Class Echinoidea Leske, 1778

Subclass Cidaroidea Claus, 1880
Order Cidaroida Claus, 1880

The use of cidaroid spines and isolated coronal plates in systematic studies is problematic. While being well characterised as a group and readily recognisable even in disarticulated ossicles generic and specific determination of such remains is very difficult. Yet the conservatism of coronal material is partly compensated for by the diversity displayed by primary spine morphology and ornamentation. In fact, Mooi et al. (2000) claim that many cidaroid species cannot be identified without information on primary spines.

Cidaroids are known to exhibit a wide range of spine morphologies on a single individual. Additionally, spine morphology is correlated (to an unknown extent) with the habitat. Nevertheless, these spines often represent the only remains of taxa (often very common) in the fossil record and hence need to be considered. Data on test morphology is scare or entirely missing. Following Cutress (1980) disarticulated spine and coronal material is grouped in parataxa as working-hypothesis, although the author is aware that these groupings do not represent species in a biological sense and could be partly artificial. The attribution to the different "species" is based mostly on ornamentation and microstructure. Despite the [theoretical] problems associated with this procedure the results are reproducible.

The influence of the sedimentary environment respectively habitat on the spine ornamentation as well as the extent of individual variation is unclear and needs to be investigated in extant species, where additional independent evidence/features can be used for determination (e.g. test morphology, pedicellariae, molecular data,...). Personal observations on extant *Stylocidaris affinis* from the Mediterranean, *Eucidaris metularia*, *Prionocidaris baculosa* and *Phyllacanthus imperialis* from the Red Sea showed that spine ornamentation is very homogenous at least within a single site/region. This suggests that the method outlined above might produce reasonable biodiversity data if applied cautiously and variation due to spine position is taken into account.

Family Cidaridae Gray, 1825
Subfamily Rhabdocidarinae Lambert, 1900
Genus *Prionocidaris* Agassiz, 1863

Type-species: *Cidarites pistillaris* Lamarck, 1816; by original designation (Agassiz, 1863: 18).
Diagnosis: Corona arched or low; more or less flattened apex; primary tubercles noncrenulate adorally, noncrenulate to weakly subcrenulate aborally; areoles shallow, usually well separated, except for the most adoral which may be confluent; pores distinctly conjugate to subconjugate; primary spines usually long, tapering and ornamented with coarse thorns in longitudinal series; less commonly spines are smooth or bear large thorns arranged in whorls; oral primaries with long collar. (modified from Fell, 1966a).
Distribution: Eocene to Recent – circumtropical
Remarks: Fossil species of *Prionocidaris* (e.g. *P. avenionesis* des Moulins, 1837) were often attributed to the genus *Cyathocidaris* (e.g. Lambert, 1910b) a genus of predominantly Antarctic Late Cretaceous occurrence. First photographs of *Cyathocidaris* spines and tests are given by Néraudeau et al. (2000), whereas Lambert (1910a) gave only drawings. The photographs and description clearly show the different nature of the morphology in the Antarctic *Cyathocidaris* and the Miocene species attributed to this genus. Whereas the trumpet-shaped crown of e.g. *P. avenionensis* is formed by fused thorns, which are common also along the shaft (as in extant *Prionocidaris*), the crown of true *Cyathocidaris* species forms by an extension of the cortex and lateral flattening of the distal part of the spine. Thorns or large granules similar to extant and fossil prionocidarids are absent in the Antarctic cyathocidarids. Additionally, the coronas of the Antarctic species have also few similarities with the Mediterranean species.

Prionocidaris sismondai (Mayer, 1864)

(Pl. 1, Figs. 1-5; Pl. 2, Figs. 10-11)

*	1864	*Rhabdocidaris Sismondai*. Mayer. – Mayer: 12; pl. 1, fig. 6 [needs to be re-examined]
	1891	*Cidaris avenionensis*, Desmoulins, 1837. – Gregory: 587-589, pl. 1, fig. 1a-c
pp	1913a	*Cyathocidaris avenionensis* Desm. (*Cidarites*). – Cottreau: 44
v	1913a	*Cyathocidaris avenionensis* Desm. (*Cidarites*). – Cottreau: 23, 79-80; fig. 9 [poorly preserved misidentified *P. sismondai*]
non	1913a	*Cyathocidaris avenionensis* Desm. (*Cidarites*). – Cottreau: pl. 1, figs. 1-8
pp	1913a	*L.*[*eiocidaris*] *Sismondai* Mayer (*Rhabdocidaris*). – Cottreau: 23, 45
	1980	*Prionocidaris sismondai* (Mayer) – Challis: 69-72; pl. 21, figs. b-c; pl. 22, figs. a-c
v.	2003	*Prionocidaris* sp. – Kroh et al.: 92

Type-material:
The type material could not be located. According to the information in Mayer (1864) it is probably in the palaeontological collection in Zurich or in the collection of Bronn housed (at that time) in the mineralogical collection of Heidelberg. The types of this species need to be re-examined and newly illustrated. The Austrian material is compared with the only available good description given by Challis (1980), which is, however, based on Maltese material.

Material:
Early Badenian (Langhian) – Eisenstadt (Hartl Fm., Hartl hill), Bgld, Austria
NHMW: 1 spine fragment (NHMW 1981/56/5)
Early Badenian (Langhian) – Stotzing (sandpit Mayer), Bgld, Austria
NHMW: 1 spine fragment (NHMW 2004z0050/0002)
Early Badenian (Langhian) – Weissenegg Fm., Retznei [Lafarge (formerly Perlmoser) quarry], Styria, Austria
NHMW: 1 spine fragment (NHMW 2004z0098/0004)
Badenian (Langhian-Early Serravallian) – Forchtenau, Bgld, Austria
NHMW: 4 spine fragments (NHMW 1853.III.256)
Badenian (Langhian-Early Serravallian) – old sandpit between

Großhöflein and Kleinhöflein, Bgld, Austria
NHMW: 14 spine fragments (NHMW 2003z0081/0051, 2004z0004/0001)
Badenian (Langhian-Early Serravallian) – Rauchstallbrunngraben, near Baden, NÖ, Austria
NHMW: 2 large spine fragments (NHMW 1981/56/8, 1997z0178/0904)

Foreign material for comparison:
Badenian (Langhian- Early Serravallian) – Mátyásföld, Budapest, Hungary
NHMW: several spine fragments (NHMW 1997z0178/2093)

Description:
Spines: Primary spines, thick, straight and very robust. The shaft is ornamented with large pointed thorns which are arranged in irregular longitudinal rows. On one side of the spines (~25 % of the circumference in cross-section) the thorns are distinctly smaller, or in some cases missing and replaced by moderately large granulae arranged in distinct vertical rows. The spines are round to slightly oval in cross-section. Preserved distal ends bear a trumpet shaped whorl of thorns (Pl. 1, Fig. 5). The collar is about the same length as the distance acetabulum – milled ring. The neck is short but well developed and lacks any ornamentation. The milled ring is prominent. The acetabulum has a noncrenulate margin.

Discussion:
The specimens considered here are placed in the genus *Prionocidaris* based on the thorny nature of the spines with a trumpet shaped whorl of thorns on their distal end and a noncrenulate acetabulum. Extant *Prionocidaris* show very similar morphologies (compare Mortensen, 1928; Fell, 1966a; Dollfuss & Roman, 1981). Specific determination is more difficult with the limited material at hand. Basically three *Prionocidaris* species are recorded in the Early and Middle Miocene of the Mediterranean: *P. avenionensis*, *P. scillae* and *P. sismondai*. The investigated material fits best with *P. sismondai*, which was re-described by Challis (1980) on base of material from the Chattian to Langhian of the Maltese Islands. Some spine fragments come also close to *P. avenionensis* (compare Philippe, 1998 [under the genus *Cyathocidaris*] and Kroh, in press), but generally the investigated material shows more coarsely ornamented spines than present in that species. Unfortunately, no coronal material could be recovered. *P. sismondai* has a narrow admedian zone in contrast to *P. avenionensis* and *P. scillae* which have broader admedian zones often ornamented by distinct grooves. Literature records of *P. avenionensis* (most under the [sub-] genus *Cyathocidaris*) from the Central Paratethys are in part based on material very similar to that documented here (summarised in Kroh, 2003b). Other specimens (e.g. material of Vadász, 1915 from the Ottnangian, Karpatian and Early Badenian of Hungary in the collection of the Hungarian Geological Survey), however, are closely similar to *P. avenionensis* and it seems possible that both species are present in the Central Paratethys. Further material (especially coronal plates) is needed to explore the possibility that part of the material attributed to *P. sismondai* here might belong to *P. avenionensis* and to check if the latter species is present in the Austrian Miocene too.

Cidaris oligocenus Gregory, 1891 from the Lower Coralline Limestone of Malta is a junior synonym of *Prionocidaris sismondai* according to Challis (1980). Cottreau (1913a) and Philippe (1998), on the other hand, place it into the synonymy of *P. avenionensis* [referred to the genus *Cyathocidaris* in that papers].

Occurrence:
Austria: Badenian (Langhian to Early Serravallian)
Vienna Basin: Rauchstallbrunngraben, near Baden, NÖ ([NHMW])
Eisenstadt-Sopron Basin: Forchtenau, Bgld ([NHMW]); Großhöflein, Bgld ([NHMW]); Hartl Fm., Hartl, Eisenstadt, Bgld (Kroh et al., 2003; [NHMW])
Styrian Basin: Retznei (Weissenegg Fm., Lafarge quarry), Styria ([NHMW])

Paratethys (non-Austrian occurrences): Badenian (Langhian to Early Serravallian)
Great Hungarian Basin (Pannonian Basin): Mátyásföld, Budapest ([NHMW])

Mediterranean: ? Chattian to Langhian
Central Mediterranean: *Globigerina* Limestone, Malta (Gregory, 1891; Cottreau, 1913a; Challis, 1980)

Atlantic Ocean: Miocene
Madeira Archipelago: Porto da Calheta, Porto Santo (Mayer, 1864)

Subfamily Cidarinae Gray, 1825
Genus ? *Stylocidaris* Mortensen, 1909

Type-species: *Cidaris affinis* Philippi, 1845; by original designation (Mortensen, 1909: 52, 54).
Diagnosis: Corona usually flattened; areoles deep or shallow, usually well separated except the most adoral two or three, which may be confluent; primary tubercles noncrenulate adorally, sometimes weakly subcrenulate aborally, especially in juveniles; primary spines long, tapering; secondary spines flattened; tridentate pedicellariae slender; large globiferous pedicellariae without end-tooth (slightly modified from Fell, 1966a).
Distribution: Miocene to Recent – circumtropical
Remarks: The extant genus *Cidaris* differs only by the presence of an end-tooth in the globiferous pedicellariae, a feature rarely preserved in fossil specimens. Nevertheless, most fossil and extant cidaroids of uncertain generic position were originally referred to that genus (which was the first cidaroid genus to be established) [Moore (in Fell, 1966a: U331-U332) proposed the use of inverted commas to distinguish between *Cidaris* sensu stricto and sensu lato].

Although it cannot be excluded that the present material belongs to the genus *Cidaris* s.s., this seems to be unlikely. Instead the material is tentatively assigned to the more diverse and more widely distributed genus *Stylocidaris* on base of the high similarities in spine and coronal morphology.

Stylocidaris ? *polyacantha* (Reuss, 1860)

(Pl. 1, Figs. 11-19; Pl. 2, Figs. 1-2; Pl. 3, Figs. 1-16)

v.* 1860 *Cidaris polyacantha* n. sp. – Reuss: 223; pl. 3, figs. 4, 4a
1880 *Cidaris polyacantha* Rss. – Rzehak: 302
1900 *Cidaris polyacanthus*, Rss. – Procházka: 74
1900 *Cydarus polyacanthus*, Reuss. – Procházka: 146
1942 Cidariten (ähnlich dem *Cidaris polyacanthus* Reuss) – Toth: 525
1950 *Cidaris polyacantha* Reuss – Toth: 171
v. 1998 "*Cidaris*" sp. – Schultz: 116; pl. 52b, figs. 5a-b

Type-material:
Syntypes: 9 spine fragments (NHMW 1859.X.135)
Locus typicus: Rudolticé (= Rudelsdorf), Czech Republic
Stratum typicum: "Rudoltitzer Tegel"
Age: Badenian (Langhian-Early Serravallian), Middle Miocene

Material:
Early Badenian (Langhian) – Badener Tegel, Baden, NÖ, Austria
NHMW: 2 spine fragments (NHMW 1846.37.952), 2 spine fragments (NHMW 1862.I.241), 5 spine fragments

(NHMW 1866.I.131), 19 spine fragments (NHMW 1997z0178/0899), 1 spine fragment (NHMW 2004z0001/0010), 4 spine fragments (NHMW 2004z0001/0011), 1 spine fragment and 1 interambulacral plate (NHMW 2004z0001/0012a+b), 6 spine fragments (NHMW 2004z0001/0063a-f)

GBA: 18 spine fragments and 1 interambulacral plate (no inventory numbers)

Early Badenian (Langhian) – Badener Tegel, Vöslau, NÖ, Austria

NHMW: 65 spine fragments and 1 interambulacral plate (NHMW 2004z0001/0002), 1 spine fragment + 1 interambulacral plate (NHMW 2004z0001/0012), 1 spine fragment (NHMW 2004z0001/0014)

Early Badenian (Langhian) – Badener Tegel, Sooss, near Baden, NÖ, Austria

GBA: 17 spine fragments (no inventory numbers)

Early Badenian (Langhian) – Niederleis, NÖ, Austria

NHMW: 1 spine fragment (NHMW 2004z0001/0016c)

Early Badenian (Langhian) – Stotzing (sandpit Mayer), Bgld, Austria

NHMW: 7 spine fragments (NHMW 2004z0050/0018)

Foreign material for comparison:

Early Badenian (Langhian) – Lăpugiu des Sus (= Lapugy), Romania

NHMW: 4 spine fragments (NHMW 1859.XLV.617B.d)

Badenian (Langhian-Early Serravallian) – Hrušovany nad Jevišovkou (= Grusbach), Czech Republic

NHMW: 22 spine fragments (NHMW 1997z0178/0740), 124 spine fragments (NHMW 1981/56/3)

Badenian (Langhian-Early Serravallian) – Knínice (= Kinitz), Czech Republic

NHMW: 4 primary spine fragments and 1 secondary spine (NHMW 2004z0001/0017a-e)

Badenian (Langhian-Early Serravallian) – Lysice (= Lissitz), Moravia, Czech Republic

NHMW: 4 spine fragments (NHMW 1865.XV.Anhang.b)

Badenian (Langhian-Early Serravallian) – Rudolticé (= Rudelsdorf), Czech Republic

NHMW: 9 spine fragments (NHMW 1859.X.135 [**type material** of *C. polyacantha* Reuss, 1860])

Description:

Interambulacral plates: Each interambulacral plate bears one large perforate primary tubercle. Aborally the tubercles are weakly crenulate in the adapical part of the platform. Ambitally and adorally the primary tubercles are noncrenulate. The areoles are not confluent, but separated only by narrow ridges with smaller scrobicular tubercles ambitally. The scrobicular tubercles are eye- or lens-shaped and are about twice as large as the remaining secondary tubercles. The adradial zone is narrow bearing a single row of secondary tubercles additionally to the scrobicular tubercles. The admedian zone is wider (about twice as wide as the adradial zone) and bears 3-4 irregular rows of secondary tubercles additionally to the scrobicular tubercles. Both adradial and admedian zones show horizontally and/or radially arranged, narrow grooves. This feature is, however, not very prominent and there are only few grooves on each plate [not as prominent as in e.g. *Prionocidaris canaliculata* (Duncan & Sladen, 1884) or *Phyllacanthus titan* Fell, 1954].

Primary spines: The spines are up to 70 mm long, straight and slightly tapering distally. Their diameter ranges from 1.5 to 5.2 mm in the proximal part, just above the neck. They are ornamented by 10 to 18 well separated, longitudinal ridges bearing short, pointed thorns (Pl. 3, Figs. 3-16). These thorns are flexed distally, producing a saw-like appearance. The number of ridges decreases towards the tip of the spines. The space between the ridges, the ridges themselves and the base of the thorns are covered by small granulae. In some cases an outer layer of cortical hair is preserved in patches, looking like a fine mesh spanning the gaps between the granulae (Pl. 3, Fig. 9). In some spines remnants of what may have been the original coloration is preserved by a pinkish stain. The thinner spines often show less closely spaced, larger and more sharply pointed thorns along the ridges in the distal part of the spine (e.g. Pl. 3, Fig. 4). Rarely thin spines occur with a flattened, flaring distal part terminating in a small "crown-like" whorl of small thorns (Pl. 3, Fig. 15). The collar and base are approximately equally long and separated by a finely striated milled ring. There is a well developed neck, which is free of ornamentation, showing a smooth, glossy surface. It is a little bit longer than collar or base. Both spines with partly crenulate acetabulum (aboral spines; Pl. 3, Figs. 10, 11) and such with noncrenulate acetabulum (ambital and oral spines; Pl. 3, Figs. 9, 12, 14) are present. Few spines with intact tips were observed, some seem to terminate in a small "crown-like" whorl of small thorns.

In cross-section the spines show a microstructure similar to *Stylocidaris*-spines, with non-specialised lamellae and a moderately thick cortex (Pl. 2, Figs. 1-2).

Differential diagnosis:

Spines of *Stylocidaris* ? *schwabenaui* Laube, 1869 are overall very similar to *S.* ? *polyacantha* but differ by their ornamentation (and microstructure). The longitudinal ridges in *S.* ? *schwabenaui* are usually more numerous and more closely spaced. Moreover, the ridges are usually strongly beaded, being made up of large, closely spaced nodules (or rarely short thorns). While the tips of the thorns are sharp and free of granulae in *S.* ? *polyacantha*, they are blunt and bear granulae except on the summit in S. ? *schwabenaui*. As a whole the spines of *S.* ? *schwabenaui* are more robust and lack the delicate thorny habit of *S.* ? *polyacantha* spines. Additionally, the "naked" neck of *S.* ? *schwabenaui* spines is longer but less constricted. No flattened, distally flaring spines have been observed in this species and the tubercles are always noncrenulate.

Spines of the Ottnangian cidaroid species [referred to as Cidarinae sp. 1 here] differ by their deeper grooves between the longitudinal ridges, which are again usually more numerous than in *S.* ? *polyacantha*. Additionally, these ridges do not really bear thorns or are made up of nodules, but are simple ridges, often undulating in their width. Moreover, some spines have a triangular to T-shaped cross-section in their distal part. Co-occurring with this spines serrated oral primary spines have been observed, which were never found in association with the other two species.

Spines of the Eggenburgian species *Plegiocidaris* ? *peroni* (Cotteau, 1877) differ by their more strongly crenulate acetabula, longer striated collar and short neck. The ornamentation of the spines is more "robust" and like in *S.* ? *schwabenaui*, the thorns are completely covered with granulae.

Discussion:

In contrast to *Stylocidaris* ? *schwabenaui* Laube, 1869, which occurs most abundantly in psammitic and maerl-type sediments *S.* ? *polyacantha* is found mainly in pelitic settings. Spine-microstructure, however, differs so strongly that the hypothesis of an ecomorphological gradient between the two morphs is rejected.

Occurrence:

Austria: Early Badenian (Langhian) (Late Badenian occurrences not ascertained)

Vienna Basin: Badener Tegel, Bad Vöslau, NÖ (Schultz, 1998 as "*Cidaris*" sp. [NHMW]); Badener Tegel, Baden, NÖ ([NHMW]); Badener Tegel, Sooss, near Baden, NÖ ([NHMW])

Gaaden Bay: roadcuts between Sittendorf-Sparbach-Weissenbach, NÖ (Toth, 1942, 1950)

Paratethys (non-Austrian occurrences): Early Badenian (Langhian) (Late Badenian occurrences not ascertained)

Molasse Zone: Hrušovany nad Jevišovkou (= Grusbach), Czech Republic ([NHMW]); Lysice (= Lissitz), Moravia, Czech Republic ([NHMW]); Rudoltické (= Rudelsdorf), Czech Republic (Reuss, 1860; Procházka, 1900; [NHMW]); Židlochovice (= Gross Seelowitz), Czech Republic (Rzehak, 1880)

Transylvanian Basin: Lăpugiu des Sus (= Lapugy), Romania ([NHMW])

Mediterranean: unknown

Stylocidaris ? *schwabenaui* (Laube, 1869)

(Pl. 1, Figs. 20-30; Pl. 2, Figs. 3-4; Pl. 4, Figs. 1-11)

*	1869a	*Cidaris Schwabenaui* Laube. – Laube: 182
	1870	*Cidaris Schwabenaui* Laube. – Laube: 314
	1871	*Cidaris Schwabenaui* Laube. – Laube: 58; pl. 16, fig1.
pp	1880b	*Dorocidaris papillata*, Leske. – Manzoni: 329 [Austrian records]
?	1895	*Cidaris* cf. *Schwabenaui* Laube – Redlich: 333
non	1897	*Dorocidaris papillata* Leske. – Vinassa de Regny: 144-145
	1898	*Cidaris Schwabenaui* Lbe. – Kornhuber: 31 [spines]
v	1915	*Cidaris* (*Dorocidaris*) *papillata* Leske. – Vadász: 105-106; pl. 8 (2), fig. 16
	1939	*Cidaris Schwabenaui* Laube. – Kapounek: 74

Type-material:
Holotype: figured in Laube (1871: pl. 16, fig. 1); collection of Hofrat von Schwabenau, current whereabouts unknown
Locus typicus: St. Margarethen, Bgld, Austria
Stratum typicum: Leitha limestone of St. Margarethen
Age: Late Badenian (Early Serravallian), Middle Miocene
Remarks: Hofrat von Schwabenau was living in Linz, OÖ in the year 1864 and was probably employed at the Museum of Linz. In any case, he had a private collection and had also access to the collection at the Museum of Linz (compare Zittel, 1865: 106). Some of the specimens of his collection are now located in the systematic collection of the Naturhistorisches Museum Wien (at that time k. & k. Hofmuseum), but the type specimen is not among them.

Material:
Badenian (Langhian-Early Serravallian) – Großhöflein, Bgld, Austria
NHMW: 1 interambulacral plate (NHMW 2004z0004/0002, determination tentative)
Badenian (Langhian-Early Serravallian) – Kahlenberg, Vienna, Austria
NHMW: 5 spine fragments (NHMW 1981/56/10a)
Badenian (Langhian-Early Serravallian) – Perchtoldsdorf (Brunnergasse, Highway-ramp), NÖ, Austria
NHMW: 12 spine fragments (NHMW 1981/56/9a)
Badenian (Langhian-Early Serravallian) – Steinebrunn (= Steinabrunn), NÖ, Austria
NHMW: 4 spine fragments (NHMW 1859.XLV.634B.b)
Badenian (Langhian-Early Serravallian) – Wöllersdorf, NÖ, Austria
NHMW: 6 spine fragments (NHMW 1981/56/6)
Late Badenian (Early Serravallian) – Walbersdorf, Bgld, Austria
NHMW: 1 spine (NHMW 2004z0001/0001)
Late Badenian (Early Serravallian) –Winden am Neusiedlersee (Nirgl quarry), Bgld, Austria
NHMW: 5 spine fragments (NHMW 1859.L.833)
Late Badenian (Early Serravallian) – Winden [old quarry, N of the Ludlloch (cave), N of the village], Bgld, Austria
NHMW: test fragment consisting of 3 interambulacral plates with attached ambulacral plates (NHMW 1997z0178/1683), 6 test fragments (NHMW 2003z0082/0009, ../0036), 107 spine fragments (NHMW 2003z0082/0008), several hundred primary spine fragments (NHMW 2003z0082/0031-32, ../0035, ../0037-39, 2004z0004/0002)

Foreign material for comparison:
Late Badenian (Early Serravallian) – Sandberg, Devínska Nová Ves (= Neudorf an der March), Slovak Republic
NHMW: 46 spine fragments and 1 interambulacral plate with attached ambulacral plates (NHMW 1997z0178/1939a-b)
Late Badenian (Early Serravallian) – Devínska Nová Ves (= Neudorf an der March; = Dévény-Újfalu), Slovak Republic
NHMW: 78 spine fragments (NHMW 1857.XLV.48), 165 spine fragments (NHMW 1868.VIII.27a-h)
MAFI: 16 spine fragments (MAFI Ech 295 [material referred to as *Cidaris* (*Dorocidaris*) *papillata* Leske by Vadász, 1915: 105-106])

Interambulacral plates: Each interambulacral plate bears one large perforate noncrenulate primary tubercle. The areoles are not confluent, but separated by a narrow ridge bearing only scrobicular tubercles. The scrobicular tubercles are eye- or lens-shaped and are about twice as large as the remaining secondary tubercles. The adradial zone is narrow bearing up to two rows of secondary tubercles additionally to the scrobicular tubercles. The admedian zone is bearing 3-4 irregular rows of secondary tubercles additionally to the scrobicular tubercles. There is no naked area along the interradial suture and the suture is not depressed.
Ambulacral plates: The ambulacra are sinuous. Each plate bears a single large, oblique partitioned isopore (P1 to P2 type). Medially a single vertical row of moderately large marginal tubercles and a vertical row of inner tubercles is present in each half ambulacrum. The inner tubercles are situated in the perradial/adoral corner of each ambulacral plate and are much smaller than the marginal tubercles. Both marginal tubercles and pore pairs take up the full height of the ambulacral plates. There is no naked area along the perradial suture. 12 to 13 ambulacral plates per interambulacral plate ambitally.
Primary spines: The largest spine fragments are more than 50 mm long, a maximum spine length of up to 70 mm or more seems likely. The spines are straight and taper slightly distally. Spine diameter ranges from *c.* 1.0 to 4.0 mm, most fragments, however, have a diameter between 2.5 and 3.1 mm. The shaft is ornamented by up 12 to 20 beaded longitudinal ridges. These ridges may be relatively straight (Pl. 4, Fig. 8) to strongly beaded (Pl. 4., Fig. 10) and sometimes may bear short, blunt thorns (Pl. 4, Fig. 6). Contrary to *S.* ? *polyacantha* these thorns are never pointed and are wholly covered by small granulae (not only the bases as in *S.* ? *polyacantha*). The ridges themselves and the narrow grooves in-between are covered with small granulae as well. In some cases an outer layer of cortical hair is preserved in patches, looking like a fine mesh spanning the gaps between those granulae (Pl. 4, Fig. 10). The collar is striated and moderately long. The neck is up to twice as long as the collar, free of ornamentation and not conspicuously constricted. The acetabulum has a noncrenulate margin. Few distal spine fragments preserved, showing a blunt, worn tip.

In cross-section the spines show a microstructure similar to extant *Stylocidaris*-spines, with non-specialised lamellae and a moderately thick cortex (Pl. 2, Fig. 3-4).

Differential diagnosis:
For the differences to *S.* ? *polyacantha* see above under that species.

Spines of the Ottnangian cidaroid species [referred to as Cidarinae sp. 1 here] are generally similar to those of *S.* ? *schwa-*

benaui. Spine ornamentation differs, however, in its microstructure: whereas there are pronounced longitudinal ridges with undulating width in the Ottnangian spines, the ridges of *S.* ? *schwabenaui* are more like longitudinal rows of thorns than true ridges. Moreover the strongly serrated oral primary spines that are typical of the Ottnangian species were never observed in *S.* ? *schwabenaui*

Spines of the Eggenburgian species *Plegiocidaris* ? *peroni* (Cotteau, 1877) differ by their strongly crenulate acetabula, longer striated collar and short neck.

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 description. Thus, according to the ICZN the year 1869 has to be regarded as the valid date for this species.

Manzoni (1880b: 329) and Vinassa de Regny (1897: 144-145) considered *S.* ? *schwabenaui* as junior synonym of *Dorocidaris papillata* Leske (a junior synonym of *Cidaris cidaris* Linné, 1758; often confused with *Stylocidaris affinis* (Philippi, 1845); compare Mortensen, 1928: 289-298). When the fossil material from Austria is compared in detail, however, differences between *S.* ? *schwabenaui* and the two extant species reported under the name "*Dorocidaris papillata*" are apparent. *S.* ? *schwabenaui* has a much wider adradial and admedian zone in the ambital interambulacra than either extant species. Moreover, it shows distinct horizontal grooves in the admedian zone. Thus *S.* ? *schwabenaui* is considered a distinct species and the opinion of Vinassa de Regny is rejected.

Occurrence:

Austria: Badenian (Langhian-Early Serravallian)
- Vienna Basin: Kahlenberg, W ([NHMW]); Perchtoldsdorf, NÖ ([NHMW]); Steinebrunn (formerly Steinabrunn), NÖ (Laube, 1869a, 1871; Manzoni, 1880b; [NHMW]); Wöllersdorf, NÖ ([NHMW]); Vienna Basin (Manzoni, 1880b)
- Eisenstadt-Sopron Basin: E of Großhöflein, near Eisenstadt, Bgld (Kapounek , 1934; [NHMW]); St. Margarethen, Bgld (Laube, 1871; Manzoni, 1880b; Vadász, 1915); Walbersdorf, Bgld ([NHMW])
- Danube Basin: Mörbisch (formerly Merwisch), near Rust, Bgld (Laube, 1871; Manzoni, 1880b); Winden, Bgld (Laube, 1871; Manzoni, 1880b; [NHMW])

Paratethys (non-Austrian occurrences): Badenian (Langhian-Early Serravallian)
- Vienna Basin: Devínska Kobyla (= Thebener Kogel), near Bratislava (Kornhuber, 1898); Devínska Nová Ves (= Neudorf an der March, = Dévény-Újfalu), Slovak Republic (Laube, 1869a, 1871; Manzoni, 1880b; Vadász, 1915; [MAFI]; [NHMW]); Sandberg, Devínska Nová Ves (= Neudorf an der March), Slovak Republic ([NHMW])
- Great Hungarian Basin (Pannonian Basin): Sóskut (or Bia), Hungary (Vadász, 1915)
- Transylvanian Basin: ? Mănăstire Polovragi (= Kloster Polowratsch), Romania (Redlich, 1895)

Mediterranean: unknown

Genus *Eucidaris* Pomel, 1883

Type-species: *Cidarites metularia* Lamarck, 1816; by subsequent designation (Clark, 1909: 88, and reply by Bather, 1909: 88; see also discussions in Bather, 1908a, b; Clark, 1908; Mortensen, 1909: 39-40)
Diagnosis: The test is flattened, the areoles are well separated, only the proximal 2 to 3 are confluent. The primary tubercles are noncrenulate, except in young stages, where they may be weakly subcrenulate aborally. Madreporite slightly larger than other genital plates. The primary spines typically cylindrical, shaft is abruptly truncated and ends in a crown with central prominence. The ornamentation of the spines consists of low rounded warts disposed in regular, longitudinal series (modified from Fell, 1966a).
Distribution: Late Paleocene (Holmes, 1999) to Recent – circumtropical and southern temperate (Australasia)
Possibly from the Danian (Paleocene) on (compare the spines figured in as indeterminate cidaroid in Jagt, 2000: pl. 2, figs. 10-12)
Ecology and biogeography: Feeding experiments with *E. tribuloides* showed that this species is an opportunistic omnivore. When starved the animals consumed anything within reach, including wooden and fibre-glass parts of the aquarium. Under normal conditions they showed a preference for rock infested with the endolithic sponge *Cliona lampa*, over the sea-grass *Thalassa testudinum*, rock covered with algae and pieces of fish (McPherson, 1968b). Analysis of the gut content of animals captured in the field showed a significant amount of hard material and it seems likely that clionid sponges and other epi- and endolithic organisms constitute a large amount of the food under natural conditions. The high-feeding rate of *E. tribuloides* observed by McPherson (1968b) indicate that this species is potentially an important bioeroder. Due to the low density in the field (usually <2 indiv./m²), however, this species does not reach the importance of the major bioeroding echinoid of the Caribbean, *Diadema antillarum* (McPherson, 1968b).

Extant species of *Eucidaris* are especially abundant from the intertidal down to 20-30 metres (Kier & Grant, 1965; McPherson, 1968a; Nebelsick, 1992; Hickman, 1998), but are rarely found beyond the continental shelf (Mortensen, 1940; Fell, 1954) . *E. tribuloides* is usually observed on sandy or rocky bottoms, within turtle grass or on rocks in crevices or beneath sponges or corals; but not on clean sand, where sea grass or algae are absent (Kier & Grant, 1965; McPherson, 1968a); its distribution coincides with that of *Tripneustes ventricosus* (Kier & Grant, 1965). *E. metularia* lives on a variety of hard and soft substrates and is especially common on sand with coral patches, in coral reefs and coral carpets (Nebelsick, 1992).

E. tribuloides shows relatively slow growth with an increase of test diameter between 1 and 2 mm/month or less (McPherson, 1968a). Based on these rates McPherson (1968a) estimated a minimum age of four to five years for the largest specimens observed in the field. Aquarium kept specimens may live up to seven years. This species is preyed upon by cassid gastropods, crabs and a variety of fishes (McPherson, 1968a)

The spatial distribution of *Eucidaris* was summarised by Fell (1954: 20), who found that it is well correlated with the 15° C winter surface isotherms.

Eucidaris zeamays (Sismonda, 1842)

(Pl. 2, Figs. 5-6; Pl. 6, Figs. 1-21; Pl. 7, Figs. 1-30)

*	1842	*Cidarites zea-mays* mihi. – Sismonda: 391
	1846	[*Cidaris*] *Zea-Mays* E. Sism. – Agassiz & Desor: 336
	1847	*Cidaris Zea-mays*. Sism. – Michelotti: 67
	1847	*Cidaris Zea-mays* E. Sism. – Sismonda: 8
	1852	[*Cidaris*] *zea-mays*, E. Sism. – d'Orbigny: 142
	1858	[*Cidaris*] *Zea-mays* E. Sism. – Desor: 38
.	1901	*Cidaris zeamais* Sism. – Airaghi: 167-168; pl. 19, figs. 49-57
#	1901	*Cidaris fragilis* n. f. – Airaghi: 165; pl. 19, figs. 63-64 [based on test fragments]
#	1907a	*Cidaris sardica* Lambert. – Lambert: 14-15; pl. 1, figs. 7-8
	1907	*Cidaris zeamays* Sism. – Vadász: 370, 422
	1910	*P.*[*legiocidaris*] *zea-mays* Sismonda (*Cidaris*). – Lambert & Thiéry: 134

	1913a	*Plegiocidaris zea-mays* Sism. (*Cidaris*). – Cottreau: 45
	1915	*Cidaris* cf. *zeamays* Sism. – Májer: 34
?	1915	*Cidaris melitenni* Forbes.– Májer: 35, 88
.	1915	*Cidaris zeamays* Sism. – Vadász: 105; pl. 8 (2), fig. 17
v.	1915	*Cidaris* cfr. *zeamays* Sism. – Vadász: 105; pl. 8 (2), fig. 15
v	1915	*Cidaris melitensis* Forbes. – Vadász: 104; pl. 8 (2), fig. 4
? pp	1915	*Plegiocidaris Peroni* Cott. sp. – Vadász: 104; pl. 8 (2), figs. 18-19
	1927b	*Cidaris zeamaïs* Sismonda, 1842 – Lambert: 84-85
	1928	*Cidaris Zeamays* Sism. – Kutassy: 8
?	1928	*Cidaris Desmoulinsi* Sism. – Kutassy: 8
	1934	*Cidaris* cf. *zeamays* Sism. – Horusitzky: 324
	1966	*Cidaris* cfr. *zeamays* Sism. – Kókay: 83
	1969	*Plegiocidaris peroni* (Cott.) – Gábos & Ghiurca: 82; pl. 1, fig. 1 [misidentified adapical test fragment of *E. zeamays*]
	1969	*Cidaris melitensis* Forbes – Gábos & Ghiurca: 82-86; pl. 1, fig. 2 [misidentified interambulacral plate of *E. zeamays*]
	1969	*Cidaris zeamays* Sism. – Gábos & Ghiurca: 86; pl. 1, fig. 3
	1974	*Cidaris zeamaïs* Sismonda, 1842 – Chavanon: 51-52; pl. 3, fig. 5a-c
	1974	*Cidaris tribuloïdes* (Lamarck) – Philippe: 7 [misidentification, fide Philippe (1998: 46)]
.	1977	*Cidaris* cf. *desmoulinsi* Sismonda, 1842 – Mączyńska: 194; pl. 1, figs. 7, 13
pp	1977	*Cidaris* sp. div. – Mączyńska: 194; pl. 1, figs. 4-6, 9-12, 14-15
non	1977	*Cidaris* sp. div. – Mączyńska: 194; pl. 1, fig. 16
?	1981	*C.* cf. *melitensis* Forb. – Halmai: 106
?	1981	*C.* cf. *zeamays* Sism. – Halmai: 106
.	1984	*Plegiocidaris zeamaïs* (Sismonda, 1842) – Philippe: 86; pl. 5, fig. 11
.	1987	*Cidaris zeamaïs* Sismonda, 1842 – Mączyńska: 146, 148; pl. 1, fig. 1
.	1987	*Cyathocidaris avenionensis* (Desmoulins, 1837) – Mączyńska: 145-146, 148; pl. 1, figs. 4-7; pl. 2, figs. 1a-d
	1987	*Cidaris desmoulinsi* Sismonda, 1842 – Mączyńska: 148
.	1988	*Cidaris zeamaïs* Sismonda, 1841 – Mączyńska: 60; pl. 1, figs. 1-3
.	1989	*Eucidaris zeamaïs* – Philippe: 27; tab. 1
.	1993	*Cidaris zeamaïs* Sismonda, 1842 – Mączyńska: 105; pl. 1, fig. 1; pl. 6, figs. 1a, 4
?	1993	*Cidaris* cf. *desmoulinsi* Sismonda, 1842 – Mączyńska: 106; pl. 1, fig. 2
.	1993	*Cyathocidaris avenionensis* (Desmoulins, 1837) – Mączyńska: 106; pl. 1, figs. 3-4; pl. 6, fig. 1c
?	1993	*Cidaridae* – Mączyńska: pl. 1, figs. 8
?pp	1993	*Plegiocidaris peroni* (Cotteau, 1877) – Mączyńska: 106-107; pl. 1, fig. 5
.	1996	*Cidaris zeamaïs* Sismonda, 1842 – Mączyńska: 40; pl. 1, fig. 1
.	1996	*Cyathocidaris avenionensis* (Desmoulins, 1837) – Mączyńska: 40-41; pl. 1, figs. 2-3
.	1998	*Eucidaris zeamaïs* (Sismonda, 1842) – Philippe: 44-46; pl. 4, figs. 8-15
v.	2002b	*Eucidaris zeamays* – Kroh: 12
v.	2003a	*Eucidaris zeamays* (Sismonda, 1842) – Kroh: 158-159; pl. 1, figs. 1-11
	2003b	*Eucidaris zeamays* (Sismonda, 1842) – Kroh: 248
v.	2003	*Eucidaris zeamays* (Sismonda) – Kroh et al.: 92

Type-material:
Cidaris zeamays Sismonda, 1842:
Type-material: current whereabouts unknown
Locus typicus: Colli di Torino, Italy
Stratum typicum: "terreno terziario medio"
Age: Early to mid Miocene

Cidaris fragilis Airaghi, 1901:
Type-material: figured by Airaghi (1901: pl. 19, figs. 63-64); private collection of Mr. Rovesenda; current whereabouts unknown
Type area: Colli Torinesi (Baldissero, Val Geppi, Pian dei Boschi, Rio Batteria, Grangia, Val Saufrà, S. Antonio), Italy
Age: Elveziano (Early – Mid Miocene)

Cidaris sardica Lambert, 1907:
Type-material: figured by Lambert (1907a: pl. 1, figs. 7-8); current whereabouts unknown
Locus typicus: Santa Reparata (Cap de la Testa), Sardinia
Stratum typicum: Calcaire à Poissons
Age: "Helvétien", Early to mid Miocene

Material:
Early Badenian (Langhian) – Bad Vöslau (?), NÖ, Austria
NHMW: 11 spines (NHMW 1997z0178/1328, 1328a-d)
Early Badenian (Langhian) – Eisenstadt (Hartl Fm.), Bgld, Austria
NHMW: 36 spines (NHMW 1869.L.802)
Early Badenian (Langhian) – Forchtenau, Bgld, Austria
NHMW: 9 spines (NHMW 2004z0001/0015a)
Early Badenian (Langhian) – Gainfarn, NÖ, Austria
NHMW: 6 spines (NHMW 2004z0076/0007-12, ../0060), 1 test fragment (NHMW 2004z0076/0043)
Wanzenböck coll.: 58 primary spine fragments; 2 test fragments
Neitz coll.: 16 primary spine fragments
Early Badenian (Langhian) – Grund Formation, Grund, NÖ, Austria
NHMW: 1 spine (NHMW 2002z0086/0001)
Early Badenian (Langhian) – Niederleis, NÖ, Austria
NHMW: 10 interambulacral plates (NHMW 2002z0087/0048-49, 2002z0087/00052), 166 primary spines (NHMW 2002z0087/0040-47, 2002z0087/0050, 2002z0088/0002, 2002z0089/0006) and 1 genital plate (NHMW 2002z0087/0051), 5 spines (NHMW 2004z0001/0016a)
Early ? Badenian (Langhian) – Rauchstallbrunngraben (bryozoan marl), near Baden, NÖ
NHMW: 6 test fragments (NHMW 2004z0121/0001-4, ../0009-10), 7 primary spines (NHMW 2004z0121/0009-17), 2 genital plates (NHMW 2004z0121/0005-06), 2 ocular plates (NHMW 2004z0121/0007-08), 2 demipyramids (NHMW 2004z0121/0018-19), 2 epiphyses (NHMW 2004z0121/0020-21), 4 rotulae (NHMW 2004z0121/0022-25), 1 tooth (NHMW 2004z0121/0026), 4 secondary spines (NHMW 2004z0121/0027-30)
Early Badenian (Langhian) – Retznei [Weissenegg Fm., Lafarge quarry (formerly Perlmoser)], Styria, Austria
NHMW: 1 spine (NHMW 2004z0098/0003)
Early Badenian (Langhian) – Stotzing (sandpit Mayer), Bgld, Austria
NHMW: 60 spines (NHMW 2004z0050/0001, ../0027-30), and 20 test fragments (NHMW 2004z0050/0019, .../0020-25)
Early Badenian (Langhian) – Wagna (brickyard Wagna), Styria, Austria
NHMW: 1 spine (NHMW 2004z0001/0040)
Badenian (Langhian-Early Serravallian) – Bruck an der Leitha, NÖ, Austria
NHMW: 14 spine fragments (NHMW 2004z0001/0021a)

Badenian (Langhian-Early Serravallian) – old sandpit between Großhöflein and Kleinhöflein, near Eisenstadt, Bgld
NHMW: 348 spines (NHMW 2003z0081/0003, ../0046-0050), 105 test fragments (NHMW 2003z0081/0004) and 20 demipyramids (NHMW 2003z0081/0005)
Badenian (Langhian-Early Serravallian) – Pöls, near Wildon, Styria, Austria
NHMW: 3 spines (NHMW 1862.XXXIII.93)
Badenian (Langhian-Early Serravallian) – Steinebrunn (formerly Steinabrunn), NÖ, Austria
NHMW: 1 spine (NHMW 1846.37.954a), 9 spines (NHMW 1859.XLV.634B.a), 40 spine fragments (NHMW 1865.I.612a), 2 spine fragments (NHMW 2004z0001/0020b), 1 spine fragment (NHMW 2004z0001/0024a)
Badenian (Langhian-Early Serravallian) –Teischl quarry, (? Hartl Fm., Eisenstadt, Bgld), Austria
NHMW: 4 test fragments (NHMW 2004z0001/0008a)
Late Badenian (Early Serravallian) – Winden (quarry north of the village), Bgld, Austria
NHMW: 1 primary spine (NHMW 2003z0082/0034)

Foreign material for comparison:
Early Badenian (Langhian) – Coşteiu de Sus (= Kostej), Romania
NHMW: 5 spines (NHMW 2004z0001/0003a), 1 epiphysis (NHMW 2003z0084/0003)
Early Badenian (Langhian) – Kemence, Hungary
MAFI: 3 vials with several hundred spines and spine fragments [MAFI Ech 442 (including material figured as *Cidaris* cfr. *zeamays* Sism. by Vadász, 1915: 105; pl. 8, fig. 15; additionally to the *E. zeamays* spines there are numerous other cidaroid and diadematid spine fragments, as well as annelids of the genus *Ditrupa* in these vials)], 13 test fragments [MAFI Ech 443 (the vial includes also an ambulacral plate of a diadematoid)]
Early Badenian (Langhian) – Lăpugiu des Sus (= Lapugy), Romania
NHMW: 2 spines + 1 interambulacral plate (NHMW 1859.XXXVII.59a), 24 spines, 4 interambulacral plates + 1 demipyramid (NHMW 2004z0001/0004a), 68 spines + 1 interambulacral plate (NHMW 1859.XLV.617B.a), 1 test fragment + 4 spines (NHMW 2004z0001/0027a)
Badenian (Langhian-Early Serravallian) – Lysice (= Lissitz), Moravia, Czech Republic
NHMW: 1 spine (NHMW NHMW 1865.XV.Anhang.a)
Badenian (Langhian-Early Serravallian) – Nový Rybik (= Portzteich), near Sedlec, W Lednice, Czech Republic
NHMW: 22 spine fragments (NHMW 2004z0001/0009)
Late Badenian (Early Serravallian) – Budapest-Budaörs, Hungary
MAFI: 2 test fragments [MAFI Ech 1397 (material figured as *Cidaris melitensis* Forbes by Vadász, 1915: 104; pl. 8, fig. 4)]
Late Badenian (Early Serravallian) – Buituri (= Bujtur), Romania
NHMW: 3 spine fragments + 3 interambulacral plates (NHMW 2004z0001/0005a), 21 spine fragments (NHMW 1852.II.1603a)

Description:
Size and shape: The corona, as could be reconstructed from isolated test segments, is small, its diameter rarely exceeding 2 cm. It is flattened orally and aborally and has a circular outline. The peristomal opening and the apical disc are of about equal size.
Apical disc: The genital plates associated with this species have a near hexagonal shape, wider at their adapical border than on their abapical margin. They are ornamented by large rounded granules along the margin of the plates and smaller ones in the centre of the plates. The genital pores are large rounded pores, one on each plate, about halfway between the centre and abapical margin. The madreporite bears many small madreporic pores which are closely spaced between the rounded granules in the centre of the plate. The ocular plates are distinctly smaller and have a triangular shape The long side (= the abapical side) is strongly indented. The ocular pores are small and rounded and lie at the tip of the indentation of the abapical side.
Ambulacra: The ambulacra are slightly sinuous and consist of small plates with C2 isopores orally and C1 isopores adapically. The transition of the two pore types is gradually. The pores in each pair are oval and subequal in size and shape. The neural canals are small and are positioned adorally on the perradial pores. Adjacent pore pairs are well separated by a broad wall. Each ambulacral plate bears one large marginal tubercle with prominent boss. Larger specimens have also one inner tubercle per ambulacral plate, except in the most adoral plates. In smaller specimens the inner tubercles are only present at the ambital ambulacral plates. The poriferous zones are slightly wider than the interporiferous zones. Each interambulacral plate is bordered by 4 to 8 ambulacral plates.
Interambulacra: The interambulacra are up to four times the width of the ambulacra. Each column contains 4 to 6 plates. One large perforate, noncrenulate primary tubercle with undercut mamelon is present on each plate. The platform is small and the parapet weakly defined in most specimens. The areoles are well defined and surrounded by a ring of scrobicular tubercles, which are slightly larger than the secondary tubercles. In the ambital plates of large specimens the areoles may be confluent (e.g. Kroh, 2003a: pl. 1, fig. 10) or nearly so with very narrow ridges separating the areoles. The admedian zone is wider than the adradial zone.
Primary spines: The spines are short, relatively stout and ornamented by longitudinal rows of large granules. These granules are enlarged in more or the less regular intervals and may form whorls along the shaft. Towards the tip, the size of the granules decreases and they grade into longitudinal ridges, which form a crown at the tip of the spine. The acetabulum has a noncrenulate margin. The milled ring is prominent and indistinctly striated. The collar is short and distinctly striated. Spine cross-section is consistent with that of extant *Eucidaris*.

In some outcrops (e.g. Niederleis, Austria or Lapugy, Romania) the spines still show traces of their original coloration. They are banded with broad dark (dark pink to brownish) and thin light bands, the latter coinciding with the whorls of the ornamentation. Very similar coloration is found in extant *E. metularia* (Lamarck) and *E. tribuloides* (Lamarck).

In bulk samples isolated spine bases and regenerating spines (Pl. 6, Fig. 17) are commonly found. The former result from breakage of the spine through the proximal part of the collar, a process possibly associated with autotomy (Cutress, 1965).
Secondary spines: The secondary spines are small, flattened and have a rectangular outline.
Demipyramids: The demipyramids are typical cidaroid demipyramids, with a very shallow foramen magnum.
Rotulae: cidaroid type
Epiphyses: cidaroid type
Teeth: The teeth are grooved longitudinally and have a pointed tip.

Differential diagnosis:
E. zeamays differs from *E. metularia* (Lamarck), an extant species of the Red Sea by its more coarsely ornamented spines (no whorls of coarse thorns are present in *E. metularia*) and more slender spines (compare Plate 6). Likewise *E. tribuloides* (Lamarck), an Pliocene to extant species of the Caribbean has much less strongly ornamented and, additionally, much larger spines than *E. zeamays*.

E. desmoulinsi (Sismonda, 1842) differs from *E. zeamays* by its larger spines (usually 15 to 25 mm in length), which show a more or less regular ornamentation consisting of 15 to 18 longitudinal rows of small granulae. There are no whorls or other