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Echinoids from the Belpberg Beds (Obere Meeresmolasse, Middle Burdigalian) in the area of Bern (Switzerland)

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Key words: Echinoidea, Belpberg Beds, Upper Marine Molasse (OMM), Early Miocene, Switzerland, palaeobiogeography
Schlüsselwörter: Echinoidea, Belpberg Schichten, Obere Meeresmolasse (OMM), Unter-Miozän, Schweiz, Paläobiogeographie

ABSTRACT

The present paper deals with the echinoid fauna of the Belpberg Beds, a lithostratigraphic unit in the Upper Marine Molasse cropping out southeast of Bern (Switzerland). In this unit, echinoids, in contrast to mollusks, are rare and of low diversity. The scarcity of echinoids is related to the environmental setting dominated by monotonous siliciclastic deposits and strong diagenetic alteration.

The echinoid fauna consists of three species: *Psammechinus dubius dubius*, *Echinocardium deikei* and *Hemipatagus ocellatus*? *Psammechinus dubius dubius* and *H. ocellatus* typically occur in Burdigalian sediments in the Paratethys and help to confirm the dating obtained from the microfossils and molluscs of the Belpberg Beds. Furthermore, the Belpberg echinoid fauna is especially relevant for the palaeobiogeography with species common to both the Rhône Basin and the Central Paratethyan faunas.

ZUSAMMENFASSUNG

Die vorliegende Arbeit beschäftigt sich mit der Echinidenfauna der Belpberg Schichten (Obere Meeresmolasse) bei Bern. Im Gegensatz zu den Mollusken sind die Echiniden selten und wenig divers. Dies kann einerseits auf das sedimentäre Regime, und andererseits auf diagenetische Ursachen zurückgeführt werden.

Insgesamt konnten drei Arten nachgewiesen werden (*Psammechinus dubius dubius*, *Echinocardium deikei* und *Hemipatagus ocellatus*?). Zwei davon treten in der Paratethys charakteristischerweise im Burdigalium auf und lassen ein ebensolches Alter für die Belpberg Schichten als wahrscheinlich erscheinen. Aus paläobiogeographischer Sicht ist die Belpberg-Echinidenfauna von besonderem Interesse, das sie ein Bindeglied zwischen Rhône Becken und Zentraler Paratethys darstellt.

1. Introduction

Apart from the early papers by Agassiz (1839, 1840) and de Loriol (1875–1876), the Neogene echinoid fauna of Switzerland and the Western Paratethys is poorly known. Additionally, a few general papers on the fauna of the Swiss Molasse mention echinoderm remains (Studer 1825; Heer 1865; Bachmann 1867, 1868; Kaufmann 1872; Kissling 1890; Thalmann 1923; Rutsch 1928). The only modern work deals with Pliocene echinoids from southern Switzerland (Ragaini 1996). In contrast, the echinoid faunas of the adjacent regions, the Rhône Basin and the Central Paratethys, have been recently the focus of renewed research (Philippe 1998; Kroh 2005). The echinoid fauna of the Belpberg Beds has never been studied in detail before. The echinoid collections of the Naturhistorisches Museum Bern give us this opportunity.

2. Geological setting

The Upper Marine Molasse (OMM, from the German term "Obere Meeresmolasse") of the study area in the vicinity of Bern (Switzerland) was deposited during the Early Miocene in the perialpine Molasse Basin (Pfister & Wegmüller 1994). The special position of this area, represents a transitional zone between the Central Paratethys in the East and the Rhône Basin and the Mediterranean in the West, reflected by its mollusk (e.g. Pfister & Wegmüller 1994, 1998, 1999, 2000, 2001) and echinoid fauna (this study). Elements of both regions are represented.

Since Ritter (1742), the Belpberg Beds have been the focus of several palaeontological and geological publications. Studer (1825), Bachmann (1867) and Kissling (1890) described the fossil fauna around Bern. The work of Rutsch (1928) was for a

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Upper Marine Molasse (OMM)	Niedermatt Beds (della Valle 1965)		
	Belpberg Beds sensu lato (Rutsch 1926)	Sädel Conglomerate (Rutsch 1928)	
		Belpberg Beds sensu stricto (Rutsch & Schlüchter 1973)	Utzigen Beds (Gerber 1926) with Muschelsandstein (Rutsch 1926) and "Petrefactenlager" (Studer 1825)
			Upper Muschelsandstein (Gerber 1926) and/or Conglomerate with Oysters
		Bütschelbach Conglomerate (Rutsch 1967) and/or Lower Muschelsandstein (Gerber 1926)	
	Sense Beds (Rutsch 1967)		

Fig. 1. Lithostratigraphic units and subunits of the Upper Marine Molasse in the study area (modified from Gruner 2001).

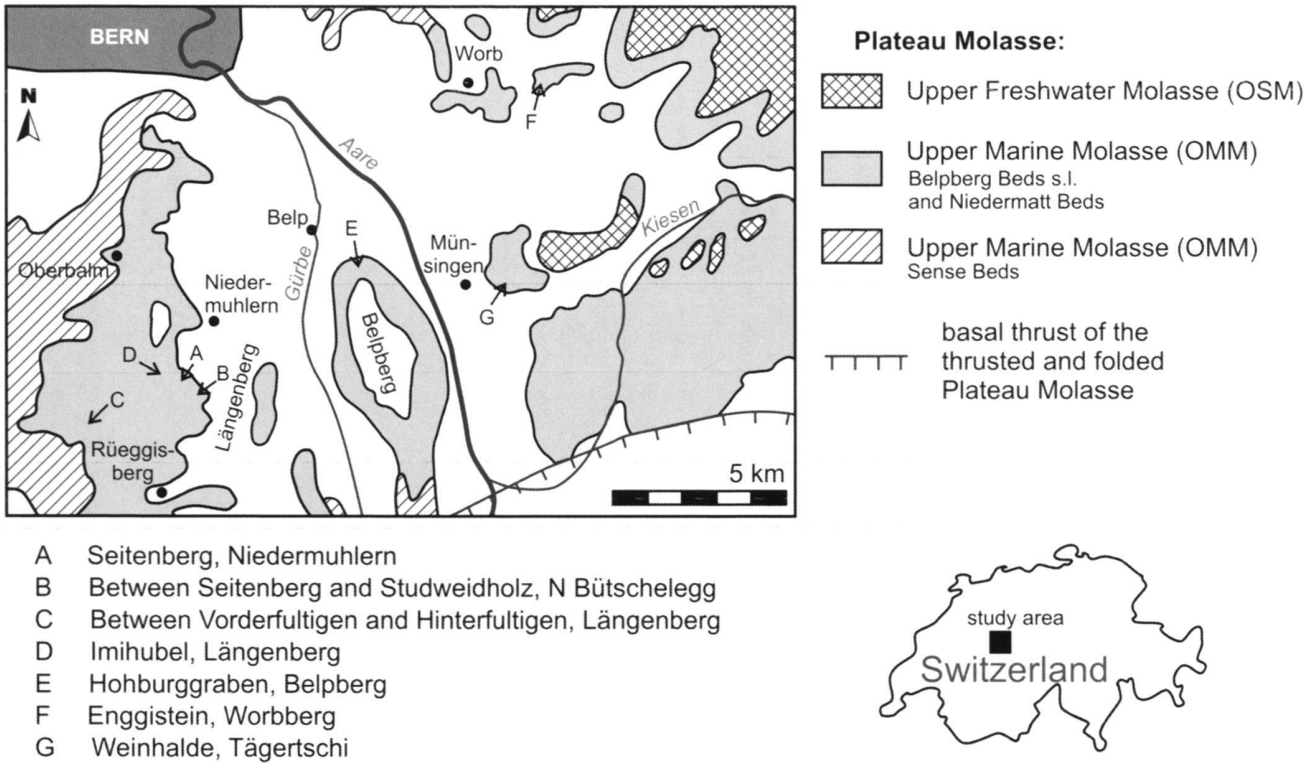


Fig. 2. Location and simplified geological map of the study area, indicating the different localities of the reported echinoids (modified from Pfister & Wegmüller 1994; Kellerhals et al. 1999).

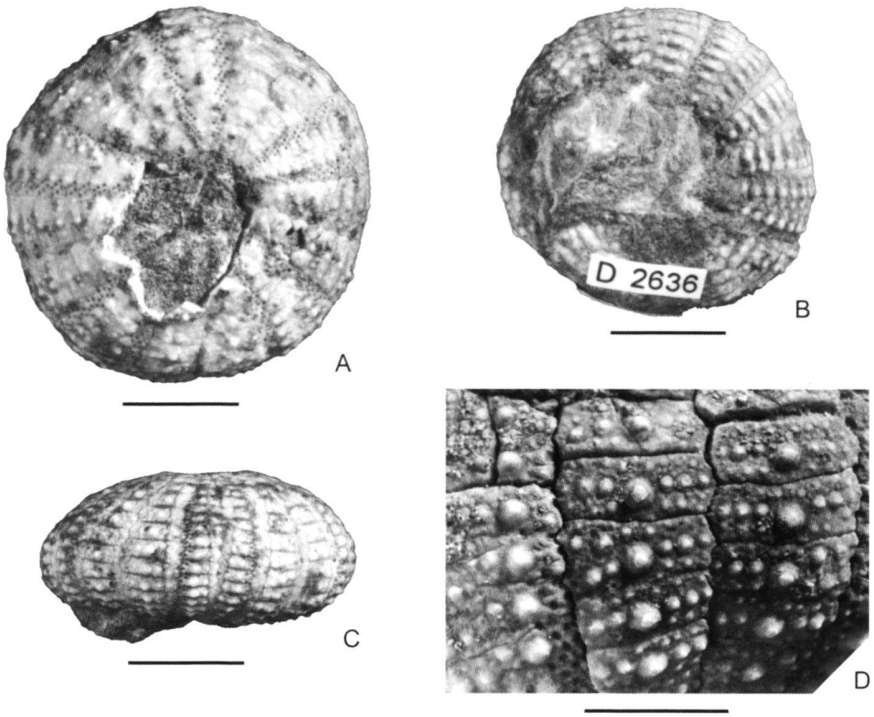


Fig. 3. *Psammechinus dubius dubius* (AGASSIZ 1840). A) NMBE 5011426 in aboral view; B), C) NMBE 5011439 in oral and lateral view; D) NMBE 5011435, detail of the ambital tuberculation. All these specimens are from Hohburggraben (Middle Burdigalian, Belpberg, Switzerland). Scale bars: A-C (10 mm); D (5 mm).

long time the most comprehensive palaeontological and geological study of the Belpberg sediments. Keller (1989) and Schoepfer (1989) have published new results on sedimentological and stratigraphical aspects. More recently, Pfister & Wegmüller (1994, 1998, 1999, 2000, 2001) have published a series of papers on the mollusc fauna.

The sediments in the area have become known as the Belpberg Beds (Fig. 1). Initially, including a much wider range of lithostratigraphic units (Rutsch 1926), the beds have subsequently been restricted to the Upper Muschelsandstein and the Utzigen Beds (Rutsch & Schlüchter 1973). All the echinoid material originates from this restricted part of the Belpberg Beds, which crop out in the southeast of Bern (Fig. 2).

Gruner (2001) described the lithology of the Belpberg Beds s.s. as a fine- to medium grained sandstone, rich in mica, with intermediary marly layers and/or conglomerates. Rapid changes in facies are typical. The thickness of the Belpberg Beds s.s. ranges from 250 to 300 m and shows a tendency to decrease towards the northeast. Sedimentary interpretations by Schoepfer (1989) and Pfister & Wegmüller (1994) indicate a depositional environment within a storm influenced delta front, ranging into protected shallow-water prodelta bay environments.

Biostratigraphical correlations of the Belpberg Beds were given by Martini (1971), Rutsch (1971), Rutsch & Salaj (1974, 1980), Müller (1982), Schoepfer (1986), Schoepfer & Berger (1989), Keller (1989), Demarq (1990) and Engesser (1990). Index forms are rare and age interpretations are controversial (Schoepfer 1989; Pfister & Wegmüller 1994). Strontium isotope measurements on pectinid shells from the Belpberg Beds (section Aarwald, Belpberg), in contrast, yielded an absolute age of 15.7 million years ago (Fischer 1985), correlating with the Early Langhian. However, these strontium data seem questionable in light of the strong diagenetic alteration of the material: aragonitic shells are preserved as moulds or casts only, pectinid and echinoid calcite shows a strong diagenetic overprint. Recently, Gruner (2001) assigned the Belpberg Beds to the Middle Burdigalian, based on conclusions of Schoepfer (1989) and Pfister & Wegmüller (1994). This is in agreement with earlier results obtained from calcareous nannoplankton samples, indicating an assignment from upper part of zone NN2 (equaling Early to Middle Burdigalian) to the border between zone NN3 and NN4 (correlating with the Middle Burdigalian; Schoepfer 1989; Demarq & Schoepfer 1990). In the Central Paratethys this interval corresponds to the Upper Eggenburgian to the Lower Ottnangian (Schoepfer 1989; Pfister & Wegmüller 1994). See Harzhauser et al. (2003) for additional discussion on the age of the Belpberg Beds (and the "Helvetian", an outdated term used for the studied time interval) and Berger et al. (2005a, b) for an overview on the lithostratigraphy and palaeogeography of the Swiss Molasse.

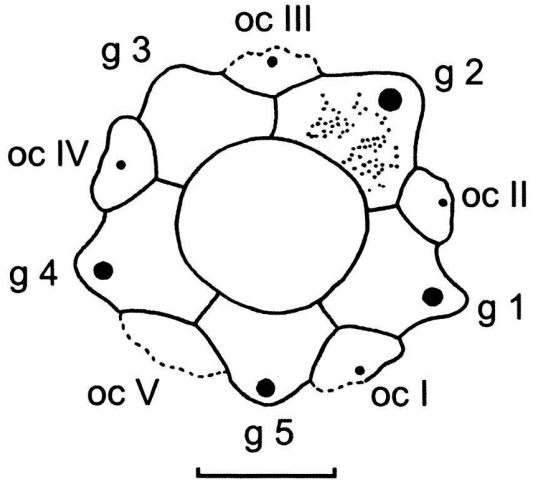


Fig. 4. *Psammechinus dubius dubius* (AGASSIZ 1840). Drawing (using a camera lucida) of the apical disc of NMBE 5011427 from Hohburggraben (Middle Burdigalian, Belpberg, Switzerland). Poorly visible sutures are stippled, gonopore in genital plate 3 is not visible. Ocular plates are indicated by "oc" and their Lovenian number in Roman font. Genital plates are marked by "g" and their Lovenian number in Arabian font. Scale bar: 1 mm.

3. Material and methods

The material used in the present study is housed at the Naturhistorisches Museum Bern (NMBE). It originates from the collections of R. Hadorn, A. Hoerning, B. Hostettler, B. Schott, E. Wyttenbach and the excavations by the NMBE.

The described material originates from the upper part of the Belpberg Beds s.s. (Fig. 1). Most of the specimens come from the Hohburggraben section (Fig. 2E) and other localities at Belpberg. Additional material is derived from the localities Enggistein, Imihubel, Längenberg Seitenberg and Weinhalde (Fig. 2A-D, F, G).

The upper part of the Belpberg Beds s.s. (Fig. 1) is composed of a sequence of sandstones and marls. The sequence includes two conspicuous fossiliferous beds: the "Petrefactenlager" (fossiliferous horizons in the upper part of the sandstone and marl succession) in the middle part and the "Muschelsandstein" (coarse sandstone with bivalves, pebbles and shark teeth) at the top. Echinoids have only been found in the "Petrefactenlager". Only a single specimen (NMBE 5011432) can be assigned to a particular horizon (layer 13, Hohburggraben section), in the lower part of the succession of sandstones and marls. All the other sixteen specimens were collected loose from the uppermost layers of the sequence, or from fallen blocks belonging to these horizons.

During fieldwork, the investigated sections were repeatedly sampled to obtain washable material, but many horizons turned out to be too strongly lithified for washing and sieve analysis. The few samples that could be processed did not yield any echinoderm remain (J. Wegmüller, pers. comm.).

4. Systematic palaeontology

Phylum Echinodermata DE BRUGUIERE 1791 (ex KLEIN 1734)
Class Echinoidea LESKE 1778
Order Echinoida CLAUS 1876
Family Echinidae GRAY 1825
Genus *Psammechinus* AGASSIZ & DESOR 1846

Psammechinus dubius dubius (AGASSIZ 1840)

(Figs. 3A-D; Fig. 4)

*1840	*Echinus dubius* AG. – AGASSIZ: 84–85; pl. 22, figs. 4–6
1875	*Psammechinus dubius*, AGASSIZ. – DE LORIOL: 29–30; pl. 2, figs. 6, 6a-c; 7, 7a, b
1883	*Psammechinus mirabilis*, NICOL. (*Echinometra*). – GUTZWILLER: 46
1998	*Psammechinus dubius* (AGASSIZ 1840) – PHILIPPE: 65–67; pl. 8, figs. 5-8 [cum syn.]
2005	*Psammechinus dubius dubius* (AGASSIZ 1840) – KROH: 25–26; pl. 14, figs. 1–4 [cum syn.]

Type material. – Figured in Agassiz (1840: pl. 22, figs. 4–6); current location unknown.

Type horizon and type locality. – ? Upper Marine Molasse, Middle Burdigalian, Chaux-de-Fonds, Switzerland.

Material. – 2 specimens from Cheergraben, Belpberg (NMBE 5014152, 5014155); 16 specimens from Hohburggraben, Belpberg, (NMBE 5011426-5011440, 5011442); 1 specimen from Seitenberg, near Niedermuhlern (NMBE 5011443); 1 specimen from between Seitenberg and Studweidholz, N Bütschelegg (NMBE 5011444).

Dimensions (in mm). –

Specimen no.	Diameter	Height	Remarks
NMBE 5011426	33.0	13.1	
NMBE 5011427	16.7	9.5	apical disc preserved
NMBE 5011431	27.4	13.8	
NMBE 5011432	25.0	12.1	
NMBE 5011436	18.2	9.6	
NMBE 5011439	~28.0	12.9	deformed
NMBE 5011440	21.2	8.1	depressed
NMBE 5011442	19.5	8.9	
NMBE 5014152	28.0	19.0	
NMBE 5014155	27.0	6.0	

Description. – Test of small to medium size, with diameter ranging from 16.7 to 33 mm. The outline of the corona is more or less circular. The aboral surface is highly arched, the oral surface flattened and depressed around the peristome. The ambitus is tumid. The apical disc is preserved in specimen NMBE 5011427. It is dicyclic with clearly exsert ocular plates (Fig. 4). Ornamentation and/or tuberculation are obscured. The ambulacra consist of trigeminate plates belonging to the echinoid compound type. The pores are partitioned isopores and are arranged in arcs of three. Each plate bears one large noncrenulate, imperforate marginal tubercle and few smaller inner tubercles. The most perradially situated inner tubercle is distinctly enlarged. The interambulacra are about 1.5 times as

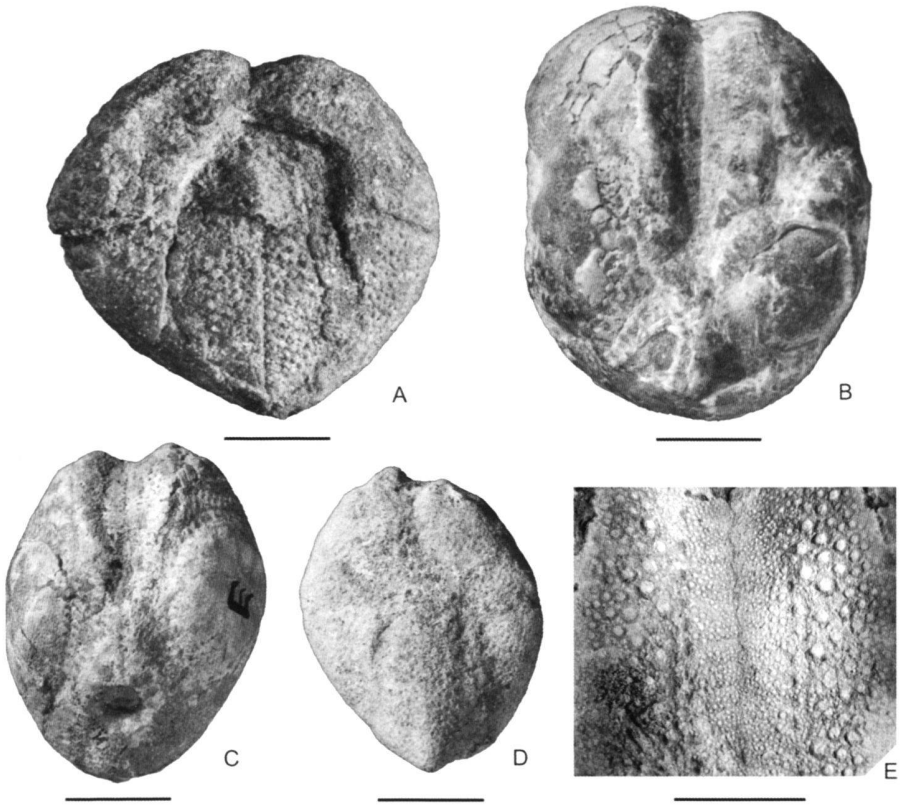


Fig. 5. *Echinocardium deikei* DESOR 1858. A) NMBE 5011449 in oral view, from Belpberg or Weinhalde (Tägertschi); B) NMBE 5011448 in aboral view, from Hohburggraben (Belpberg); C) NMBE 5011447 in aboral view, from Enggistein (Worbberg); D) NMBE 5011445 in oral view, collected between Vorder- and Hinterfultigen (Längenberg); E) NMBE 5011448, detail of ambulacrum III, from Hohburggraben (Belpberg). All the mentioned localities are from the Middle Burdigalian of Switzerland. Scale bars: A-D (10 mm); E (5 mm).

wide as the ambulacra at the ambitus. Each plate bears one noncrenulate, imperforate primary tubercle, lying slightly adorally of the centre of each plate. The secondary tuberculation is moderately dense. At the ambitus, two to four secondary tubercles are distinctly enlarged on each side of the primary tubercle. These secondary tubercles and the primary tubercles are arranged in more or less horizontal rows. The peristome is moderately large, being about 37 % of the test diameter. It has a circular outline and only faint buccal notches (formerly termed gill slits). The periproct is enclosed by the genital plates and has a circular outline. It is 2.1 mm in diameter in specimen NMBE 5011427.

Remarks. – Although poorly preserved, the specimens can be assigned to *Psammechinus dubius dubius* without doubt. All features correspond well to the original description. A thorough revision of closely related taxa was recently published by Philippe (1998). Reports of this subspecies from the Badenian (Middle Miocene) of the Central Paratethys (e.g. Mączyńska 1979, 1987, 1988) are doubtful and need to be re-examined (Kroh 2005).

Due to the strong diagenetic overprint, the skeletal material is strongly altered. This is expressed in the present specimens by a nearly complete loss of the stereom microstructure. Interestingly, the individual stereom types reacted differently to the alteration resulting in darker and lighter areas tracing the original structures. This accounts also for the dark horizontal bands seen in many specimens (e.g. Fig. 3B, C), which might erroneously be interpreted as sutural gaps (in Fig. 3D, by contrast, sediment compaction led to partial crushing of the test and breaking of sutures).

Occurrence. – Paratethys: Eggenburgian (Early Burdigalian), Karpatian (Late Burdigalian), ? Badenian (Langhian-Serravallian): various localities in Austria and Hungary (Kroh 2005); Mediterranean: Aquitanian to Serravallian: circum-Mediterranean.

Order Spatangoida CLAUS 1876
Family Loveniidae LAMBERT 1905
Genus Echinocardium GRAY 1825

Echinocardium deikei DESOR 1858

(Fig. 5A-D)

*1858 [*Echinocardium*] *Deikei* DESOR nov. sp. – DESOR: 408
1875 *Echinocardium Deikei*, DESOR. – DE LORIOL: 122; pl. 22, fig. 6, 6a, b
1883 *Echinocardium Deikei*, DES. – GUTZWILLER: 46
1890 *Echinocardium Deikei* DESOR – KISSLING: 68; pl. 1, fig. 1
non1979 *Echinocardium deikei* DESOR 1857 – MĄCZYŃSKA: 33; pl. 9, figs. 2; 4 [= *E. peroni* fide PHILIPPE 1998]
non1979 *Echinocardium deikei* DESOR 1857 – MĄCZYŃSKA: 33; pl. 9, fig. 3 [= deformed schizasterid]
?1985 *Echinocardium* cf. *deikei* DESOR 1858 – MIHÁLY: 245; pl. 5, fig. 6

Type material. – Reported to from the collection Deike according to Desor (1855–1858: 408), current location unknown.

Type horizon and type locality. – "Molasse de Krobell près St.-Gall" (Desor 1858: 408).

Material. – 2 specimens from between Vorder- and Hinterfultigen, Längenberg (NMBE 5011445, 5011446); 1 specimen from Enggistein, Worbberg (NMBE 5011447); 1 specimen from Hohburggraben, Belpberg (NMBE 5011448); 1 specimen from Belpberg or Weinhalde, Tägertschi (NMBE 5011449).

Dimensions (in mm). –

Specimen no.	Length	Width	Height	Remarks
NMBE 5011445	31.1	22.5	12.9	slightly deformed
NMBE 5011446	23.3	23.8	26.0	deformed
NMBE 5011447	32.7	25.0	13.5	deformed
NMBE 5011448	41.6	34.0	21.9	posterior and left lateral parts missing
NMBE 5011449	34.9	37.6	15.2	deformed

Description. – Test of medium size with heart-shaped, antero-posteriorly elongated outline. A shallow frontal notch is developed. Aborally ambulacrum III and the adjacent interambulacral columns (2b and 3a) form a broad groove between the apical disc and the ambitus. Posterior end obliquely truncate with distinctly pointed subanal heel. In profile the test is slightly wedge shaped. The highest point lies posteriorly in interambulacrum 5. Apical disc is not preserved in any of the investigated specimens, but lies posteriorly, approximately 60 to 65 % of test length from the anterior margin. The ambulacra are petaloid and are moderately depressed on the aboral side between the apical disc and the ambitus. The paired ambulacra are greatly widened adapically. The frontal ambulacrum, in contrast, is narrower and more strongly depressed. Within the paired petals, the pores are large elongate isopores. In the frontal ambulacrum the pores seem to be minute partitioned isopores (poorly visible). The interambulacra are slightly inflated between the petals forming narrow, rounded keels. Tuberculation details are largely obscured due to poor preservation, but tubercles on the oral side and especially on the plastron are considerably larger than on the aboral surface. Fascioles are not preserved. The periproct lies high on the obliquely truncated posterior face of the test. It is subcircular with a diameter of 3.7 mm in NMBE 5011447. Peristome is not preserved.

Remarks. – Although the fascioles are not preserved, the material can clearly be assigned to the genus *Echinocardium* based on the overall shape and structure of the ambulacra. The studied specimens seem to be conspecific with *Echinocardium deikei* DESOR 1858 as re-described by de Loriol (1875: 122; pl. 22, fig. 6, 6a-b). Comparison with other species of *Echinocardium* from the Early Miocene of the Mediterranean and Paratethys is difficult due to the poor preservation of all known *E. deikei* specimens. *Echinocardium depressum* (AGASSIZ 1847) from the Burdigalian of the Rhône Basin differs from the present material by its subcentral apical disc, narrower ambulacrum III (respectively narrower groove) and more rounded outline (based on the re-description in Philippe 1998 and on material from the Early Burdigalian of the Central Paratethys). The relation between *E. deikei* and *E. depressum*, however, is a very close one and it may turn out that the two are conspecific upon a re-examination of the type material of *E. deikei*. *Echinocardium peroni* COTTEAU 1877 from the Burdigalian of the Rhône Basin and the Middle Miocene of Corsica differs by lacking a frontal notch, its rounded outline and its anteriorly eccentric apical disc (Cotteau 1877; Philippe 1998).

Echinocardium deikei DESOR 1857 from the Middle Miocene of Poland reported by Mączyńska (1979, 1991) was reassigned to *E. peroni* by Philippe (1998: 231).

Occurrence. – Paratethys: Obere Meeresmolasse (Middle Burdigalian) of Switzerland.

Echinocardium? sp.

(Fig. 6)

Material. – 1 fragment from the Belpberg Beds, Hohburg, Belpberg (NMBE 5011450).

Description. – Small (~ 22 x 20 mm) antero-lateral fragment of the aboral surface. The fragment preserves the aboral part of ambulacrum IV and interambulacral column 4a. The petal widens strongly adapically and seems to have been confluent with the posterior petal V. It bears widely spaced elongate isopores. Interambulacral column 4a shows traces of a dense and homogenous tuberculation. There are no traces of enlarged or camellate primary tubercles.

Remarks. – The present fragment is tentatively assigned to the genus *Echinocardium* based on the structure of the single preserved petal and the lack of enlarged or camellate primary tubercles in interambulacral column 4a. This genus is well documented by better preserved specimens from the locality Hohburg and other, nearby localities of the Belpberg Beds (this study).

Genus *Hemipatagus* DESOR 1858

Hemipatagus ocellatus? (DEFRANCE 1827)

(Fig. 7)

*1827	*Spatangus ocellatus* – DEFRANCE in BLAINVILLE et al.: vol. 50, 96-97 [not seen, fide PHILIPPE 1998]
1839	*Spatangus Nicoleti* AG. – AGASSIZ: 33; pl. 4, figs. 7; 8
1847	[*Spatangus*] *ocellatus* DEFR. – AGASSIZ & DESOR: 7
1858	[*Spatangus*] *ocellatus* DEFR. – DESOR: 422
non1864	*Spatangus ocellatus*, DEFRANCE. – WRIGHT: 487-488; pl. 21, fig. 1a, b [= *Lovenia duncani* GREGORY 1891 fide CHALLIS 1980]
1876	*Spatangus ocellatus*, DEFRANCE. – DE LORIOL: 132-134; pl. 23, figs. 2, 2a; 3
1915	*Hemipatagus ocellatus* DEFRANCE (*Spatangus*), 1827 – LAMBERT: 189-192; pl. 14, figs. 17; 18
1998	*Maretia ocellata* (DEFRANCE 1827) – PHILIPPE: 220-223; pl. 22, figs. 6; 7; 8a, b; 9a, b; 10a-c
2005	*Hemipatagus ocellatus* (DEFRANCE 1827) – KROH: 191-194; fig. 94; pl. 81, figs. 1-4; pl. 82, figs. 1; 2 [cum syn.]



Fig. 6. *Echinocardium*? sp. NMBE 5011450 in aboral view, from Hohburg (Middle Burdigalian, Belpberg, Switzerland). Scale bar: 10 mm.



Fig. 7. *Hemipatagus ocellatus*? (DEFRANCE 1827). NMBE 5011451, internal view of the aboral side, from Imihubel (Middle Burdigalian, Längenberg, Switzerland). Scale bar: 10 mm.

Type material. – Holotype unknown; Neotype designated by Lambert (1915: pl. 14, fig. 17); coll. Lambert, Muséum national, Paris (Philippe 1998: 220).

Type horizon and type locality. – Burdigalian of Saint-Paul-Trois-Châteaux, France (Philippe 1998: 220); Neotype from the Burdigalian of Taulignan.

Material. – 1 fragment from the Belpberg Beds, at Imihubel, Längenberg (NMBE 5011451).

Description. – Small (~ 15 x 43 mm) antero-lateral fragment of the aboral surface, exposed from the inside of the corona. Numerous camellate primary tubercles in interambulacra 3b and 4a are visible. The tubercles take up nearly the whole plate height and are extremely closely spaced, their areoles nearly touching each other. These tubercles extend from the adradial to the interradial suture both in interambulacra 3b and 4a. In the preserved fragment, there are at least 8 such tubercles in interambulacrum 3b and 16 in 4a. Additionally, the tip of petal IV is preserved. The petal is closed distally and bears large, conjugate, elongate isopores.

Remarks. – Although the specimen is a very small and poorly preserved fragment, it can be tentatively assigned to *Hemipatagus ocellatus* due to the presence and arrangement of the characteristic camellate primary tubercles and the shape of the preserved petal. Another possible species, *Lovenia duncani* (GREGORY 1891), can be ruled out because of its less numerous and less densely arranged camellate tubercles. Moreover, the latter species seems confined to the Central Mediterranean region (Challis 1980). There is only a single record from the Southern Rhône Basin (Philippe 1998) and none from the Western and Central Paratethys. In contrast *Hemipatagus ocellatus*is a common member of the Burdigalian fauna of the Rhône Basin (Philippe 1998), the Western Paratethys (Agassiz 1839, under the name *Spatangus nicoleti*; de Loriol 1876) and the Central Paratethys (Schaffer 1912, under the name *Spatangus* (*Maretia*) *perornatus*; Kroh 2005). A possible attribution to *Spatangus*, another common genus in the Neogene of the Paratethys and the Mediterranean, can clearly be ruled out. *Spatangus* also has enlarged aboral primary tubercles (e.g. Néraudeau et al. 1998; Kroh 2005), but their structure is very different (Fig. 8). In *Hemipatagus ocellatus* and *Lovenia*, the aboral primary tubercles have deeply sunken areoles, clearly showing as bulbs on the inside of the corona (Fig. 8A). In *Spatangus*, on the contrary, the areoles are only slightly sunken and are not visible on the inside of the corona (Fig. 8B). In the present specimen, which is visible from the inside the *Hemipatagus*/*Lovenia*-type of tubercles is

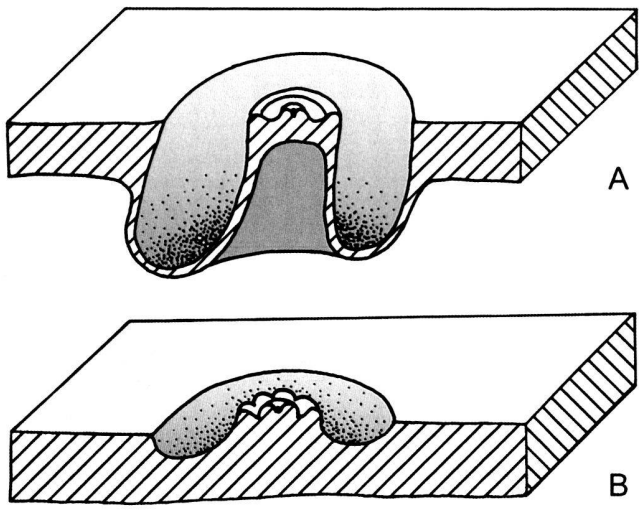


Fig. 8. Schematic comparison between the enlarged aboral primary tubercles of loveniid type (A) and the spatangid type (B), in cross section. The fragment illustrated in Fig. 7 corresponds to the loveniid type, with pillar-like boss exposed trough abrasion of the internal bulb.

clearly visible (Fig. 7). The innermost parts of the bulbs are partially eroded, exposing the pillar-like central part of the tubercles.

Earlier this species was assigned to the genus *Maretia* (e.g. Mortensen 1951), a member of the Spatangidae. However, Kroh (2005, in press) has shown that the type species of *Hemipatagus* as well as *H. ocellatus* are loveniids and not closely related to *Maretia*. *Hemipatagus* is structurally more closely related to *Lovenia* and it may often be difficult to distinguish from this genus on the base of poorly preserved material, a fact noted already by Mortensen (1951). This is notably expressed by the conspicuous adapical field of tubercles found in *Hemipatagus* that is invariably associated with an internal fasciole in all other known genera that share this feature. The presence of this specialized structure could indicate that an internal fasciole is initially present in juvenile *Hemipatagus*, but lost during ontogeny. Fasciole loss during ontogeny is not so uncommon in the Spatangoida (e.g. Mortensen 1950, 1951; Jeffery 1998), and has caused considerable confusion when too much emphasis was placed in fasciole absence/presence in taxonomy. Other features include the depth of the frontal notch, the shape of the subanal fasciole, the structure of the phyllodes and primordial plates of the interambulacra and the constricted nature of the oral antero-lateral ambulacra.

Occurrence. – Paratethys: Burdigalian of the Swiss Molasse Basin and Early to Late Eggenburgian (Early Burdigalian) of the Austrian Molasse Basin; records from the Badenian (Langhian-Early Serravallian) of Hungary and Romania are highly questionable (Kroh 2005); Mediterranean: Burdigalian to ?Langhian of the Rhône Basin, Vence Basin and Sardinia.

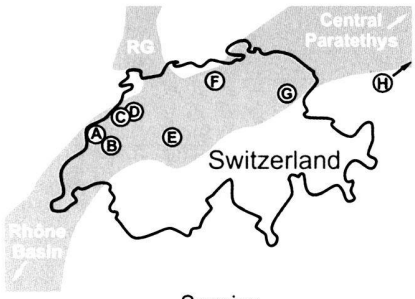
5. Discussion and conclusions

5.1. Palaeoecology

The echinoid fauna of the Belpberg Beds is of low abundance and diversity. This is in strong contrast to the mollusc fauna which is both abundant and diverse (Pfister & Wegmüller 1994, 1998, 1999, 2000, 2001). The scarcity of the echinoderm material may also account for the lack of respective publications, with the exception of occasional notes in geological mapping reports (Studer 1825; Bachmann 1867; Kissling 1890; Thalmann 1923; Rutsch 1928) and the commonly mentioned ophiuroid resting traces. The latter were interpreted as asteroid body fossils or casts (e.g. as "*Astrerias aranciacea*" by Studer 1825 and as "*Astropecten helveticus*" by Mayer 1872 and Kaufmann 1872) until critically re-studied by Seilacher (1953). The strong diagenetic alteration and lithification of the sediment may in part explain the scarcity of echinoderm remains in the Belpberg Beds. Additionally, the sedimentary facies of the succession is rather monotonous, being dominated by fine grained, sandy sediments from a setting influenced by fluvial input (cf. 2. Geological setting). Such sediments facilitate only a reduced spectrum of echinoderms, which are much more common and diverse in biogenic carbonates or fully marine clays (Smith 1984). Moreover, the lack of washable sediment reduces the chances to find rare echinoderm groups (e.g. Donovan 2001), that can in most instances only be documented by bulk sample analysis. Cidaroid remains, for example, reported as rare by earlier authors (Bachmann 1867; Kissling 1890), were not recovered.

Extant sedimentary settings similar to those documented from the Belperg Beds are inhabited by the same echinoid genera. *Echinocardium* and *Psammechinus*, for example, are very common in extant near-shore settings influenced by siliciclastic fluvial input (e.g. the German North Sea coast, Schäfer 1962; Krönke et al. 2001). Unfortunately, the majority of the reported specimens comes from scree and could not be related precisely to the horizons. It could not be established whether the species under discussion belong to a single assemblage or originate from different beds. The sediment adhering to the investigated specimens suggests the former, but provides no conclusive evidence due to the rather monotonous sedimentary succession.

Echinocardium is relatively rare in Miocene strata (Néraudeau et al. 2001; Kroh 2005), with the exception of the Burdigalian of the Southern Rhône Basin (Philippe 1998). It is usually found in infralittoral sands, often in association with echinaceans (e.g. *Psammechinus*, *Schizechinus*) and sometimes with *Spatangus* (Videt & Néraudeau 2002). In contrast *Psammechinus* is a generally found in Miocene shallow water echinoderm assemblages, both in siliciclastic and carbonate settings.



Species	Rhône Basin	Swiss Molasse							Central Paratethys
		Ⓐ Les Verrières, NE	Ⓑ Ste-Croix, VD	Ⓒ La Chaux-de-Fonds, NE	Ⓓ Crêt du Locle, NE	Ⓔ Berne Region	Ⓕ Aargau Region	Ⓖ St. Gallen Region	Ⓗ Eggenburg Region
Prionocidaris avenionensis (DES MOULINS 1837)	6		3, 5	1, 3, 5					
Cidaroida indet.						2, 4			
Arbacia catenata (DESOR 1858)	6			5					7
Psammechinus dubius dubius (AGASSIZ 1840)	6	3, 5	3, 5	1, 3, 5	5	x			7
Parascutella paulensis (AGASSIZ 1841)	6					3	3		7
Echinolampas scutiformis (LESKE 1778)	6	3, 5		3, 5					
Schizaster sp.	6				5				
Brissopsis crescentica WRIGHT 1855	6	3, 5							
Spatangus delphinus DEFRANCE 1827	6	3, 5							
Echinocardium deikei (DESOR 1858)						x		3	
Echinocardium depressum (AGASSIZ 1847)	6			5	5				7
Hemipatagus ocellatus (DEFRANCE 1827)	6	3, 5		1, 3, 5		x			7

1 by AGASSIZ 1839, 1840; 2 by BACHMANN 1867; 3 by DE LORIOL 1875, 1876; 4 by KISSLING 1890; 5 by LAMBERT 1925; 6 by PHILIPPE 1998; 7 by KROH 2005; x in the present paper; NE = Neuenburg; RG = Rhine Graben; VD = Vaud

Fig. 9. Comparison of the Belpberg echinoid fauna with that of the whole Swiss Molasse and its adjacent basins (Rhône Basin and Central Paratethys). The inset shows the position of the localities mentioned in the table and the general distribution of the marine Molasse sediments (in grey).

Various authors have commented on the potential environmental preferences of fossil species of *Psammechinus*, noting a possible association with detrital facies, coralline algal debris, seagrass meadows, and possibly reefal environments (Roman 1984; Roman & Lachkhem 1993; Blondel & Philippe 1992). *Psammechinus dubius dubius* is morphologically similar to the extant *P. miliaris*, the ecology of which is well known thanks to ecological and aquacultural studies (Kelly & Cook 2001 for a synthesis). *Psammechinus miliaris* is an omnivore, found in a variety of habitats from low tide level to deeper, sublittoral settings (down to 100 m depth). It is obviously not very selective in respect to the settled sediment, as it has been reported from boulders and rocky bottoms, as well as sands and mud. In many cases, *P. miliaris* is associated with brown algal patches, oyster banks and *Zostera* meadows.

Hemipatagus ocellatus is usually encountered in coarse sands and biodetrites in shallow-water palaeoenvironments (Roman 1984; Kroh & Harzhauser 1999). It probably had similar ecological requirements as the members of its most closely related extant genus, *Lovenia*, which is a shallow burrowing detrivore living in sand or gravel bottoms in sheltered settings from the low tide zone of the sublittoral (Miskelly 2002; Schultz 2005).

5.2. Biostratigraphy

From a biostratigraphic point of view, the dating indicated from the echinoids of the Belpberg Beds is consistent with that defined earlier based on microfossils, which indicated Early to Middle Burdigalian age (Schoepfer 1989). Based on the ranges of the studied taxa in the Western and Central Paratethys, the presence of *Psammechinus dubius dubius* and *Hemipatagus ocellatus?* indicates a late Early Burdigalian, respectively Late Eggenburgian age (cf. Kroh 2005). Although they have also been mentioned from younger strata of the Central Paratethys, these records were interpreted as doubtful notably because of misidentifications (Kroh 2005).

5.3. Palaeobiogeography

The Swiss Molasse Basin is a transitional area between the French Rhône Basin (westwards) and the Central Paratethys

(eastwards) (Fig.9). As such it is a key region for the understanding of the biogeographic relation of these two areas. The Belpberg echinoid fauna, despite its low diversity, includes forms common to both the Rhône Basin and the Central Paratethyan faunas. This is consistent with the echinoid fauna of the whole Swiss Molasse (Fig. 9). All species, except one (*E. deikei*), reported from the Swiss Molasse are also found in the Rhône Basin, and about 50 percent of the species are shared with the Eggenburg region of the Central Paratethys. This can be interpreted as a further evidence to support the theory of an echinoid immigration of the Late Eggenburgian (Early Miocene) Central Paratethyan forms via the Molasse trough (Kroh & Harzhauser 1999).

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