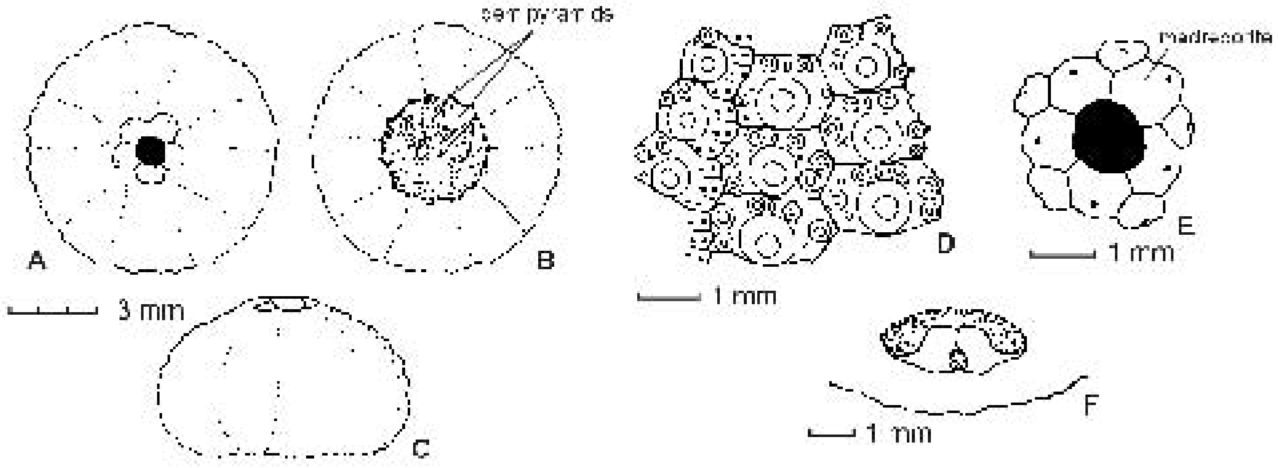

Figure 16: *Psammechinus* sp. juv.: aboral (A), oral (B) and lateral view (C), detail of supra-ambital tuberculation (D), apical disc (E) and apophyses (F) (Fürnkranz coll.; Oslip, Bgld).

tributed to the genus *Psammechinus* on base of the tuberculation pattern. Despite the good preservation of the individual ossicles (no rim cement) a specific determination of such small (young) specimens is difficult. The tuberculation patterns are similar to those of the Early Miocene species *Psammechinus dubius dubius* (see above), but not identical. Until more material becomes available this species is left in open nomenclature.

Additionally, disarticulated coronal plates from the Badenian of Gainfarn are attributed to the genus *Psammechinus*. Poor preservation, lack of whole coronas and the scarcity of the material preclude a more refined determination at the time being.

The material discussed under this heading is identifiable to genus rank only. Its unified discussion under the heading "*Psammechinus* sp." does not imply that they are conspecific.

Psammechinus sp. is mentioned several times in the geological literature of Austria. These records could not be revised, since the material on which they are based could not be located. Some of them might actually be based on misidentified *Schizechinus* or *Arbacina* species.

Juvenile *Psammechinus* specimens (Figs. 16.A-F) can be distinguished from juvenile *Arbacina* specimens by their less dense secondary tuberculation and from *Schizechinus* by the lack of finely granular surface between the tubercles.

Occurrence:

Austria: Ottnangian (Late Burdigalian), Badenian (Langhian-Early Serravallian)

Molasse Zone: Allerding, OÖ ([Danninger coll.])

Vienna Basin: Gainfarn, NÖ (Kroh, 2002b [NHMW]); ? Müllendorf (Mühlendorfer Kreide AG quarry), Bgld (Schaffer, 1961); ? Steinebrunn (= Steinabrunn), NÖ (Sieber, 1958b)

Paratethys (non-Austrian occurrences): Badenian (Langhian-Early Serravallian)

Molasse Zone: Kralice nad Oslavou (= Kralitz), Moravia, Czech Republic (Toula, 1893);

Fore-Carpathian Basin: ? Korytnica Clays, Korytnica, Poland (Mączyńska, 1987); ? Mykolaiv (= Mikołajów), S of Lwów, western Ukraine (Hilber, 1882)

Family Echinometridae Gray, 1825
Genus *Echinometra* Gray, 1825

Type-species: *Echinus lucunter* Linné, 1758, p. 665; by original designation (Gray, 1825: 426).

Diagnosis: Test oval in outline, with long axis passing through ocular I and genital plate 3. Apical disc dicyclic to hemicyclic (ocular V commonly exsert). Ambulacra polygeminate with 4-10 pore-pairs. Pore pairs arranged in arcs in the type species; arcs separated by adradial secondary tubercles. One large imperforate, noncrenulate primary tubercle on each ambulacral and interambulacral plate. Peristome subcircular to slightly oval, with shallow gill slits. No phyllodes. Spines stout and pointed; usually a little less than the test diameter long (modified from Fell & Pawson 1966 and Smith "*The Echinoid Directory*", 26.01.04)

Distribution: Early Miocene to Recent – circumtropical

Echinometra mathaei (de Blainville, 1825)

(Pl. 16, Figs. 1a-f)

* 1825 *Echinus mathaei* – de Blainville: tome 37, p. 94 [not seen; fide Philippe (1998)]
* 1902 *Echinometra miocenica* – de Loriol: 12-13; pl. 3, figs. 4-5 [not seen; fide Philippe (1998)]

1906 *Echinometra lucunter* (Leske). – Gregory: 253 [misidentified *E. mathaei* fide Philippe (1998)]

1910a *Ellipsechinus miocenicus* de Loriol (*Echinometra*), 1902. – Lambert: 47-48; pl. 3, figs. 21-23

1913a *Echinometra miocenica* de Loriol. – Cottreau: 85-86; text-fig. 12

1931 *Echinometra mathaei* (de Blainville) – Brighton: 324

1943b *Echinometra Mathaei* (Balinville). – Mortensen: 381-393; figs. 155-194; pl. 42, figs. 1-10; pl. 47, figs. 1-4; pl. 65, figs. 16-26 [cum. syn.]

1960 *Echinometra miocenica* Loriol 1902 – Kojumdgieva & Strachimirov: 229; pl. 9, fig. 2a-c

? 1968 *Echinometra miocenica* Lor. – Stancu & Andreescu: 466, 468, tab.; fig. 79 [very small juvenile, ~2-3 mm TL]

1981 *Echinometra mathaei* (Blainville, 1825) Blainville, 1830 – Dollfuss & Roman: 7274; pl. 18, figs. 3-6; pl. 19, figs. 5-7

1985 *Echinometra mathaei* (Blainville) – Ali: 285; fig. 3

. 1990 *Echinometra mathaei* (Blainville) – Negretti et al.: 446-450; pl. 1, figs. 1-4; pl. 2, figs. 1-4

. 1998 *Echinometra mathaei* (de Blainville, 1825) – Philippe: 78-81; pl. 6, figs. 1-4

v. 2004a *Echinometra mathaei* – Kroh: 229

Material:
Badenian (Langhian-Early Serravallian) – Hundsheim, near Deutsch Altenburg, NÖ, Austria
NHMW: 1 specimen (NHMW 1939 No.2)

Dimensions (in mm)**:**

Inv. No.	TL	TW	TH	ps ø
NHMW 1939 No.2	38.9	32.8	18.6	17.5

Description:
Size and shape: Test of medium size with oval outline. In profile test cushion-shaped with tumid ambitus. Oral surface slightly concave in lateral view.
Apical disc: not preserved
Ambulacra: The ambulacra consist of tetrageminate plates of the echinoid compound type. In some of the ambulacra there few quinquegeminate plates in the aboral part of the ambulacra {IIb: 3rd plate, IIIb: 4th plate, IVa: 3rd and 5th plates, IVb: 3rd plate, Va: 6th and 7th plates, Vb: 6th plate [counted from the (missing) apical disc towards the ambitus; numbering of ambulacra based on the assumption that the long axis passes through ocular I and genital plate 3 as in the extant specimens]}. The pores are partitioned isopores and belong to the P1 type aborally, respectively P2 to P3 type adorally. The pore pairs are arranged in arcs, separated by adradial secondary tubercles. Each plate bears one large noncrenulate, imperforate marginal tubercle and few small inner tubercles. The ambulacra are nearly half as wide as the interambulacra at the ambitus.
Interambulacra: Each interambulacral plate bears one large noncrenulate, imperforate primary tubercle, situated halfway along the adoral margin of the plate. Secondary tuberculation consists of a vertical adradial row of tubercles in each half-interambulacrum and a zigzagging row of secondary tubercles along the interradial suture. Remaining secondary/miliary tubercles small and inconspicuous.
Peristome: The peristome is large and has a subcircular outline. Shallow gill slits are present.
Periproct: not preserved

Discussion:
Comparison with extant specimens of *Echinometra mathaei* from the Philippines revealed no significant differences, besides a slightly smaller peristome (relative to overall size) and slightly smaller primary tubercles. These two features vary, however, also within the extant material at hand and are considered irrelevant. Like in the fossil specimens, some of the extant specimens also have few quinquegeminate plates in their aboral ambulacra. For a throughout synonymy, biogeographical data of the extant animals and differential diagnoses for this and the other living congeners see Mortensen (1943b).

Echinometra miocenica de Loriol, 1902 from the Early Miocene of Southern France was placed in the synonymy of *E. mathaei* by Negretti et al. (1990) and recently re-described by Philippe (1998).

This record is just the third record of *Echinometra* from the Paratethys and the first one from Austria. The first record is from Bulgaria and is based on two specimens, one of them well preserved. (Kojumdgieva & Strachimirov, 1960). The second record, from Romania (Stancu & Andreescu, 1968), is dubious as it is based on an extremely small juvenile (TL ~ 2-3 mm). Although highly abundant in extant settings (see below) *Echinometra* is obviously extremely rare in the sediments of the Mediterranean and the Paratethys. The reason for the rarity of this genus is connected to the poor preservation potential in its preferred habitat (Kier, 1977: 171; Greenstein, 1993: 590-591, appendix; compare also Donovan & Gordon, 1993) and the poor preservation potential of these rocky intertidal and extremely shallow subtidal environments, where erosion prevails (Kier, 1977: 171; Schopf, 1978: 267). The situation is similar in the Caribbean, where two extant species of *Echinometra* occur abundantly in the shallow water habitats, yet are only rarely documented in the fossils record (Gordon, 1991; Gordon & Donovan, 1992; Donovan & Gordon, 1993; Donovan & Collins, 1997).

Palaeoecology:
Today *Echinometra mathaei* lives in the rocky intertidal and sublittoral down to approximately 30 metres. The population density can be quite high (up to 100 animals/m^2) and thus this species is an important bioeroder and sediment producer. *E. mathaei*, like its congeners, is restricted to the tropical climate zone. Successful reproduction takes place in a narrow temperature interval between 28 to 36° C, although normal development only occurs at temperatures below 34° C (Rupp, 1973). The animals are epibenthic grazers and feed mainly upon epi- and endolithic algae, as well as on algal drift (McClanahan & Muthiga, 2001). *Echinometra* forms boreholes in the rocky intertidal by repeatedly removal of the uppermost millimetres of rock with its lantern. These boreholes are a common feature of the upper margin of rocky intertidal and reef flat zones, where they form a distinct zone at mean low water line (Schoppe & Werdings, 1996).

The single specimen from Hundsheim lacks ambital tuberculation in the columns 3b, IVa, IVb, 4a and 4b. There the test surface is scratched by irregularly arranged grooves (Pl. 16, Fig. 1d). Some of these grooves are arranged in an inconspicuous stellate pattern. These traces are interpreted as gnawing marks/grazing traces produced by regular sea urchins (probably by this species [not specimen] itself). Such gnawing marks have been introduced as *Gnathichnus pentax* Bromley, 1975 into the trace fossil literature (see Bromley, 1975). Later several other ichnospecies have been established for similar traces (Michalik, 1977; Breton et al., 1992), but their validity has been questioned (Radwańska, 1999). Such traces have been found on a variety of substrates including other echinoids, crinoids, asteroids, brachiopods, oysters, and others (Bromley, 1975; Radwańska, 1999; Neumann, 2000; Carrasco, 2003 and references therein). Some patches of epibiont overgrowth of corallinaceans and (subsidiary) bryozoans is still preserved on the studied specimen.

Occurrence:

Austria: Badenian (Langhian-Early Serravallian)
Vienna Basin: Hundsheim, near Deutsch Altenburg, NÖ (Kroh, 2004a; [NHMW])

Paratethys (non-Austrian occurrences): Badenian (Langhian-Early Serravallian)
Transylvanian Basin: Rugi-Delineşti, Romania (Stancu & Andreescu, 1968)
Lom Basin (Bulgaria): Ochrid, Palilula, and Urovene, Northern Bulgaria (Kojumdgieva & Strachimirov, 1960)

Mediterranean: Late Burdigalian or Tortonian
Western Mediterranean: Florinas, Sardinia (Negretti et al., 1990)
Rhône Basin: Sériège, Hérault, France (de Loriol, 1902; Lambert, 1910a; Cottreau, 1913a; Negretti et al., 1990; Philippe, 1998)

Indian Ocean and Red Sea: Early Pliocene to Recent (see Mortensen, 1943b; Dollfuss & Roman, 1981; Ali, 1985)

Family Toxopneustidae Troschel, 1872
Genus *Schizechinus* Pomel, 1869

Type-species: see remarks
Diagnosis: Corona large, more or less hemispherical; ambulacral plates trigeminate with a single marginal tubercle on each; inner tubercles form regular series parallel to the marginal series; interambulacra with up to 6 rows of subequal tubercles

(secondary tubercles nearly as large as primary tubercle) in each half ambulacrum; apical disc hemicyclic with oculars I and V insert; peristome with distinct, moderately deep gill slits (strongly modified from Fell & Pawson, 1966).
<u>Distribution</u>: Miocene to Pliocene – circum-Mediterranean
<u>Remarks</u>: Lambert & Thiéry (1914: 247) designated *Anapesus tuberculatus* Pomel, 1887 as type-species of this genus. As this species was not included into original paper of Pomel (1869: XLII) this cannot be a valid designation (ICZN, 4th ed.). Three of the four species mentioned by Pomel (1869) are extant forms that are not at all related with what is considered as *Schizechinus* today. As the fourth species (*Echinus serresii* des Moulins, 1837) is a hybrid species (of a Late Cretaceous taxon and an Early Miocene one) a proposal to the ICZN was submitted to suppress *E. serressii* des Moulins, 1837, to validate *Echinus serresii* Agassiz & Desor, 1846 and designate the latter as type-species of *Schizechinus* (decision pending).
<u>Palaeoecology and biogeography</u>: As the genus *Schizechinus* is only known from fossils little is known on its biology. It occurs commonly in carbonatic and less commonly siliciclastic shallow water sediments throughout the Mediterranean and the Central Paratethys. It is common in Northern Africa (from Morocco in the west to Egypt in the East), Saudi Arabian and reaches a far north as Poland and the western Ukraine. Recently it has also been reported from the Miocene of Barrow Island in north-western Australia (McNamara & Kendrick, 1994) and the Pliocene of Papua New Guinea (Lindley, 2003).

Schizechinus seems to be closely related to the extant *Sphaerechinus*, a monotypic genus of the Mediterranean and Eastern Atlantic Ocean. In the Mediterranean *S. granularis* occurs between 1 to 120 m depth, but is commonest between 8-12 metres, on coarse sandy to gravel bottoms with sea grass (Riedl, 1983; Ernst, 1973a). According to Ernst (1973a), however, water depth is not relevant for the distribution of this echinoid, instead it is controlled by the presence of suitable substrates and most important the presence of macroalgae on which the urchin feeds.

Schizechinus hungaricus (Laube, 1869)

(Figs. 17-19; Pl. 17, Figs. 1-6; Pl. 18, Figs. 1-19)

	1869a	*Psammechinus Serresii* Desmou. sp. – Laube: 182
pp	1869a	*Psammechinus mirabilis* Nicolet sp. – Laube: 182
	1869a	*Psammechinus Duciei* Wright. – Laube: 182
* v.	1869a	*Echinus hungaricus* Laube. – Laube: 182
# v.	1869a	*Echinus dux* Laube. – Laube: 182
	1870	*Psammechinus Serresii* Derm. – Laube: 314
pp	1870	*Psammechinus mirabilis* Nic. – Laube: 314
	1870	*Psammechinus Duciei* Wright. – Laube: 314
v.	1870	*Echinus dux* Laube. – Laube: 314
v.	1870	*Echinus hungaricus* Laube. – Laube: 314
	1871	*Psammechinus Serresii* Desmoulins sp. – Laube: 58-59
pp	1871	*Psammechinus mirabilis* Nicolet sp. – Laube: 59
	1871	*Psammechinus Duciei* Wright. – Laube: 59
v.	1871	*Echinus hungaricus* Laube. – Laube: 60-61; pl. 16, figs. 3, 3a
v.	1871	*Echinus dux* Laube. – Laube: 60; pl. 16, figs. 2, 2a
non	1880b	*Echinus hungaricus*, Laube. – Manzoni: 330-331 [= *Schizechinus serialis* Pomel, 1887, fide Borghi (1993: 9)]
pp	1891	*Echinus duciei*, Wright, 1855. – Gregory: 590
pp	1891	*Echinus hungaricus*, Laube, 1871. – Gregory: 592
	1892a	*Echinus* cf. *Hungaricus* Laube. – Procházka: 734, 743
non	1897	*Echinus hungaricus* Laube. – Vinassa de Regny: 147 [= *Schizechinus serialis* Pomel, 1887, fide Borghi (1993: 9)]
non	1898	*Echinus aff. hungaricus* Laub. – Airaghi: 364; pl. 1, fig. 4 [= *Schizechinus serialis* Pomel, 1887, fide Borghi (1993)]
non	1901	*Anapesus hungaricus* (Lbe.) Lamb. – Airaghi: 174; pl. 19 (1), fig. 3
non	1908	*Echinus hungaricus* Lbe. – Airaghi: 255, 256-257, 259 [= *Schizechinus serialis* Pomel, 1887, fide Borghi (1993: 9)]
	1930	*Schizechinus hungaricus* Laube. – Vendl: 76
	1953	*Schizechinus duciei* (Wright), 1855 – Szörényi: 12, 58-59; pl. 8, figs. 1, 1a, 2
	1953	*Schizechinus hungaricus* (Laube), 1871 – Szörényi: 12, 59-60; pl. 1, fig. 1
?	1958a	*Schizechinus duciei* (Wright) – Sieber: 152
?	1979	*Schizechinus duciei* (Wright, 1855) – Mączyńska: 30, pl. 1, figs. 3-5
	1979	*Schizechinus dux* (Laube, 1871) – Mączyńska: 30-31, pl. 1, fig. 6; pl. 2, fig. 1
	1988	*Schizechinus dux* (Laube, 1871) – Mączyńska: 60; pl. 1, fig. 10-11
	1988	*Schizechinus* cf. *hungaricus* (Laube, 1871) – Mączyńska: 60; pl. 2, fig. 2
? pp	1988	*Arbacina* sp. – Mączyńska: 60; pl. 1, fig. 5 [misidentification]
v.	1998	*Psammechinus mirabilis* Nicolet – Schultz: 116; pl. 52b, figs. 6
v.	2001	*Schizechinus dux* (Laube) – Schmid et al.: 13; pl. 2; pl. 3, fig. 1
v.	2002	*Schizechinus* – Nebelsick & Kroh: 381

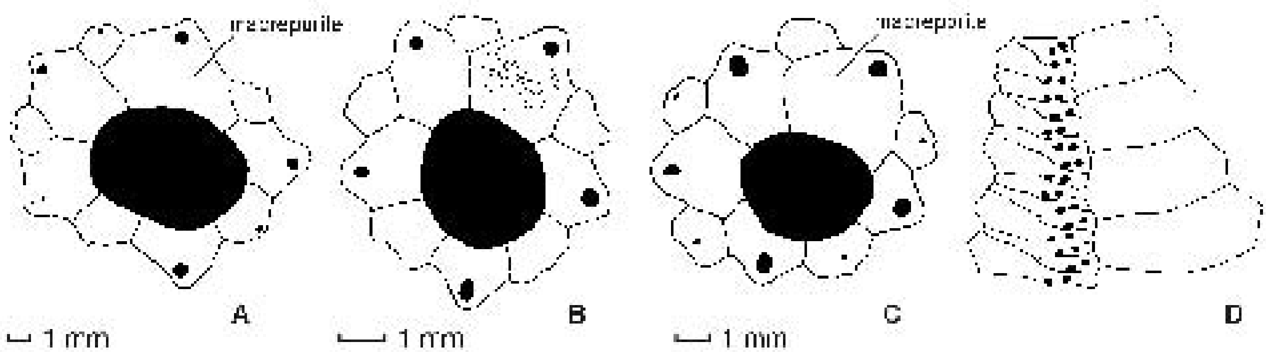

Figure 17: *Schizechinus hungaricus* (Laube, 1869): apical disc (A-C) and ambulacral plate structure (D) (A: St. Margarethen, Bgld, NHMW 1986/118/1; B: Winden, Bgld, Wanzenböck coll.; C: Oslip, Bgld, Wanzenböck coll.; D: Winden, Bgld, NHMW 1992/0084). In the great majority of the specimens oculars I and V are insert, in a single, abnorm specimen (C) only ocular I is insert. Figure A was drawn from the inside of the test and is mirrored for easier comparison.

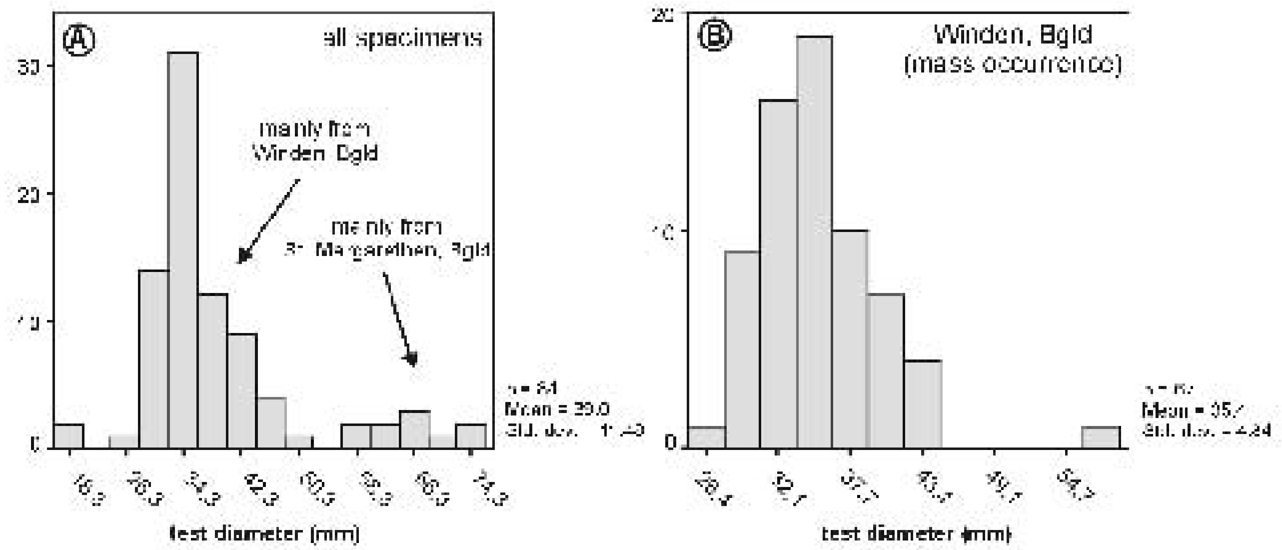

Figure 18: *Schizechinus hungaricus* (Laube, 1869): size frequency diagrams of all specimens (A) and the subset from the mass occurrence at Winden, Bgld (B).

Type-material:
<u>*Echinus hungaricus* Laube, 1869</u>:
Holotype: specimen MAFI Ech 227 from Bia, Hungary, figured by Laube (1871: pl. 16, figs. 3, 3a); located in the collection of the Geological Museum at the Geological Survey of Hungary in Budapest.
Locus typicus: Biatorbágy (= Bia), Hungary
Stratum typicum: Leitha limestone
Age: Late Badenian (Early Serravallian), Middle Miocene

<u>*Echinus dux* Laube, 1869</u>:
Lectotype (designated herein; Pl. 17, Fig. 4): specimen NHMW 1859.XLV.632 from Steinebrunn, figured by Laube (1871: pl. 16, figs. 2, 2a); located in the Naturhistorisches Museum Wien.
Locus typicus: Steinebrunn (formerly Steinabrunn), NÖ
Age: Badenian (Langhian-Early Serravallian), Middle Miocene
Remarks: The second specimen mentioned by Laube (1871: 60) from Valtice (= Feldsberg), Czech Republic could not be located in the Austrian and Hungarian collections.

Material:
Early Badenian (Langhian) – Wiesfleck (sandpit Hohlreich), Bgld, Austria
NHMW: 1 specimen (NHMW 2004z0001/0031)
Badenian (Langhian-Early Serravallian) – Purbach, Bgld, Austria
NHMW: 2 specimens (NHMW 2003z0033/0002-3)
Badenian (Langhian-Early Serravallian) – Ritzing, Bgld, Austria
NHMW: 1 specimen (NHMW 1848.III.61)
Badenian (Langhian-Early Serravallian) – Steinebrunn (formerly Steinabrunn), NÖ, Austria
NHMW: 1 corona (**lectotype** of *E. dux* Laube, 1869; NHMW 1859.XLV.632), 1 test fragment (NHMW 1861.XXXV.138), 2 coronas (NHMW A1050, 1997z0178/0771)
Late Badenian (Early Serravallian) – Biatorbágy (= Bia), Hungary
MAFI: 1 specimen [MAFI Ech 227 (**holotype** of *Echinus hungaricus* Vadász, 1915)]
Late Badenian (Early Serravallian) – St. Margarethen (Kummer quarry), Bgld, Austria
NHMW: 1 test fragment (NHMW 1976/1844/53)
Wanzenböck coll.: slab with three specimens preserving spines and lantern (no inv. no.)
Late Badenian (Early Serravallian) – Winden (Nirgl quarry, N of the village), Bgld, Austria
NHMW: 4 test fragments, 1 demipyramid (NHMW 1859.L.831a)
Late Badenian (Early Serravallian) – Winden [old quarry, N of the Ludlloch (cave), N of the village], Bgld, Austria
NHMW: 62 specimens (NHMW 1992/0084), 80 partially fragmented coronas (2004z0003/0001), 1 partial corona (NHMW 2004z0001/0025a), 182 test fragments (NHMW 2003z0082/0001, ../0025, ../0029-30), 5 genital plates (NHMW 2003z0082/0002, ../0026-27), 113 demipyramids (NHMW 2003z0082/0003, ../0010-12), 11 epiphyses (NHMW 2003z0082/0004, ../0020-21), 42 rotulae (NHMW 2003z0082/0005, ../0014-17), 11 teeth (NHMW 2003z0082/0006, ../0013), 112 spines (NHMW 2003z0082/0007, ../0022-24, ../0028, ../0043-45), 2 compass elements (NHMW 2003z0082/00018-19)

Dimensions (in mm)**:**

Inv. No.	test ø	TH	ps ø	pc ø
NHMW 2004z0001/0031	16.8	8.8	~ 7.8	-
NHMW 1848.III.61	~28	13.8	-	-
NHMW A1050	33.8	17.3	-	2.7
NHMW 1859.XLV.632	~ 47	23.7	-	-

Description:
<u>Size and shape</u>: The test is of medium to large size, ranging from 15 to 75 mm test diameter in the material studied. The outline of the test is circular to very slightly pentagonal. In profile the test is moderately high and arched to high and domed. The ambitus is tumid.
<u>Apical disc</u>: The apical disc lies centrally on the aboral side, it is relatively small, measuring between 15 to 17 % TL along the III-5 axis. It is hemicyclic, oculars I and V being insert, all others exsert (Figs. 17.A-B). The only exception is a single specimen from Oslip, Bgld (coll. Wanzenböck) in which only ocular I is insert (Figs. 17.C). The genital plates are large and perforated by a single rounded gonopore. The madreporite is the largest of the genital plates and bears many small madreporic pores. The ocular plates are much smaller than the genital plates and bear a small ocular pore each.
<u>Ambulacra</u>: The ambulacra consist of trigeminate plates compound in the echinoid type (Fig. 17.D). The pores are partitioned isopores of the P2 type and are arranged in arches of three. Adjacent pore pairs are separated by broad, granulate

walls. Each plate bears one large noncrenulate, imperforate marginal tubercle with undercut mamelon and several smaller inner tubercles. The one lying perradially to the marginal tubercle is distinctly enlarged and nearly as large as the marginal tubercle in ambital ambulacral plates. This feature forms a pattern of four parallel series of tubercles per ambulacrum. The interporiferous zone of a single ambulacral column is about one and a half times as wide as the poriferous zone at the ambitus.

Interambulacra: The interambulacra are about twice as wide as the ambulacra at the ambitus. Each plate bears one large noncrenulate, imperforate primary tubercle with undercut mamelon. The secondary tubercles besides the primary tubercles are distinctly enlarged and nearly as large at the ambitus. They form regular series parallel to the series of primary tubercles on the ambulacra. The number of enlarged secondary tubercles per plate increases from the apex, where they are not present, or only slightly enlarged, to the ambitus. In large specimens there may be as many as six parallel rows in each half interambulacrum. On each second plate the number of enlarged secondary tubercles adradial to the primary tubercle is doubled vertically (compare Pl. 17, Fig. 6). "Normal" secondary tubercles and miliary tubercles are spread loosely among the larger tubercles, but are most common along the adapical border of each plate.

Peristome: Peristome circular with moderately deep gill slits. The diameter of the peristome varies between 30 and 33 % test diameter. Auricles are present in the perignathic girdle.

Periproct: The periproct is irregularly oval and elongated roughly along the 1-IV or I-3 axis. Its long axis is about 50 to 55 % of the length of the apical disc respectively 7.3 – 9.5 % of TL.

Spines: The spines are short, with a smooth base, a granulated ring and noncrenulate acetabulum. The shaft is longitudinally striated.

Lantern: The lantern is camarodont, the foramen magnum is closed by the epiphyses. The demipyramids are camarodont demipyramids, with a striated interpyramidal face and a well developed styloid process. The shape of the rotulae and compass elements can be seen on Plate 18 (rotulae: Figs. 5-8; compass elements: Figs. 9-10). The teeth are keeled and have a bluntly pointed tip.

Differential diagnosis:

S. duciei (Wright, 1855), a species from the Messinian of Malta, differs from the species considered here by its consistently flatter profile and the presence of zigzagging walls between the pore pairs (Wright, 1855; Cottreau, 1913a; Challis, 1980; but see discussion). *S. saheliensis* (Pomel) was considered a synonym of the former species by Cottreau (1913a). *S. pentagonalis* (Kier, 1972), from the Miocene of Saudi Arabia and Iran (NHMW coll.), differs by its pentagonal outline and less prominent tuberculation. *S. angulatus* (Pomel, 1887) has also a markedly pentagonal outline. *S. tuberculatus* (Pomel, 1887) has much larger gill slits, judging by Pomel's figure, but is otherwise very similar. *S. chateleti* Lambert, 1910 is based on a single specimen of dubious provenience and is probably synonymous to *S. duciei* (Philippe, 1998). *S. serialis* Pomel, 1887 from the Pliocene of Algeria and Northern Italy differs by its more prominent gill slits, higher ambital interambulacral plates (usually 25% of plate width; vs. ~ 20 % in *S. hungaricus*) and smaller tubercles (diameter usually ~ 50% of corresponding plate height vs. ~ 70% in *S. hungaricus*) (compare Fig. 19, and description and illustrations in Borghi, 1993).

Discussion:

Until now this species has been attributed to Laube (1871). In Laube's 1869a paper, however, this species is already mentioned, accompanied by a differential diagnosis. Thus, according to the ICZN the year 1869 has to be regarded as the valid date for this species.

Although, at a first glance it may seem possible to distinguish two separate species within the material studied. More detailed investigations reveal that only overall size and height of the test separate these two morphotypes and that all other features i.e. tuberculation are identical. Statistical analysis of the complete data set (Kolmogorov-Smirnov test on normal distribution) reveals that the test diameter is not normally distributed ($p=0.002$; Fig. 18.A). Most specimens belong to the smaller morphotype and were found in a mass occurrence preserved in

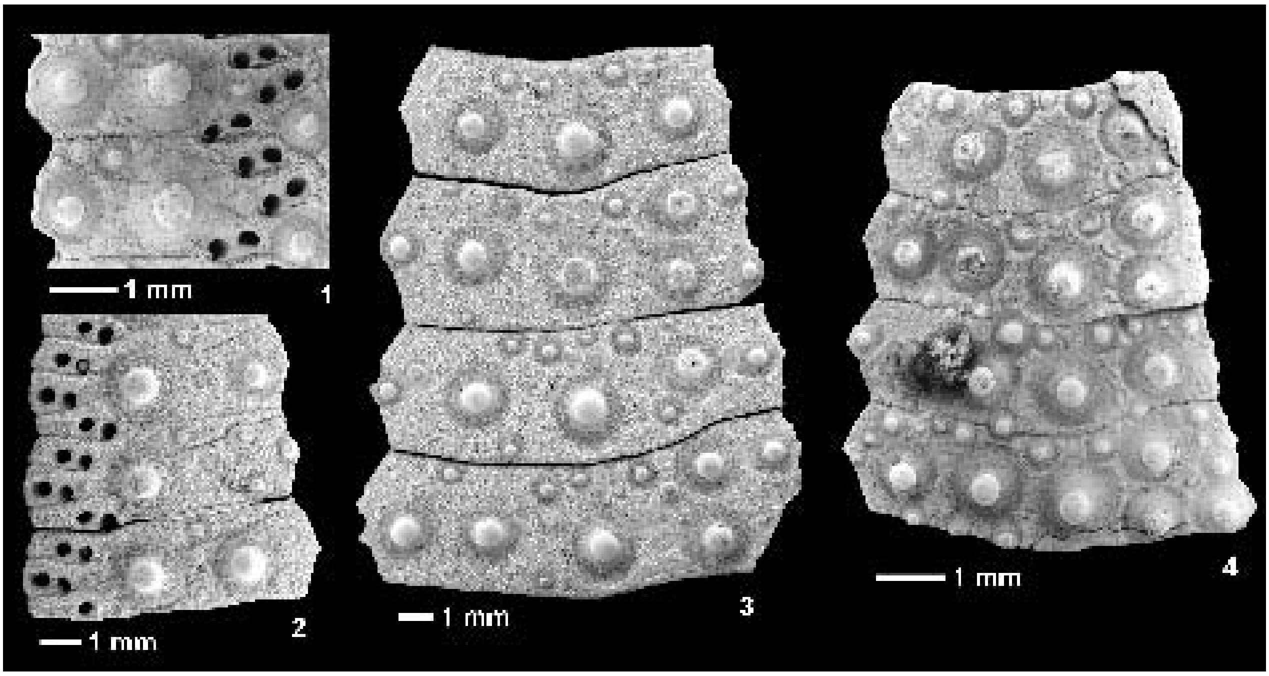

Figure 19: Comparison between *Schizechinus hungaricus* (Laube, 1869) [1, 4: Badenian (Middle Miocene) of Winden, Bgld; NHMW 2003z0082/0029-30] and *Schizaster serialis* (Pomel, 1887) [2, 3: Late Pliocene (Gelasian) of the Stirone Rive (Salsomaggiore-Parma), Northern Italy; NHMW coll., don. E. Borghi]

a single bed at the locality Winden (Bgld). This occurrence is interpreted as representing a local mass-mortality event (Kroh et al., 2002). Albeit such mass mortality events do usually not contribute significantly to the fossil record (see discussion of the *Diadema antillarum* mass mortality event in 1983-84 in Lessios, 1988 and Greenstein, 1989) in this case the skeletal material was preserved due to the special sedimentary setting. Size-frequency diagrams (Fig. 18.B) of the test diameter of the specimens from this deposit show, that only a narrow size range is preserved and that the data set is normally distributed (Kolmogorov-Smirnov test, p=0.291). Most probably only a single year-class is present in this material. Thus, the smaller morphotype is over-represented in the fossil record and is considered here as young adult of the larger morphotype.

Other authors (e.g. Laube, 1871; Mączyńska, 1979) placed the smaller morphotype into the species *Schizechinus duciei* (Wright), a species from the Messinian of Malta. According to Mączyńska (1979) *S. hungaricus* differs from *S. duciei* by the larger size of the test, flatter base and lower profile [although she states that the test height of her two specimens (of *S. dux*) "displays a considerable variability" (Mączyńska, 1979: 31)].

Here only a single species of *Schizechinus* is recognised in the Badenian (Langhian-Serravallian) strata of the Central Paratethys. The oldest available name for which is *S. hungaricus* (Laube, 1869). The relation to the Messinian *S. duciei* (Wright, 1855) from the Maltese islands remains to be investigated, but the two may well turn out to be conspecific as suggested already by Gregory (1891: 592).

The names *E. dux* and *E. hungaricus* were simultaneously published. Vinassa de Regny (1897: 147-148), following a suggestion of Manzoni (1880b: 331), placed *E. dux* in the synonymy of *E. hungaricus*. According to the ICZN rule of "the First Reviser" (4th ed., Article 24.2.) the name *E. hungaricus* thus has priority over *E. dux* (it is irrelevant in this context that the material of both Manzoni and Vinasse de Regny was not conspecific with *E. hungaricus/dux*).

According to Ernst (1973a) length/height ratio in extant regular sea urchins is very variable and clearly influenced by environmental parameters. Thus, care should be taken to overemphasis differences in the height of fossil regular echinoids, especially when the specimens come from the same or adjacent outcrops or related contemporaneous strata.

Part of the types and reference material of Laube (1869a, 1870 and 1871) could be traced in the collections of the Naturhistorisches Museum Wien (NHMW), the Geological Survey of Austria (GBA) and the Museum of the Geological Survey of Hungary (MAFI). Material attributed to the taxa *Psammechinus duciei* (Wright), *Psammechinus serresii* (des Moulins), *Psammechinus monilis* (Desmarest), *Psammechinus mirabilis* (Nicolet), *Echinus dux* Laube and *Echinus hungaricus* Laube represent growth stages of a single taxon, namely *Schizechinus hungaricus* (Laube). During the growth of *Schizechinus* (but also of many other toxopneustids, like e.g. *Sphaerechinus granularis*, *Toxopneustes pileolus*, *Tripneustes ventricosus*) the number of subequal tubercles on each interambulacral plate (and to a lesser extent on the ambulacral plates) increases. Thus a specimen with 16.8 mm TD (NHMW 2004z0001/0031, Wiesfleck, Bgld) has one large primary tubercle roughly in the centre of each plate. Ambitally one secondary tubercle on each side of the primary tubercle is distinctly enlarged in that specimen (Pl. 17, Fig. 1a-b). In another specimen (NHMW 1848.III.61, Ritzing, Bgld; referred to *P. serresii* by Laube, 1871) these two secondary tubercles are as large as the primary tubercle ambitally (Pl. 17, figs. 2a-b). In a 33.5 mm specimen (NHMW A1050, Steinabrunn, NÖ; referred to *P. mirabilis* by Laube, 1871) a third enlarged secondary tubercle appears interradially at the ambitus (Pl. 17, figs. 3a-b). In the lectotype of *E. dux* with 46.7 mm largest test diameter (NHMW 1859.XLV.632) there are already five subequal tubercles in each interambulacral column ambitally (Pl. 17, Fig. 4). Finally, in the type of *E. hungaricus* with *c*. 75 mm TD (MAFI Ech 227) there are up to six subequal tubercles on each interambulacral plate ambitally. Therefore, it is impossible to use the number of subequal tubercles in the interambulacra and ambulacra to differentiate between species in the way Laube (1871) did.

Lambert (1897: 120; in a literature review) remarked that *Echinus dux* and *E. hungaricus* are closely related to *Anapesus* Holmes, an opinion that was followed by Airaghi (1901). The later, however, is today considered as junior synonym of *Arbacia* (Fell & Pawson, 1966: U409). There is no doubt that *E. dux* and *E. hungaricus* belong to the genus *Schizechinus*, based on their multiple subequal primary tubercles, hemicyclic apical disc with oculars I and V insert and the deep gill slits.

Fragmented material of *Schizechinus* from the Badenian of Rybnica, Poland was attributed to the genus *Arbacina* (Mączyńska, 1988). This, however, can be ruled out based on tuberculation pattern and size of the fragments. This material is tentatively assigned to this species based on the co-occurrence with whole coronas at the same locality.

Occurrence:

Austria: Early to Late Badenian (Langhian-Early Serravallian)
- Vienna Basin: Steinebrunn (formerly Steinabrunn), NÖ (Laube, 1869a, 1871; ? Sieber, 1958a; Schultz, 1998; [NHMW])
- Eisenstadt-Sopron Basin: St. Margarethen (Kummer quarry), Bgld (Schmid et al., 2001; [NHMW]); Walbersdorf, Bgld (Procházka, 1892a)
- Danube Basin: Purbach, Bgld ([NHMW]); Winden, Bgld ([NHMW])
- Oberpullendorf Bay: Ritzing, Bgld (Laube, 1869a; [NHMW]); Wiesfleck, Bgld ([NHMW])

Paratethys (non-Austrian occurrences): Early to Late Badenian (Langhian-Early Serravallian)
- Vienna Basin: Úvaly (= Garschenthal), near Valtice (=Feldsberg), Czech Republic (Laube, 1869a, 1871; Gregory, 1891)
- Eisenstadt-Sopron Basin: Fertörákos, Györ-Monson-Sopron, Hungary (Vendl, 1930)
- Great Hungarian Basin (Pannonian Basin): Biatorbágy (= Bia or Bid), Pest, Hungary (Laube, 1869a, 1871; Gregory, 1891; [MAFI])
- Fore-Carpathian Basin: Huta Lubycka, southeastern Poland (Mączyńska, 1979); Monastyrz, Ukraine (Mączyńska, 1979); Potylicz, near Rawa Ruska, western Ukraine (Szörényi, 1953); Rybnica, Southern Poland (Mączyńska, 1988); Szuszkowce, near Białozurka, , Ukraine (Szörényi, 1953);? Trzęsiny, southeastern Poland (Mączyńska, 1979); Wybranówska, western Ukraine (Szörényi, 1953)

Mediterranean: unknown (but may be represented by *S. duciei*, see discussion)

Schizechinus sp.

(Pl. 12, Figs. 7-8)

v. 2002b *Schizechinus* sp. – Kroh: 12
v. 2003a *Schizechinus* sp. – Kroh: 162-163; pl. 3, figs. 7-10

Material:

Early Badenian (Langhian) – Eisenstadt (Hartl Fm., Hartl hill), Bgld, Austria
- Wanzenböck coll.: 1 test fragment (W30)

Early Badenian (Langhian) – Gainfarn, NÖ, Austria
- NHMW: 1 test fragment (NHMW 2004z0076/0006), 1 rotula (NHMW 2004z0076/0017)

Early Badenian (Langhian) – Niederleis, NÖ, Austria

NHMW: 15 test fragments (NHMW 2002z0087/0057-62, 2002z0089/0008, 2002z0090/0007-8)
Badenian (Langhian-Early Serravallian) – Grinzing, Vienna, Austria
NHMW: 2 test fragments (NHMW 1846.37.953d)
Badenian (Langhian-Early Serravallian) – Steinebrunn (formerly Steinabrunn), NÖ, Austria
NHMW: 2 test fragments with preserved apical disc (NHMW 1846.37.955)
Late Badenian (Early Serravallian) – Müllendorf (Mühlendorfer Kreide AG quarry), Bgld, Austria
NHMW: 23 juvenile coronas (NHMW 2004z0006/0004, 0021, 2004z0045/0005)
GBA: 30 juvenile coronas (GBA 2004/1/2)
Late Badenian (Early Serravallian) – St. Margarethen (Kummer quarry), Bgld, Austria
NHMW: 1 natural cast (NHMW 2004z0001/0042), 1 fragment (NHMW 2004z0001/0043)

Dimensions (juveniles)**:**
Test diameter ranging from 4.4 to 15.8 mm, most common between 7.1 and 11.8 mm
Test height ranging from 2.1 to 6.3 mm, most common between 3.4 to 5.9 mm

Description:
Ambulacra: The ambulacra consist of trigeminate plates of the echinoid compound type. The pores are partitioned isopores and are arranged in arcs of three, forming a zigzag pattern. Each plate bears one large noncrenulate, imperforate marginal tubercle with undercut mamelon and several smaller inner tubercles.
Interambulacra: Each interambulacral plate bears one large noncrenulate, imperforate primary tubercle with undercut mamelon. The secondary tubercles besides the primary tubercles are distinctly enlarged, forming a horizontal row. The number of these subequal tubercles increases with test size and position on the corona. On many plates (usually every second plate, at the ambitus) there are two enlarged secondary tubercles arranged in a vertical row adradially of the primary tubercle. "Normal" secondary tubercles and miliary tubercles are spread loosely among the larger tubercles, but are, commonest along the adapical border of each plate.
Peristome: The peristome shows moderately deep gill slits.

Discussion:
Although the material is highly fragmentary it can be assigned to the genus *Schizechinus* without much doubt. Based on a comparison with specimens of *Schizechinus* from Winden and St. Margarethen (Bgld, Austria), where this genus is fairly common and where specimens preserving apical disc, associated spines and jaws are known (compare e.g. Schmid et al., 2001: pl. 2; pl. 3, fig. 1). Diagnostic features are the tuberculation pattern, the arrangement of the ambulacral pores and the presence of moderately deep gill slits. Although most of the remains will probably belong to *S. hungaricus* (Laube, 1869) (see above), this cannot be proven as such fragmentary and disarticulated material lacks enough diagnostic features for identification to species level.
Juvenile of *Schizechinus* (e.g. Pl. 12, Figs. 7-8) are easily confused with juveniles and subadult specimens of the genera *Arbacina* and *Psammechinus*. In *Schizechinus*, however, secondary tuberculation is always less dense and the primary tubercles are larger than in the other two genera. Moreover, the remaining surface of the coronal plates (i.e. that not occupied by tubercles) is always distinctly granular, a feature not present in the other two genera.

Occurrence:
Austria: Early to Late Badenian (Langhian Early Serravallian)
Vienna Basin: Gainfarn, NÖ (Kroh, 2002b; [NHMW]); Grinzing, W ([NHMW]); Müllendorf (Mühlendorfer Kreide AG quarry), Bgld ([GBA]; [NHMW]); Niederleis, NÖ (Kroh, 2003a; [NHMW]); Steinebrunn (formerly Steinabrunn), NÖ ([NHMW])
Eisenstadt-Sopron Basin: Eisenstadt (Hartl Fm., Hartl hill), Bgld, ([NHMW]); St. Margarethen (Kummer quarry), Bgld ([NHMW])

Genus *Tripneustes* Agassiz, 1841b

Type-species: *Echinus ventricosus* Lamarck, 1816, by original designation (Agassiz, 1841b: 7).
Diagnosis: Corona large, hemispherical to sub-spherical; ambulacra trigeminate with primary tubercles on each 3rd or 4th plate; ambulacral pores arranged in three vertical series in each half ambulacrum; conspicuous naked median space in both ambulacra and interambulacra; apical disc with oculars I and V insert (modified from Fell & Pawson, 1966).
Distribution: Early Miocene to Recent – circumtropical
Ecology and biogeography: Extant *Tripneustes ventricosus* lives in subtidal environments between 0 to 55 metres (Hendler et al., 1995), where it inhabits a variety of habitats ranging from coral reefs to sea grass beds on sand bottoms (compare data summarised in Lawrence & Agatsuma, 2001: tab. 1). Juveniles may also be common in the intertidal, but adults are generally restricted to the subtidal (Moore et al., 1963). Most records are from *Thalassa testudinum* sea grass beds, where it reaches densities of up to 2.5 individuals/m² (Lawrence & Agatsuma, 2001: tab. 1, 2). Data reported for *T. gratilla* are comparable, although densities up to 20 individuals/m² are reported (during spawning periods, Régis & Thomassin 1982) and depth range of this species is larger (0-75 metres, Mortensen, 1943a). Extant *Tripneustes* feed mainly on sea grass and (to a lesser extent) macro algae, although coralline algae and other endolithic microalgae are also reported. Variation of diet seems to depend on availability and habitat (Lawrence & Agatsuma, 2001). Growth in extant *Tripneustes* is very rapid cage experiments by Lewis (1960) showed that the urchins reach test diameters of about 80 to 90 mm in the first year and had a life span of about two years.
Today *Tripneustes* is limited to the tropical climate zone, its poleward distribution being limited by temperature. Successful reproduction and normal embryonic development is limited to a narrow temperature range. The critical temperature for spawning lies around 22 °C in *T. ventricosus* (Moore et al., 1963), below it spawning does not occur. Plutei mortality at 20 and 30 °C is *c.* 100 % in contrast to 10 % at 25 °C (Cameron et al., 1985). Individual animals can withstand winter temperatures below 15 °C (*T. gratilla*, Dafni, 1992), but mass mortalities have been reported to occur when the temperature drops below 20 °C (*T. gratilla*: Tokioka, 1963, 1966; *T. ventricosus*: Moore et al.,1963). The highest latitude of *T. gratilla* is in the south-eastern Pacific Easter Islands (Fell, 1974), for which a temperature range of 17.5 to 24 °C is reported (DeSalvo et al., 1988).

Tripneustes planus Agassiz in Agassiz & Desor, 1846

(Pl. 19, Figs. 1-4)

	1840b	*Echinus planus* Ag. – Agassiz: 12 [*nomen nudum*]
*	1846	[*Tripneustes*] *planus* Agass. – Agassiz in Agassiz & Desor: 364, no. X 63
#	1846	[*Tripneustes*] *Parkinsoni* Agass. – Agassiz in Agassiz & Desor: 364, no. S 60
	1858	*Tripneustes Parkinsoni* Agass. – Desor: 132; pl. 18, fig.9
	1858	[*Tripneustes*] *planus* Agass. – Desor: 132-133
	1877	*Hipponoe parkinsoni* (Agassiz), Cotteau, 1877 – Cotteau in Locard: 233-235; pl. 8, figs. 13-16