3 % in *O. occidentalis*) (CLARK & TWITCHELL 1915).

◀ Fig. 11: Overview of species of the genus *Orthopsis*, with schematic drawings of ambulacral and interambulacral zones; the width of the ambulacral zones is the same for all drawings. Explanation of colours: violet Triassic, dark blue Middle Jurassic, light blue Upper Jurassic, dark green Lower Cretaceous, light green Upper Cretaceous. *Orthopsis pomeraniae* after KONGIEL (1957); *O. willei* after VADET & WILLE (2002); *O. peroni* after COTTEAU (1885); *O. saemanni* after COTTEAU (1885); *O. varusensis* after COTTEAU (1885); *O. titicacana* after COOKE (1949); *O. similis* after STOLICZKA (1873); *O. ruppelli* after EL-QOT *et al.* (2016); *O. miliaris* after SMITH & BENGTSON (1991) and SMITH (1995); *O. occidentalis* after CLARK & TWITCHELL (1915); *O. grossouvrei* after specimen MNHN.F.J00860; *O. haugi* after specimen MNHN.F.J00881.

O. kiseljaki sp. nov. differs from *O. ruppelli* by the significantly smaller size of the test (12.2 mm test diameter *vs.* 63 mm in *O. ruppelli*), in significantly larger peristome (60% of the test diameter *vs.* 37% in *O. ruppelli*), and a slightly smaller periproct (16 % of the test diameter *vs.* 17% in *O. ruppelli*) (El Qot *et al.* 2016).

O. kiseljaki sp. nov. differs from *O. willei* by the smaller size of the test (12.2 mm test diameter *vs.* 30 mm in *O. willei*), a significantly larger peristome (60% of the test diameter *vs.* 41% in *O. willei*), and a larger periproct (16% of the test diameter *vs.* 19 % in *O. willei*). *O. willei* shows larger, well developed primary tubercles (Vadet & Wille 2002).

O. kiseljaki sp. nov. seems to be the smallest candidate of the genus *Orthopsis* with the largest peristome (60% of the test diameter) and a large periproct (16% of test diameter). Only the trigeminate plated *O. peroni* shows a similar large peristome with 58% of the test diameter (Cotteau 1885). All others have a much smaller peristome ratio. Regarding the periproct ratio, the values are not quit as clear. *O. miliaris* and *O. ruppelli* have slightly different values compared to *O. kiseljaki*. Unlike all *Orthopsis* species listed above, *O. kiseljaki* shows only one big, well developed and one smaller primary tubercle on the interambulacral plate. The large primary tubercle on each third ambulacral element is a common feature in *Orthopsis*. The presence and number of smaller tubercles beside the big primary tubercle is different from species to species (Fig. 11).

Palaeoecology

Records of the coral *Retiophyllia clathrata* Emmrich, 1853 point to a shallow marine environment. According to Tomašových (2006), *Atreta intusstriata* Emmrich, 1853 and *Rhaetina gregaria* Suess, 1854 are indicative of the carbonate interval between normal storm wave base and maximum storm wave base. The rare tests with spines (*e.g.* NHMW 2020/0182/0009) show that the embedding – after a possibly not very long transport after death – was a relatively fast process.

Conclusions

Echinoid fossils in Rhaetian deposits are exceptionally rare. The phylogenetic tree of the class Echinoidea published by Kroh & Smith (2010) shows that the Rhaetian record is still incomplete and that there is a large potential for further research. Therefore, any new discovery is important and might help to fill this gap. This is the case in the Rhaetian with the genus *Orthopsis*. The new discovery from the Kössen Formation suggests that *Orthopsis* is much older than previously assumed and obviously survived the Triassic–Jurassic extinction event.

Acknowledgements

The author is grateful to Renato Kiseljak for years of friendship and countless joint excursions, and thank the HOLCIM Company and the BSL GmbH & Co KG (Brech- und

Siebwerk Lorüns) for repeated access to the Lorüns Quarry, making this research possible. Many thanks to Dr. Andreas KROH (NHMW), Prof. Dr. Christian MEYER (University Basel), Christian OBRIST (Rickenbach, Switzerland), Dr. John W. M. JAGT (Natuurhistorisch Museum Maastricht, Limburg, Netherlands), Iwona PUZNIAK (Geological Library and Museum of Polish Geological Institute, Warszawa) for help accessing the relevant literature. In addition, many thanks are extended to Hendrik KLEIN (Saurierwelt Paläontologisches Museum, Neumarkt, Germany) for the correction of the first English manuscript. Special thanks are due to the reviewers Dr. John W. M. JAGT (Natuurhistorisch Museum Maastricht, Limburg, Netherlands) and Dr. Rich MOOI (California Academy of Sciences, San Francisco, California, USA) for their critical and constructive reviewing the manuscript. Cordial thanks to Dr. Andreas KROH for interesting discussions about anatomical features of echinoids, helpful tips, help in producing SEM images, his role as a manager of the fossil echinoderm collection (NHM Vienna), and his great help as editor.

References

AGASSIZ, L. (1832): Untersuchungen über die fossilen Fische der Lias-Formation. – Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde, **3**: 139–149.

AGASSIZ, L. (1834): Abgerissene Bemerkungen über fossile Fische. – Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde, **4**: 379–390.

AGASSIZ, L. (1841): Monographies d'échinodermes vivans et fossiles, Seconde Monographie: Des Scutelles. – 126 pp., Neuchâtel en Suisse (Aux frais de l'auteur).

AGASSIZ, L. & DESOR, P.J.E. (1846): Catalogue raisonné des familles, des genres, et des espèces de la classe des échinodermes. – Annales des Sciences Naturelles, 3e Série, Zoologie, **6**: 305–374.

ALBERTI, F.A. von (1834): Beitrag zu einer Monographie des Bunten Sandsteins, Muschelkalks und Keupers und die Verbindung dieser Gebilde zu einer Formation. – 366 pp., Stuttgart, Tübingen (Verlag der J.G. Cotta'schen Buchhandlung).

BARTRAM, A.W.H. (1977): The Macrosemiidae, a Mesozoic family of holostean fishes. – Bulletin of the British Museum Natural History, Geology, **29**/2: 137–234.

BRITO, I.M. (1964): Equinoides cretácicos do Estado da Bahia. – Universidade da Bahia Escola de Geologia, Publicaçáo Avulsa, **1**: 1–11.

BROUGH, J. (1935): On the structure and relationships of the hybodont sharks. – Memoirs and Proceedings of the Manchester Literary and Philosophical Society, **79**/4: 35–50.

BÜRGIN, T. & FURRER, H. (2004): Fossile Knochenfische aus der Kössen-Formation (Obertrias; Rhaet) von Lorüns (Vorarlberg, Österreich). – Vorarlberger Naturschau, **14**: 67–86.

CHECCHIA-RISPOLI, G. (1933): Illustrazione di alcuni Echinidi del Maestrichtiano della Tripolitania raccolti da Ignazio Sanfilippo. – Memorie della Società Geologica Italiana, **1**: 1–22.

CLARK, W.B. & TWITCHELL, M.W. (1915): The Mesozoic and Cenozoic Echinodermata of the United States. – Monographs of the United States Geological Survey, **54**: 1–227.

COOKE, C.W. (1949): Two Cretaceous echinoids from Peru. – Journal of Paleontology, **23**/1: 84–86.

COOKE, C.W. (1955): Some Cretaceous echinoids from the Americas. – United States Geological Survey Professional Paper, **264**/E: E87–E112.

COQUAND, H. (1862–1863): Géologie et Paléontologie de la Région sud de la Province de Constantine. – Mémoires de la Société d'émulation de la Provence, **2**: 5–342.

COTTEAU, G.H. (1864): Terrain Crétacé, Échinides. (Paléontologie Française. Description des animaux invertébrés fossiles de la France, 7). – pp. 374, 550, Paris (Victor Masson et fils).

COTTEAU, G.H. (1867): Terrain Crétacé, Échinides. (Paléontologie Française, Description des animaux invertébrés, 7). – 895 pp., Paris (Victor Masson et fils).

COTTEAU, G.H. (1875): Terrain Jurassique, Échinides réguliers. Familles des Cidaridées et des Salénidées. (Paléontologie Française. Description des Animaux Invertébrés, 10). – 48 pp., Paris (Victor Masson et fils).

COTTEAU, G.H. (1882): Échinides nouveaux ou peu connus. 2ème série, article 1. – Bulletin de la Société Zoologique de France, **7**: 406–424.

COTTEAU, G.H. (1885): Terrain Jurassique, Échinides réguliers. (Paléontologie Française, Description des fossiles de la France, 10). **–** 960 pp., Paris (Victor Masson et fils).

COTTEAU, G.H. & GAUTHIER, V. (1895): Mission scientifique en Perse par J. de Morgan. – Études géologiques des échinides fossiles, **3**: 1–107.

CRAGIN, F.W. (1893): A contribution to the invertebrate paleontology of the Texas Cretaceous. – Texas Geological Survey Annual Report, **4**/9: 139–294.

CRAGIN, F.W. (1894): Descriptions of invertebrate fossils from the Comanche series in Texas, Kansas, and Indian Territory. – Colorado College Studies, **5**: 49–68.

D'ARCHIAC, A. (1837): Formation Crétacée du sud-ouest de la France. – Mémoires de la Société Géologique de France, **12**/2: 157–191.

DESOR, E. (1855): Synopsis des échinides fossils. – 490 pp., Paris (Reinwald).

DUNCAN, P.M. (1865): A description of the Echinodermata from the strata on the southeastern coast of Arabia and at Bagh on the Nerbudda, in the collection of Geological Survey. – Quarterly Journal of the Geological Society of London, **21**: 349–363.

DUNCAN, P.M. (1887): Note on the Echinoidea of the Cretaceous series of the Lower Narbadá Valley, with remarks upon their Geological age. – Records of the Geological Survey of India, **20**: 81–92.

DUNCAN, P.M. (1889): A revision of the genera and great groups of the Echinoidea. – Journal of the Linnean Society, Zoology, **23**: 1–311.

EL QOT, G.M., ABDELHAMID, M.A. & ABDELGHANY, M.S. (2016): Revision of Cenomanian regular echinoids in collections at the Cairo Geological Museum, Egypt. – Cretaceous Research, **67**: 91–125.

EMMRICH, A. (1853): Geognostische Beobachtungen aus dem östlichen bayerischen und den angrenzenden österreichischen Alpen. II. Aus dem Gebiete des Alpenkalkes. – Jahrbuch der kaiserlich-königlichen Geologischen Reichsanstalt, **4**: 326–394.

FELBER, R., WEISSERT, H.J., FURRER, H. & BONTOGNALI, T.R.R. (2015): The Triassic–Jurassic boundary in the shallow-water marine carbonates from the western Northern Calcareous Alps (Austria). – Swiss Journal of Geosciences, **108**: 213–224.

FELL, H.B. & PAWSON, D.L. (1966): Echinacea. – In: MOORE, R.C. (ed.): Treatise on Invertebrate Paleontology, Part U, Echinodermata, **3**/2. – pp. U437–U439, New York & Lawrence (The Geological Society of America & University of Kansas Press).

Forner i Valls, E., Hual i Ortí, V. & Gombau i Valanzuela, E. (2015): Revisió d'*Orthopsis royoi* Lambert, 1935 (Echinoidea) del Cretaci Inferior de Vallibona (Els Ports, conca del Maestrat, NE de la península Ibèrica). – Nemus, Revista de l'Ateneu de Natura, **5**: 27–43.

Furrer, H. (1993): Stratigraphie und Facies der Trias/Jura-Grenzschichten in den Oberostalpinen Decken Graubündens. – Unpublished PhD thesis, 99 pp., Switzerland (University of Zurich).

Gras, A. (1848): Description des Oursins Fossiles du Département de l'Isère. Supplément et errata au Mémoire sur les oursins fossiles du Département de l'Isère. – Bulletin de la Société de Statistique des Sciences Naturelles et des Arts industriels du Département de l'Isère, **4**: 1–451.

Hauer, F. Ritter von (1853): Ueber die Gliederung der Trias-, Lias- und Juragebilde in den nordöstlichen Alpen. – Jahrbuch der kaiserlich-königlichen Geologischen Reichsanstalt, **4**/4: 715–784.

Jagt, J.W.M., Hersi O.S., Al-Zeidi, H.S. & Smith, A.B. (2018): Mid-Cretaceous echinoids from the Dhalqut Formation of Dhofar, southern Oman – Taxonomy and biostratigraphical implications. – Cretaceous Research, **89**: 75–91.

Kier, P.M. (1977): Triassic echinoids. – Smithsonian Contributions to Paleobiology, **30**: 1–88.

Kier, P.M. & Lawson, M.H. (1978): Index of Living and Fossil Echinoids 1924–1970. – Smithsonian Contributions to Paleobiology, **34**: 1–182.

Kongiel, R. (1957): Remarques sur les échinides suprajurassiques de Czarnoglow et de Swietoszewo en Poméranie occidentale. – Bulletin de la Service Géologique de Pologne, **105**: 5–74.

Kroh, A. (2010): Index of Living and Fossil Echinoids 1971–2018. – Annalen des Naturhistorischen Museums Wien, Series A, **112**: 195–470.

Kroh, A. (2020): Chapter 1. Phylogeny and classification of echinoids. – In: Lawrence, J.M. (ed.): Sea Urchins: Biology and Ecology, 4th Edition. (Developments in Aquaculture and Fisheries Science, 43). – pp. 1–17, Amsterdam (Elsevier). https://doi.org/10.1016/B978-0-12-819570-3.00001-9

Kroh, A. & Smith, A.B. (2010): The phylogeny and classification of post-Palaeozoic echinoids. – Journal of Systematic Palaeontology, **8**/2: 147–212.

Lamarck, J.B.P.A. (1799): Prodrome d'une nouvelle classification des coquilles, comprenant une rédaction appropriée des caractères génériques, et l'établissement d'un grand nombre de genres nouveaux. – Mémoires de la Société d'Histoire Naturelle de Paris, **1**: 63–91.

Lambert, J. (1911): Étude sur les Échinides Crétacés de Rennes-les-Bains et des Corbières. – Bulletin de la Société d'études scientifiques de l'Aude, **22**: 66–183.

Lambert, J. (1922): Échinides fossiles de la Province de Santander. – Trabajos del Museo National de Ciencias Naturales, Serie Geologica, **28**: 1–26.

Lambert, J. (1924): Sur un échinide nouveau du Rhetien des Prealpes bernoises. – Eclogae Geologicae Helvetiae, **18**/3: 448–450.

Lambert, J. (1935): Échinides crétacés d'Espagne II. Sur quelques Échinides crétacés d'Espagne communiqués par M. le Prof. Royo y Gómez. – Boletín de la Real Sociedad Española de Historia Natural, **35**: 521–526.

Lambert, J. (1937): Échinides fossiles du Maroc. – Protectorat de la République Française au Maroc, Service des Mines et de la Carte Géologique, Notes et Mémoires, **39**: 39–109.

Leske, N.G. (1778): Jacobi Theodori Klein naturalis dispositio echinodermatum ..., edita et descriptionibus novisque inventis et synonomis auctorem aucta. Addimenta ad I. T. Klein naturalem dispositionem Echinodermatum. – 278 pp., Leipzig (Beer).

Maldonado-Koerdell, M. (1953): Los equinoides regulares del Mesozoico de México. – Anales de la Escuela nacional de Ciencias biologicas, **7**: 15–44.

Mandl, G.W. (2000): The Alpine sector of the Tethyan shelf. – Examples of Triassic to Jurassic sedimentation and deformation from the Northern Calcareous Alps. – Mitteilungen der Österreichischen Geologischen Gesellschaft, **92**: 61–77.

McRoberts, C.A., Furrer, H. & Jones, D.S. (1997): Palaeoenvironmental interpretation of a Triassic–Jurassic boundary section from Western Austria based on palaeoecological and geochemical data. – Palaeogeography, Palaeoclimatology, Palaeoecology, **136**: 79–95.

Mérian, P. (1857): Ueber verschiedene Petrefacten aus der Stockhornkette, den italienischen Alpen und der Umgebung von Lugano. – Verhandlungen der Naturforschenden Gesellschaft zu Basel, **1**: 314–320.

Meyer, M. von (1858): *Psephoderma alpinum* aus dem Dachstein-Kalke der Alpen. – Palaeontographica, **6**: 246–252.

Néraudeau, D., David, B. & Al-Muallem, M.S. (1995): The Cretaceous echinoids from Central Saudi Arabia. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **197**/3: 399–424.

Plieninger, T. (1847): Abbildungen von Zähnen aus der oberen Grenzbreccie des Keupers bei Degerloch und Steinenbronn. – Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg, **3**: 164–167.

Pomel, A. (1883): Classification Méthodique et Genera des Échinides vivants et fossiles. – Thèses présentées à la Faculté de Sciences de Paris. – 132 pp., Alger (Adolphe Jourdan).

Portlock, J. (1843): Reports on the Geology of the County of Londonderry, and of parts of Tyrone and Fermanagh. – 784 pp., Dublin (A. Milliken, Hodges & Smyth).

Röding, P.F. (1798): Museum Boltenianum sive Catalogus cimeliorum e tribus regnis naturæ quæ olim collegerat Joa. Fried. Bolten, M. D.p.d. per XL. annos Proto physicus Hamburgensis. Pars Secunda conineus Conchylia sive Testacea univalvia, bivalvia & multivalvia. – 199 pp., Hamburg (Johan. Christ. Trapp).

Schafhäutl, K.E. (1851): Geognostische Untersuchungen des südbayerischen Alpengebirges. – 206 pp., München (Literarisch-artistische Anstalt).

Smith, A.B. (1990): Echinoid evolution from the Triassic to the Lower Jurassic. – Cahiers Université Catholique de Lyon, Séries Science, **3**: 79–117.

Smith, A.B. (1995): Late Campianian–Maastrichtian echinoids from the United Arab Emirates-Oman border region. – Bulletin of the Natural History Museum, London (Geology), **51**/2: 121–240.

Smith, A.B. (2010): The Cretaceous Bagh Formation, India: a Gondwanan window onto Turonian shallow-water echinoid faunas. – Cretaceous Research, **31**: 368–386.

Smith, A.B. & Bengtson, P. (1991): Cretaceous echinoids from north-eastern Brazil. – Fossils and Strata, **31**: 1–89.

Smith, A.B. & Rader, W.L. (2009): Echinoid diversity, preservation potential and sequence stratigraphical cycles in the Glen Rose Formation (early Albian, Early Cretaceous), Texas, USA. – Palaeobiodiversity and Palaeoenvironments, **89**: 8–52.

STAUB, R. (1923): Tektonische Karte der Alpen 1:1,000,000. Spezialkarte Nr. 105 A. – Beiträge zur geologischen Karte der Schweiz, Neue Folgen, Lieferung **52**, Bern (Landesgeologie).

STEFANINI, G. (1924): Il Retico nei dintorni di Selvena (Siena) e i suoi fossili. – Bollettino della Società Geologica Italiana, **42**: 48–57.

STENSIÖ, E. (1919): Einige Bemerkungen über die systematische Stellung von *Saurichthys mougeoti* AGASSIZ. – Senckenbergiana, **1**/6: 177–181.

STOLICZKA, F. (1873): Cretaceous fauna of southern India. The Echinodermata. – Memoirs of the Geological Survey of India, Palaeontologia Indica, **4**/3: 71–129.

STOLLEY, E. (1920): Beiträge zur Kenntnis der Ganoiden des deutschen Muschelkalks. – Palaeontographica, **63**: 25–86.

STOPPANI, A. (1857): Studi geologici e paleontologici sulla Lombardia. – 461 pp., Milano (Presso Carlo Turati Tipografo-Ediore)

STOPPANI, A. (1860–65): Géologie et Paléontologie des couches à Avicula contorta en Lombardie. – Paléontologie Lombarde ou déscription des fossils de Lombardie publiée à l'aidé de plusieurs savants, **3**: 267 pp.

SUESS, E. (1854): Über die Brachiopoden der Kössener Schichten. – Denkschriften der mathematisch-naturwissenschaftlichen Classe der kaiserlichen Akademie der Wissenschaften, **7**: 1–42.

TOMAŠOVÝCH, A. (2006): Brachiopod and bivalve ecology in Late Triassic (Alps, Austria): onshore-offshore replacements caused by variations in sediment and nutrient supply. – Palaios, **21**/4: 344–368.

VADET, A. & WILLE, E. (2002): Quelques oursins du Lusitanien du Portugal. – Annales de la Société d'Histoire Naturelle du Boulonnais, **2**/1: 8–17.

WHITE, C.A. (1887): Contribuições á paleontologia do Brazil. – Archivos do Museu Nacional do Rio de Janeiro, **7**: 1–273.

WHITNEY, M.I. & KELLUM, L.M. (1966): Echinoids of the Glen Rose Limestone of Texas. – Papers of the Michigan Academy of Science, Arts and Letters, **51**: 241–263.

WRIGHT, T. (1855): On a new genus of fossil Cidaridae, with a synopsis of the species included therein. – The Annals and Magazine of Natural History, **16**: 94–100.

WRIGHT, T. (1857–1878): Monograph on the British Fossil Echinodermata of the Oolitic Formations. Volume 1. The Echinoidea. (Monograph of the Palaeontographical Society London). – 481 pp., London (Palaeontographic Society).

WULFEN, X. (1793): Abhandlungen vom kärnthenschen pfauenschweifigen Helmintholith oder dem sogenannten opalisirenden Muschelmarmor. – 124 pp., Erlangen (Johann Jakob Palm).

ZUGMAYER, H. (1880): Untersuchungen über rhätische Brachiopoden. – Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients, **1**: 1–42.