

Taxonomy and palaeoecology of Cenomanian-Turonian (Upper Cretaceous) echinoids from eastern Sinai, Egypt

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EL QOT, G., FÜRSICH, F. T., ABDEL-GAWAD, G. & HANNAA, W. 2009. Taxonomy and palaeoecology of Cenomanian-Turonian (Upper Cretaceous) echinoids from eastern Sinai, Egypt. - *Beringeria* **40**: 55-98, 13 text-figs., 5 pls., 1 tab.; Würzburg.

Abstract. The Cenomanian-Turonian rocks of Gebel Aref El-Naqa and Wadi Quseib (eastern Sinai) yield associations of echinoids and other macrobenthic faunal elements (e.g. oysters, gastropods, corals). Twenty-six echinoid species (thirteen regular and thirteen irregular) belonging to sixteen genera, fourteen families, and eight orders are identified, systematically described, and their stratigraphic and palaeogeographic distribution is discussed. Based on a functional morphological analysis, the mode of life and feeding of the different taxa is reconstructed. Two main types of facies have been recognized in the studied sections: marl and reefal carbonates. The marly facies is dominated by burrowing and ploughing irregular echinoids, whereas the reefal carbonates are dominated by grazing epifaunal regular echinoids. Some of the echinoid tests (e.g. *Heterodiadema libycum*) together with oyster shells have been affected by bioerosion and encrustation.

■ *Egypt, Sinai, Cenomanian-Turonian, lithostratigraphy, echinoids, taxonomy, palaeoecology, taphonomy*

Zusammenfassung: Die Gesteine des Gebel Aref El-Naqa und Wadi Quseib (östliche Halbinsel Sinai) enthalten Gemeinschaften von Echinoideen und anderen Faunenelementen des Makrobenthos (z. B. Austern, Gastropoden oder Korallen). 26 Seeigel-Arten (13 „reguläre“ und 13 „irreguläre“) werden taxonomisch beschrieben und ihre stratigraphische und paläogeographische Verbreitung diskutiert. Sie gehören 16 Gattungen, 14 Familien und 8 Ordnungen an. Die Lebens- und Ernährungsweise der verschiedenen Taxa wird anhand funktionsmorphologischer Analysen rekonstruiert. Zwei Haupt-Faziestypen lassen sich in den untersuchten Profilen unterscheiden: Mergel und Riff(nahe)-Karbonate. Die Mergelfazies wird von infaunalen und semi-infaunalen „irregulären“ Echinoideen dominiert, während die Riff(nahe)-Karbonatfazies von epifaunalen „regulären“ Seeigeln dominiert wird. Einige Seeigel-Gehäuse (z. B. *Heterodiadema libycum*) waren, ebenso wie Austernschalen, von Bioerosion und Inkrustierung betroffen.

■ *Ägypten, Sinai, Cenoman-Turon, Lithostratigraphie, Echinoideen, Taxonomie, Paläoökologie, Taphonomie*

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1 Introduction

Echinoids are common members of benthic faunas occurring in a wide range of habitats both in and on the sediment and are highly facies-controlled (SMITH & BENGTON, 1991). They are also excellent tools for reconstructing palaeoenvironments depending on their morphological characters (e.g., KROH & NEBELSICK, 2003). In addition, irregular echinoids are abundant, taxonomically diverse, and environmentally widespread (BARRAS, 2008).

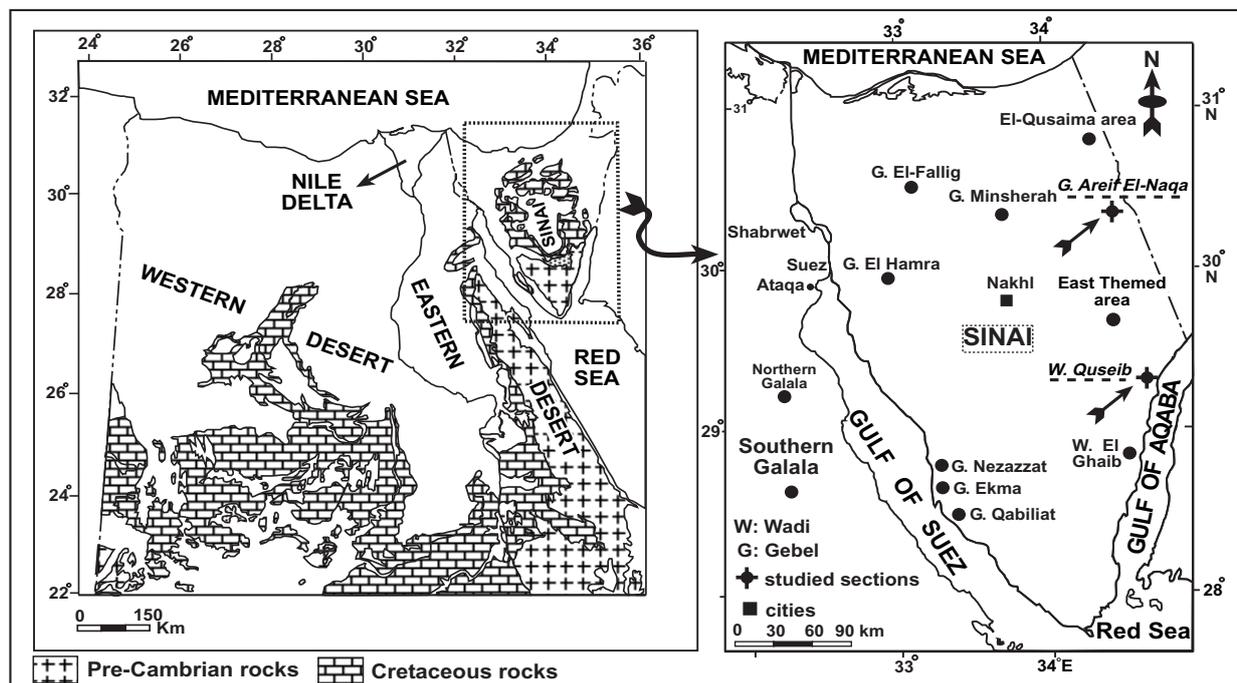
Cretaceous echinoids of Egypt have rarely been studied in the recent past, most studies being from the early 20th century (e.g., FOURTAU, 1898, 1901, 1906, 1909, 1912, 1914, 1921; LAMBERT, 1932; FAWZI, 1963; GEYS, 1989, 1992; ABDELHAMID & EL QOT, 2001; ABDELHAMID & AZAB, 2003; EL QOT, 2006). Whereas the stratigraphy, palaeogeography, structural history, and the benthic and planktonic foraminifera of the area have been studied in detail (e.g., BARTOV et al. 1980; ABED et al. 1996; LÜNING et al. 1998; BAUER et al. 2001), no

detailed studies exist about the echinoids and other macrobenthic faunal elements. Therefore, this is the first paper dealing with the systematic description and palaeoecology of the Cenomanian-Turonian echinoids of eastern Sinai.

Two sections have been studied along the eastern side of Sinai Peninsula, which is bounded by the Suez Rift to the west and the Aqaba-Dead Sea Rift to the east (Text-fig. 1). The northeastern section is Gebel Areif El-Naqa, which lies between latitudes 30°20' and 30°24'N and longitudes 34°24' and 34°30'E, about 40 km south of El-Qussaima area. The southeastern section is Wadi Quseib, near the Gulf of Aqaba, 140 km south of Gebel Areif El-Naqa (coordinates: 29°16'47"N and 34°43'12") (See text-fig. 1).

The material on which this study is based is housed in the collections of the Geology Department, Faculty of Science of El-Menoufiya University (MU), Egypt.

Text-fig. 1. Location map of the studied sections.



2 Lithostratigraphy

The Cenomanian-Turonian succession in the studied sections has been subdivided into the following four formations, from base to top: Halal Formation (Late Albian-Cenomanian of the Areif El-Naqa section), Galala Formation (Cenomanian of the Wadi Quseib section), Abu Qada Formation (Early-Middle Turonian), and Wata Formation (Late Turonian) (Text-figs. 2-3). The Galala Formation (ABDALLAH & EL ADINDANI, 1963) is characterized by containing less carbonates than the Halal Formation of north Sinai (SAID, 1971) but by having a higher carbonate content than the Raha Formation of west-central Sinai as described by GHORAB (1961).

The Cenomanian-Turonian succession at Wadi Quseib is 268 m thick. The Galala Formation (112 m) has been subdivided into three informal members, which arranged from the base to top are a lower shale member (33 m thick), middle siliciclastic/carbonate member (56 m), and upper carbonate member (23 m). It unconformably overlies multicoloured, kaolinitic, ferruginous, and cross-bedded sandstones of the Lower Cretaceous Malha Formation and is conformably underlain by fossiliferous shale of the Abu Qada Formation (Lower Turonian). The lower part of the Galala Formation consists mainly of green, glauconitic, gypsiferous, highly fissile shale (about 75% of the total thickness of the lower shale member), with intercalations of hard, ledge-forming sandstone. In the upper part of the member, the fissile shale grades upwards into nodular marly limestone thus forming a gradational contact with the middle siliciclastic/carbonate member above (Text-fig. 3). The middle siliciclastic/carbonate member is composed of carbonate rocks with highly fossiliferous shale and marl beds. The carbonate rocks are represented by fossiliferous limestone and dolomitic limestone (56% of the total thickness of the member). The member is highly fossiliferous, containing for example the bivalves *Rhynchostreon suborbiculatum* (LAMARCK), *Ilymatogyra africana* (LAMARCK), *Ceratostreon flabellatum* (GOLDFUSS), *Pycnodonte (Phygraea) vesicularis vesiculosa* (J. DE. C. SOWERBY), *Costagyra olisiponensis* (SHARPE), the gastropods *Nerinea gemmifera* COQUAND, *Pterodonta deffisi* THOMAS & PERON, the coral *Aspidiscus cristatus* (LAMARCK), *Tortoflabellum* sp. the ammonite *Neolobites vibrayanus* (D'ORBIGNY), and the trace fossil *Thalassinoides* isp. The upper carbonate member is composed mainly of greyish-yellow, hard, thick-bedded, fossiliferous, jointed, cliff-forming dolomitic limestone. The topmost part of this member is rich in corals (*Cladocora* sp.), rudist fragments (*Praeradiolites* sp.), recrystallized coralline sponges (*Actinostromarianina* sp.), and *Chondrodonta* fragments.

The Cenomanian sediments at Gebel Areif El-Naqa

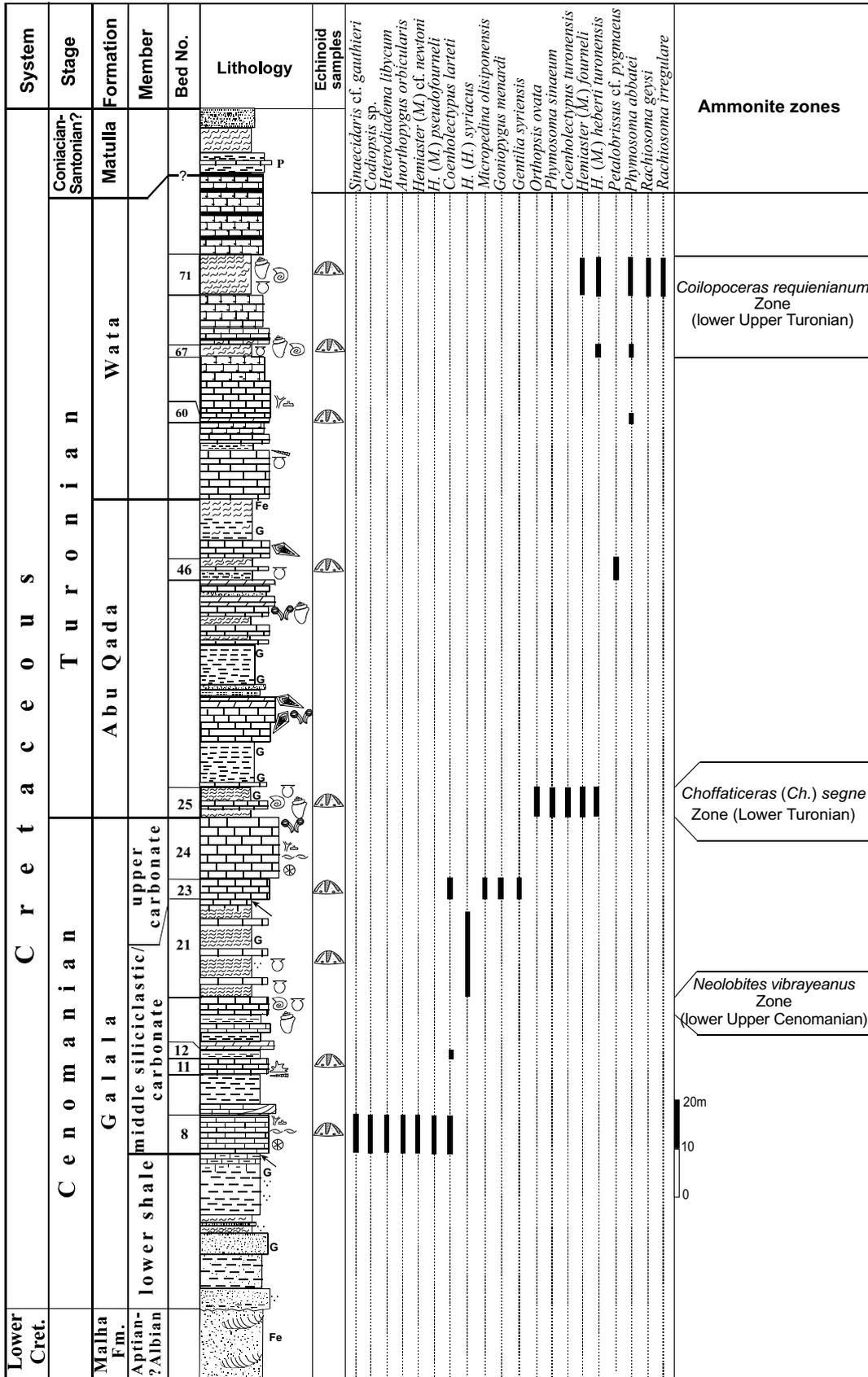
are represented by the Halal Formation (SAID 1971). It is about 301 m thick and composed mainly of carbonate rocks (about 65% of the total thickness of the formation) which alternate with siliciclastic facies (Text-fig. 2). The carbonates are represented by ledge-forming hard limestone, dolostone, and dolomitic limestone, while the terrigenous siliciclastics are represented by highly fossiliferous marl, shale, and sandy shale. The Halal Formation is subdivided into three informal members, a lower marly member (90 m), middle carbonate member (130 m), and upper marly carbonate member (81 m). The lower 75 m of the lower member are assigned to the Late Albian. The ammonite *Knemiceras deserti* Zone (Upper Albian) and inoceramid *Mytiloides concentricus* Zone (Upper Albian) have been recorded from the lower part of the Halal Formation. Therefore; the Halal Formation at the Areif El-Naqa section belongs to the Late Albian-Cenomanian.

The Abu Qada Formation (GHORAB 1961) in Wadi Quseib section is 73 m thick and is made up of yellowish-green, moderately hard, gypsiferous shale (about 55% of the total thickness of the formation) with greyish-yellow, hard to very hard, jointed limestone and dolomitic limestone beds in the middle and upper parts (35% of the total thickness). The rest of the Abu Qada Formation consists of moderately hard, fossiliferous marl (Text-fig. 3). In the Areif El-Naqa section, this formation is about 96 m thick and can be subdivided into three informal members (lower, middle, and upper members).

The formation mainly consists of marl and shale (lower and upper members) separated by thick-bedded limestones and chalky limestones (middle member) (Text-fig. 2).

The lower part of the Abu Qada Formation starts with highly fossiliferous marl with limestone intercalations (ammonite bed), which yielded *Neoptychites cephalotus* (COURTILLER), *Choffaticeras (Choffaticeras) securiforme* (ECK), *Choffaticeras (Ch.) segne* (SOLGER), and *Kamerunoceras turoniense* (D'ORBIGNY), together with other faunal elements such as the bivalve *Plicatula auresensis* COQUAND and the trace fossil *Thalassinoides* isp.

The Wata Formation can be recognized in the field by the disappearance or reduction of green siliciclastic facies and the beginning of light-coloured carbonates. Palaeontologically, this formation is not as rich in macrofauna as the underlying Abu Qada and Galala formations. In Wadi Quseib, the Wata Formation (82 m) overlies the Abu Qada Formation and underlies the Coniacian-?Santonian Matulla Formation. It is composed mainly of thick-bedded, hard, massive limestone and chalky limestone, flinty, dolomitic, cliff-forming in the lower part with marl and sandstone intercalations



Text-fig. 3. Stratigraphy, ammonite zones, and echinoid distribution of the Cenomanian-Turonian succession at Wadi Quseib.

in the middle part. The early Late Turonian ammonite *Coilipoceras requienianum* (D'ORBIGNY) was found at two levels and associated with other benthic elements e.g., the bivalve *Phelopteria grandidieri* (COQUAND), the gastropods *Tylostoma* (*Tylostoma*) *cossoni* THOMAS & PERON, *Tylostoma* (*T.*) *globosum* SHARPE, and the echinoid *Hemiaster* (*Mecaster*) *fourneli* (DESHAYES). In Gebel Areif El-Naqa, this formation is about 60 m thick.

The Cenomanian-Turonian boundary is drawn in the lower part of the Abu Qada Formation between the extinction of Cenomanian oysters e.g., *Costagyra olisi-*

ponensis (SHARPE) and the appearance of early Turonian ammonites e.g., *Choffaticeras* (*Ch.*) *segne* (SOLGER). This Ammonite Bed overlies the Cenomanian rudist-bearing beds of the upper part of the Halal and Galala formations. In agreement with BARTOV et al. (1980), the absence of the earlier Lower Turonian biozones indicates that the study area was a structural high during that time. Similarly, BAUER et al. (2001) noted that the first appearance of late Early Turonian ammonites above the Cenomanian deposits is a good indicator of a hiatus between the Cenomanian and Turonian deposits.

3 Systematic palaeontology

The systematic classification of echinoids follows the classification of Cretaceous echinoids from Great Britain (SMITH & WRIGHT 1989, 1990, 1993, 1996, 1999, and 2000) and from the United Arab Emirates-Oman border region (SMITH, 1995). The terminology used in the description of the taxa is that of DURHAM & WAGNER (1966).

All linear measurements (taken with Vernier Caliper) are given in millimeters. The abbreviations of measured parameters are:

D= test diameter;
 dp= diameter of peristome (in regular echinoids);
 H= test height;
 L= test length;
 W= test width;
 Ls= length of apical disc;
 Lk= length of periproct;
 Lp= length of peristome;
 Wp= width of peristome;
 Wa= width of ambulacral area at ambitus;
 Wi= width of interambulacral area at ambitus;
 LI= length of petal I or V;
 LII= length of petal II or IV;
 LIII= length of petal III up to the peripetalous fasciole;
 NI= number of pore pairs in petal I or V;
 NII= number of pore pairs in petal II or IV;
 NIII= number of pore pairs in ambulacral III until fasciole;
 WQ: Wadi Quseib;
 AEN: Gebel Areif El-Naqa.

Phylum Echinodermata KLEIN, 1734

Class Echinoidea LESKE, 1778

Order Cidaroida CLAUS, 1880

Family Cidaridae GRAY, 1825

Subfamily Cidarinae GRAY, 1825

Genus *Sinaeacidaris* FOURTAU, 1921

Sinaeacidaris cf. *gauthieri* FOURTAU, 1921

Pl. 1, Fig. 1.

cf. 1921 *Sinaeacidaris Gauthieri* sp. nov. – FOURTAU: 9, pl. 3, fig. 11.

Material and occurrence. A single incomplete specimen from the middle siliciclastic/carbonate member of the Cenomanian Galala Formation, bed 8 (MU2009WQ.8.1) at Wadi Quseib.

Description. Adapical and adoral sides of test flattened above and below. Ambulacral area narrow (about 20% of interambulacral width) and weakly sinuous. Poriferous zone wide and uniserial. Pores rounded, equal, slightly oblique, non-conjugated, and separated by elevated ridge. Interporiferous zones nearly as wide as poriferous zones and slightly swollen, with 2-4 rows of granules that are well developed near ambitus. Interambulacral area wide, carrying two rows of large and weakly crenulated primary tubercles with 5 plates in a series. Areole moderately deep, rounded, and surrounded by about 14 scrobicular tubercles. Interradial extrascrobicular surface wider than adradial extrascrobicular surface and occupied by equal-sized, non-oriented granules. Peristome not preserved.

Temporal and spatial distribution. *Sinaeacidaris gauthieri* has been erected based on material collected from the Upper Aptian of North Sinai, Egypt (FOURTAU, 1921).

Discussion. FOURTAU's genus differs from the genus *Typocidaritis* and all other Stereocidarinae by having primary interambulacral tubercles with confluent scrobicular circles, which are separated in *Typocidaritis*. The present material shows much similarity to *Sinaeacidaris gauthieri*, which has been originally described from the Upper Aptian of Gebel Manzour by FOURTAU (1921). It is characterized by the presence of flat adapical and adoral surfaces with crenulated tubercles.

Subclass Acrochinoidea SMITH, 1981**Superorder Pedinacea MORTENSEN, 1939
[after JENSEN, 1981]****Order Pedinoida MORTENSEN, 1939****Family Pedinidae POMIÉL, 1883**Genus *Micropedina* COTTEAU, 1866*Micropedina olisiponensis* (FORBES, 1850)

Pl. 1, Fig. 2

- 1850 *Echinus olisiponensis* sp. nov. – FORBES in SHARPE: 195, pl. 25, fig. 1.
 1912 *Micropedina olisiponensis* FORBES – FOURTAU: 156, pl. 2, fig. 2.
 1914 *Micropedina olisiponensis* FORBES – FOURTAU: 27.
 1981 *Micropedina olisiponensis* FORBES – AMARD et al.: 88.
 1991 *Micropedina olisiponensis* (FORBES) – SMITH & BENGTON: 32, pl. 6/A-I, text-figs. 24, 25.
 1992 *Micropedina olisiponensis* (FORBES) – GEYS: 143, pl. 1, figs. 8-14.
 1995 *Micropedina olisiponensis* (FORBES) – NÉRAUDEAU et al.: 411, fig. 3d.
 1997 *Micropedina olisiponensis* (FORBES) – NÉRAUDEAU & COURVILLE: 840, figs. 6/1, 8, 11.
 2003 *Micropedina olisiponensis* (FORBES) – ABDELHAMID & AZAB: 854, pl. 1, fig. F.
 2003 *Micropedina olisiponensis* (FORBES) – BERNDT: 80, fig. 3/4a-c.
 2006 *Micropedina olisiponensis* (FORBES) – EL QOT: 129, pl. 30, figs. 1, 2.

Material and occurrence. One specimen from the upper carbonate member of the Galala Formation (Upper Cenomanian), bed 23 (MU 2009WQ.23.1) at Wadi Quseib.

Measurements (in mm).

n=1	D	H	H/D	Ls	Ls/D	dp	dp/D
	30	25	0.83	7	0.23	11	0.37
	Wa	Wa/D	Wi	Wi/D	Wa/Wi		
	7	0.23	12	0.40	0.58		

Description. Test medium-sized, circular in outline, subconical, its height reaches 83% of test diameter. Ambitus strongly rounded and one-third of the test height above the base. Adapical surface dome-shaped. Adoral surface flattened. Apical disc not preserved but its size can be measured (23% of test diameter). Ambulacra straight from apex to peristome, flush, relatively broad, 23% of test diameter wide at ambitus, and 58% of interambulacral width. Poriferous zone wide and straight, not narrowing or broadening near the peristome. Pore-pairs arranged in oblique weak arcs of three (arranged in triads). Interporiferous zone carrying two rows of large tubercles with occasional militaries. Interambulacra broad, 40% of the test diameter, with irregular row of small, equal-sized tubercles that are perforated and crenulated. Peristome circular, its diameter 37% of test diameter.

Temporal and spatial distribution. *Micropedina olisiponensis* is a well known Cenomanian echinoids (NÉRAUDEAU & COURVILLE, 1997). It was first described by FORBES (in SHARPE, 1850) from the Cenomanian of Portugal. The species has been also recorded from the Middle Cenomanian of Brazil (SMITH & BENGTON, 1991), Upper Cenomanian of Saudi Arabia (NÉRAUDEAU et al., 1995), Nigeria (NÉRAUDEAU & COURVILLE, 1997), Algeria (AMARD et al., 1981), and Jordan (BERNDT, 2003). It is characteristic of the Upper Cenomanian throughout the Tethys (NÉRAUDEAU et al., 1993).

In Egypt, *M. olisiponensis* is known from the Upper Cenomanian of the Eastern Desert and Sinai (GEYS, 1992: 153; EL QOT, 2006: 30).

Cohort Echinacea CLAUS, 1876**Order Orthopsida MORTENSEN, 1942****Family Orthopsidae DUNCAN, 1889**Genus *Orthopsis* COTTEAU, 1864*Orthopsis ovata* (COQUAND, 1862)

Pl. 1, Fig. 3

- 1862 *Pseudodiadema ovatum* sp. nov. – COQUAND: 256, pl. 27, figs. 19-21.
 1880 *Orthopsis ovata* COQUAND – COQUAND: 330.
 1932 *Orthopsis ovata* COQUAND – LAMBERT: 95.
 2006 *Orthopsis* cf. *ovata* COQUAND – EL QOT: 141, pl. 32, fig. 8.

Material and occurrence. One specimen from the Lower Turonian Abu Qada Formation, bed 25 (MU2009WQ.25.1) at Wadi Quseib.

Measurements (in mm).

n=1	D	H	H/D	Ls	Ls/D	Wa	Wa / D
	30	16	0.54	7	0.23	5	0.17
	Wi	Wi/D	Wa/Wi				
	13	0.43	0.38				

Description. Test medium-sized, nearly circular, its height about 54% of test diameter. Adapical surface with a depressed domal profile. Adoral surface flattened. Ambitus rounded, lying about one-third of the height above the base. Ambulacra 17% of test diameter in width at ambitus and 38% of interambulacral width. Plating trigeminate ambitally. Poriferous zone narrow, uniserial, and straight. Pores well-rounded, equal-sized, and isolated. Interporiferous zone carries two rows of perforated, non-crenulated, non-confluent primary tubercles, which are smaller than the primary tubercles of interambulacral areas. These tubercles are separated by two rows of secondary tubercles (Pl. 1, Fig. 3d). Interambulacral plates simple, wide, and slightly curved with two rows of perforated, non-crenulated primary tubercles and reaching the apical disc and peristome. In addition, two external and two internal rows of secondary tuber-

cles exist, which disappear before the apex (Pl. 1, Fig. 3c). There are also two rows of very small tubercles around the interradiial suture at the ambitus. Peristome not well preserved.

Temporal and spatial distribution. *Orthopsis ovata* have been recorded from the Cenomanian-Turonian of Algeria (COQUAND, 1862) and Turonian of Morocco (LAMBERT, 1932). In Egypt, it has been recorded from the Turonian of Sinai by EL QOT (2006). According to EL QOT (2006: 142), *O. ovata* in Egypt apparently was restricted to Turonian.

Discussion. *Orthopsis ovata* differs from *O. miliaris* (D'ARCHIAC, 1835) figured by SMITH & BENGTSON (1991: 30, pl. 8B-F; text-fig. 23) from the Lower Albian-Middle Cenomanian of Brazil in the latter being smaller, having narrower ambulacra, and less developed tubercles on the interambulacral area.

Order Arbacioida GREGORY, 1900

Suborder Arbaciina GREGORY, 1900

Family Acropeltidae LAMBERT & THIÉRY, 1914

Genus *Goniopygus* AGASSIZ, 1838

Goniopygus menardi (DESMAREST, 1825)

Pl. 1, Fig. 4

1825 *Echinus Menardi* sp. nov. – DESMAREST: 101.

1914 *Goniopygus Menardi* DESMAREST var. *Brossardi* COQUAND – FOURTAU: 40.

1921 *Goniopygus Menardi* DESMAREST var. *Brossardi* COQUAND – FOURTAU: 45.

1925 *Goniopygus Menardi* DESMAREST – BLANCKENHORN: 84.

1985 *Goniopygus menardi* (DESMAREST) – BANDEL & GEYS: 111, pl. 9, figs. 2-6.

1992 *Goniopygus menardi* (DESMAREST) – GEYS: 147, pl. 2, figs. 10-13.

1993 *Goniopygus menardi* (DESMAREST) – NÉRAUDEAU et al.: 286, pl. 1, figs. I-K.

1993 *Goniopygus menardi* (DESMAREST) – SMITH & WRIGHT: 215, text-fig. 71.

2001 *Goniopygus menardi* (DESMAREST) – ABDELHAMID & EL QOT: 18, fig. 5I-J.

2003 *Goniopygus menardi* (DESMAREST) – ABDELHAMID & AZAB: 862, pl. 3, figs. H-I.

2003 *Goniopygus menardi* (DESMAREST) – BERNDT: 81, fig. 3/5-6.

2006 *Goniopygus menardi* (DESMAREST) – EL QOT: 140, pl. 32, figs. 5-6.

Material and occurrence. 20 specimens from the upper carbonate member of the Galala Formation (Upper Cenomanian), bed 23 (MU2009WQ.23.2-21) at Wadi Quseib.

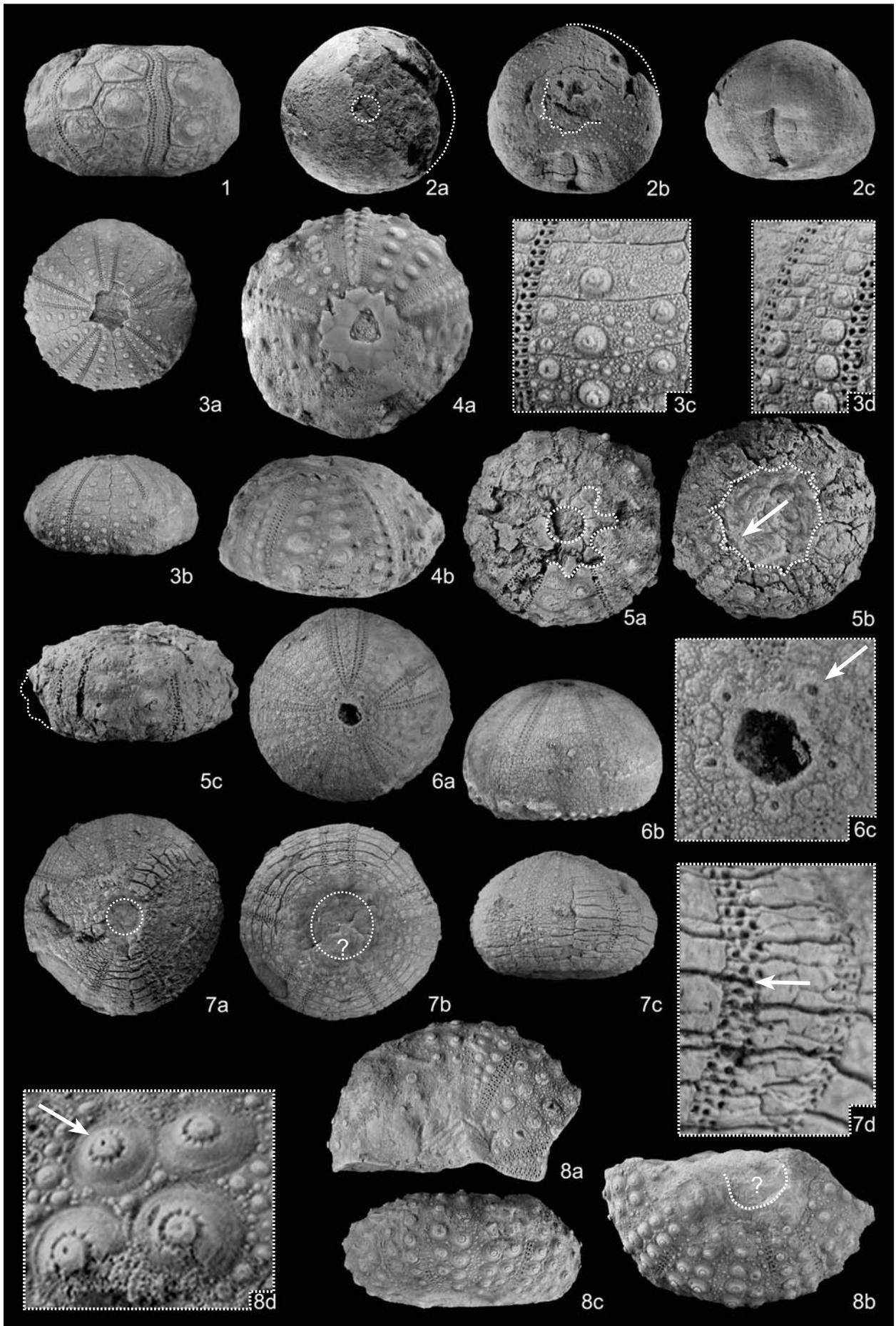
Measurements (in mm).

n=3	D	H	H/D	Ls	Ls/D	Wa	Wi	Wa/Wi
Range	6-21	11-15	0.65-0.75	7-8	0.38-0.50	3-5	7-10	0.34-0.50
Mean	18	12.7	0.70	7.6	0.43	3.7	8.7	0.42

Description. Test small-sized, hemispherical, circular in outline, its height about 70% of the total diameter. Adapical surface slightly convex with rounded ambitus. Adoral surface flattened. Apical disc large (about 53% of test diameter), flat, and sub-pentagonal to rounded. Ambulacral area narrow (42% of interambulacral width), slightly swollen, straight, and not closed adorally. Poriferous zone narrow and uniserial. Pores rounded, equal, and non-conjugated. Interporiferous zone with two rows of relatively small, imperforated, and non-crenulated primary tubercles (14-17 tubercles in each row). Interambulacral area relatively broad throughout and carrying two rows of well developed, large-sized, imperforated, and non-crenulated primary tubercles (7-10 tubercles in each row). These tubercles are not contiguous with their neighbours and surrounded by several non-contiguous secondaries. Peristome not preserved.

EXPLANATION OF PLATE 1

Fig. 1. *Sinaeccidaris* cf. *gauthieri* FOURATU, 1921 from the middle siliciclastic/carbonate member of the Cenomanian Galala Formation at Wadi Quseib. side view, x 2; MU2009WQ.8.1. **Fig. 2.** *Micropedina olisiponensis* (FORBES, 1850) from the upper carbonate member of the Cenomanian Galala Formation at Wadi Quseib. a: Adapical view, x1, b: adoral view, x1, c: side view, x1; MU2009WQ.23.1. **Fig. 3.** *Orthopsis ovata* (COQUAND, 1862) from the Lower Turonian Abu Qada Formation at Wadi Quseib. a: Adapical view, x1, b: side view, x1, c: detail of ambital interambulacrum, x4, d: detail of ambital ambulacrum, x5; MU2009WQ.25.1. **Fig. 4.** *Goniopygus menardi* (DESMAREST, 1825) from the upper carbonate member of the Cenomanian Galala Formation at Wadi Quseib. a: Adapical view, x2, b: side view, x2; MU2009WQ.23.2. **Fig. 5.** *Goniopygus* cf. *peroni* THOMAS & GAUTHIER, 1889 from the Upper Turonian Wata Formation at Gebel Areif El-Naqa. a: Adapical view, x1.5, b: adoral view, x1.5, c: side view, x1.5; MU2009AEN.31.1. **Fig. 6.** *Codiopsis* sp. from the middle siliciclastic/carbonate member of the Cenomanian Galala Formation at Wadi Quseib. a: Adapical view, x1.5, b: side view, x1.5, c: detail of apical disc, x5; MU2009WQ.8.2. **Fig. 7.** *Pedinopsis desori* (COQUAND, 1862) from the middle carbonate member of the Cenomanian Halal Formation at Gebel Areif El-Naqa. a: Adapical view, x2.5, b: adoral view, x2.5, c: side view, x2.5, d: detail of ambital ambulacrum, x12; MU2009AEN.15.1. **Fig. 8.** *Tetragramma variolare* (BRONGNIART, 1822) from the middle carbonate member of the Cenomanian Halal Formation at Gebel Areif El-Naqa. a: Adapical view, x1.5, b: adoral view, x1.5, c: side view, x1.5, d: detail of ambital interambulacrum, x8; MU2009AEN.15.2.



Temporal and spatial distribution. *Goniopygus menardi* has been recorded from the Cenomanian of Syria (BLANCKENHORN, 1925), Jordan (BANDEL & GEYS, 1985; BERNDT, 2003), and Upper Albian of England (SMITH & WRIGHT, 1993). In Egypt, it is known from the Cenomanian of Sinai and the Eastern Desert (FOURTAU, 1914; 1921; GEYS, 1992; EL QOT, 2006). The species has been also recorded from France, Germany, Portugal, Algeria, and Tunisia (GEYS, 1992: 148).

Discussion. COQUAND in COTTEAU (1865) erected *Goniopygus brossardi* as a new species from Algeria. COQUAND's species closely resembles *G. menardi* in general outline, size, and structure of the apical disc. Therefore, FOURTAU (1914) considered his species as a variety of *G. menardi*. Following BLANCKENHORN (1925) and EL QOT (2006), *G. brossardi* is regarded a junior synonym of *G. menardi*.

According to GEYS (1992), *G. innesi* GAUTHIER, 1901 in FOURTAU (1901) differs from the present species in the structure of the apical disc and in having fewer and larger ambulacral tubercles. *G. coquandi* COTTEAU, 1865, from the Cenomanian of Algeria, differs in being higher, more spherical, possessing a larger periproct, and a greater number of tubercles. The narrow interambulacral area and high test of *G. peroni* THOMAS & GAUTHIER, 1889 distinguish this species from *G. menardi* (EL QOT, 2006). The specimen, which has been described and figured by FOURTAU (1904) as *G. peroni*, is an incomplete and poorly preserved specimen. It resembles *G. menardi* more closely than *G. peroni*.

According to ABDELHAMID & AZAB (2003: 862), *G. noguesi* COTTEAU, 1863 differs from the present species in having a smaller and more depressed test and fewer granules in interambulacral areas.

Goniopygus cf. *peroni* THOMAS & GAUTHIER, 1889

Pl. 1, Fig. 5

cf. 1889 *Goniopygus Peroni* sp. nov. – THOMAS & GAUTHIER in GAUTHIER: 86, pl. 5, figs. 17-23.

cf. 1914 *Goniopygus Peroni* THOMAS & GAUTHIER – FOURTAU: 40.

cf. 2006 *Goniopygus peroni* THOMAS & GAUTHIER – EL QOT: 141, pl. 32, fig. 7.

Material and occurrence. One relatively poorly preserved specimen from the Wata Formation (Upper Turonian), bed 31 (MU2009AEN.31.1) at Gebel Areif El-Naqa.

Measurements (in mm).

n=1	D	H	H/D	Ls	Ls/D
	24	15	0.62	13	0.55
	dp	dp/D	Wa	Wi	Wa/Wi
	10	0.41	5	11	0.45

Description. Test medium-sized, subspherical, its height about 62% of total test diameter. Adapical surface slightly convex with rounded ambitus. Adoral surface

flattened and not sunken around peristome (Pl. 1, Fig. 5b). Apical disc large (about 55% of test diameter), flat, and rounded. Ambulacral area narrow (about 21% of test diameter, 45% of interambulacral width), slightly swollen, straight, and not closed adorally. Poriferous zone narrow and uniserial. Pores rounded, equal, mostly isolated and conjugated in some parts. Interporiferous zone with two rows of relatively small primary tubercles (12-14 tubercles in each row). Interambulacral area relatively broad throughout and carrying two rows of well developed, large-sized, imperforated, and non-crenulated primary tubercles. These tubercles are not contiguous with their neighbours and surrounded by several non-contiguous secondaries. Peristome rounded and slightly less than half (41%) of the test diameter. Gill slits moderately developed (Pl. 1, Fig. 5b).

Temporal and spatial distribution. *Goniopygus peroni* has been recorded from the Turonian of Tunisia (THOMAS & GAUTHIER, 1889). In Egypt, it is known from the Turonian of Sinai (EL QOT, 2006).

Discussion. The specimen is relatively poorly preserved, but it seems to be closely similar to the description and measurements of *Goniopygus peroni* THOMAS & GAUTHIER, 1889.

Family Arbaciidae GRAY, 1855

Genus *Codiopsis* AGASSIZ, 1840

Codiopsis sp.

Pl. 1, Fig. 6

Material and occurrence. A single specimen from the middle siliciclastic/carbonate member of the Cenomanian Galala Formation, bed 8 (MU 2009WQ.8.2) at Wadi Quseib.

Measurements (in mm).

n=1	D	H	H/D	Ls	Ls/D	Wa	Wi	Wa/Wi
	24	15	0.62	7	0.29	5	10	0.50

Description. Test medium-sized, rounded in outline, its height about 62% of test diameter. Adapical surface dome-like. Adoral surface flat and slightly depressed around peristome. Ambitus rounded, lying about one-third of the height above the base of the test. Apical disc medium-sized (29% of test diameter) and dicyclic with well-rounded gonopores (Pl. 1, Fig. 6c). Genital plates broad and crescentic in outline. Ocular plates small and subpentagonal. Ambulacral area about 21% of test diameter in width at the ambitus, 50% of interambulacral width, and lancet-shaped. Poriferous zones moderately wide, uniserial, straight, and close together near apical disc. Pores well-rounded, equal, and isolated. Interambulacral plates simple and with moderately developed tubercles with small granules.

Adoral surface carrying randomly oriented and well-developed tubercles, which do not extend beyond the ambitus. Peristome not preserved.

Discussion. The present material resembles *Codiopsis doma* (DESMAREST, 1825) from the Cenomanian of France as figured by DURHAM et al. (1966: U411, fig. 208b-f) in structure of the apical disc, tuberculation style, and in the plating style of ambulacra and interambulacra but the latter species differs in being higher ($H/L=79\%$ of total test height) and in having a pentagonal outline. Moreover, the oral surface of the present material is not well preserved.

Order Phymosomatoida MORTENSEN, 1904

Family Diplopodiidae, SMITH & WRIGHT, 1993

Genus *Pedinopsis* COTTEAU, 1863

Pedinopsis desori (COQUAND, 1862)

Pl. 1, Fig. 7

- 1862 *Magnosia Desori* sp. nov. – COQUAND: 254, pl. 27, figs. 13-15.
 1866 *Pedinopsis Desori* COQUAND – COTTEAU: 826, pl. 1196, figs. 6-16.
 1921 *Pedinopsis Desori* COQUAND – FOURTAU: 32.
 1925 *Pedinopsis Desori* COQUAND – BLANCKENHORN: 89, pl. 7, fig. 7.
 1990 *Pedinopsis desori* (COQUAND) – ALI: 102, fig. 3/1-3.
 2003 *Pedinopsis desori* (COQUAND) – ABDELHAMID & AZAB: 857, pl. 2, fig. A.

Material and occurrence. One specimen from the middle carbonate member of the Cenomanian Halal Formation, bed 15 (MU2009 AEN.15.1) at Gebel Areif El-Naqa.

Measurements (in mm).

n=1	D	H	H/D	Ls	Ls/D
	16	10	0.62	4	0.25
	dp	dp/D	Wa	Wi	Wa/Wi
	7	0.44	3	6	0.50

Description. Test small-sized, subconical, its height about 62% of test diameter, with strongly convex ambitus. Adapical surface dome-shaped. Adoral surface flattened, without depression around peristome. Ambulacral area slightly narrow (about 18% of test diameter and 50% of interambulacral width) and feebly swollen. Ambulacral plates compound, trigeminate adorally, and quadrigeminate at ambitus (Pl. 1, Fig. 7d). Poriferous zone wide, biserial from the apical disc to slightly below the ambitus, and nearly uniserial near peristome. Pores rounded, small adorally, wide and numerous adapically, and non-contiguous. Interporiferous zone carrying two rows of relatively small primary tubercles. Interambulacral plates narrow, simple, and separated by sutures (slightly convex adorally). Each plate with equal-sized,

crenulated primary tubercles, the middle one lying in the middle of the adoral half of the plate, the other two tubercles on the adapical half of the same plate. Primary tubercles surrounded by other irregular secondary tubercles. Peristome not well preserved but apparently rounded, centric, not sunken, and large (44% of the test diameter). Apical disc much smaller than peristome (25% of test diameter).

Temporal and spatial distribution. *Pedinopsis desori* has been recorded from the Upper Cretaceous of Algeria (COQUAND, 1862), Palestine (BLANCKENHORN, 1925), and United Arab Emirates (ALI, 1990). In Egypt, it is known from the Cenomanian of the Eastern Desert by FOURTAU (1921) and ABDELHAMID & AZAB (2003).

Discussion. The genus *Pedinopsis* is characterized by having very complex ambulacral plates, which are trigeminate adorally, and quadrigeminate or polygeminate at ambitus. It resembles the genus *Tetragramma* in having biserial ambulacral pores adapically. However, the latter genus differs in having coarse primary tubercles, the apical disc being much larger and similar in size to the peristome, and in ambulacral plates that are trigeminate or quadrigeminate but not polygeminate ambilaterally.

SMITH et al. (1990) divided *Pedinopsis* into three subgenera, based on the structure of the major ambulacral plates: *P. (Pedinopsis)* includes species having compound ambulacral plates with six platelets adapically and four adorally; *P. (Dumbea)* includes species having trigeminate compound plating throughout; and *P. (Sinaïopsis)* with trigeminate compound plating adorally and quadrigeminate compound plating adapically. However, ABDELHAMID & EL QOT (2001: 12) argued that inclusion of the genus *Dumbea* as subgenus of *Pedinopsis* does not make sense because the former differs from the latter not only in the plating style of ambulacra but also in the system of tuberculation and in having straight, low, and long interambulacral plates.

P. sinaica (DESOR) of ABDELHAMID & EL QOT (2001: 11, fig. 4E-F) from the Cenomanian of Gebel El-Hamra and G. El-Minsherah (Sinai, Egypt) differs from the present species in having biserial poriferous zones between the apical disc and slightly above the ambitus, trigeminate ambulacral plates adorally and at the ambitus and quadrigeminate plates slightly above the ambitus.

P. sphaerica SMITH et al. (1990: 50, figs. 12a-e, 13) from the Cenomanian of Oman is characterized by its globular shape (H/L ranges from 85% to 87%) and a small, not sunken peristome. FOURTAU (1921) described *P. desori* from the Cenomanian of Gebel El-Tourkmania but the globular shape of the test and biserial arrangement of the poriferous zone indicates that the species

may belong to *P. sphaerica* (for more detailed discussion, see SMITH et al., 1990: 48-54).

Genus *Tetragramma* AGASSIZ, 1840

Tetragramma variolare (BRONGNIART, 1822)

Pl. 1, Fig. 8; pl. 2, Fig. 1

- 1822 *Cidarites variolaris* sp. nov. – BRONGNIART: 84, pl. 5, fig. 9.
 1910 *Tetragramma variolare* (BRONGNIART) – LAMBERT & THIÉRY: 187.
 1914 *Diplopodia variolaris* BRONGNIART – FOURTAU: 619.
 1921 *Diplopodia variolaris* BRONGNIART – FOURTAU: 31.
 1925 *Diplopodia variolaris* BRONGNIART – BLANCKENHORN: 85.
 1985 *Tetragramma* cf. *variolare* (BRONGNIART) – BANDEL & GEYS: 107, pl. 5, figs. 3-4.
 1989 *Tetragramma variolare* (BRONGNIART) – GEYS: 131, pl. 1, figs. 9-10.
 1990 *Tetragramma variolare* (BRONGNIART) – ALI: 102, fig. 3/4-5.
 1990 *Tetragramma variolare* (BRONGNIART) – SMITH et al.: 43, fig. 8b.
 1991 *Tetragramma?* *variolare* (BRONGNIART) – SMITH & BENGTON: 26, pl. 4C-D.
 1993 *Tetragramma variolare* (BRONGNIART) – SMITH & WRIGHT: 232, pl. 79, figs. 1-9; pl. 80, figs. 1-5; pl. 81, figs. 1-8; text-figs. 74E, F, 75-76, 77A, C, 78-79.
 1995 *Tetragramma variolare* (BRONGNIART) – NÉRAUDEAU et al.: 407, fig. 3C.
 1997 *Tetragramma variolare* (BRONGNIART) – NÉRAUDEAU & COURVILLE: 839, fig. 6/4-5.
 2001 *Tetragramma variolare* (BRONGNIART) – ABDELHAMID & EL QOT: 12, fig. 4G-I.
 2001 *Tetragramma variolare* (BRONGNIART) – ABDALLAH et al.: pl. 3, fig. 11.
 2003 *Tetragramma variolare* (BRONGNIART) – ABDELHAMID & AZAB: 859, pl. 2, figs. L-M.
 2003 *Tetragramma variolare* (BRONGNIART) – BERNDT: 80, fig. 3/3a-b.
 2006 *Tetragramma variolare* (BRONGNIART) – EL QOT: 133, pl. 30, figs. 10a-b, 11a-b.

Material and occurrence. Three specimens from the middle carbonate member of the Cenomanian Halal Formation, bed 15 (MU2009 AEN.15.2-4) at Gebel Areif El-Naqa.

Measurements (in mm).

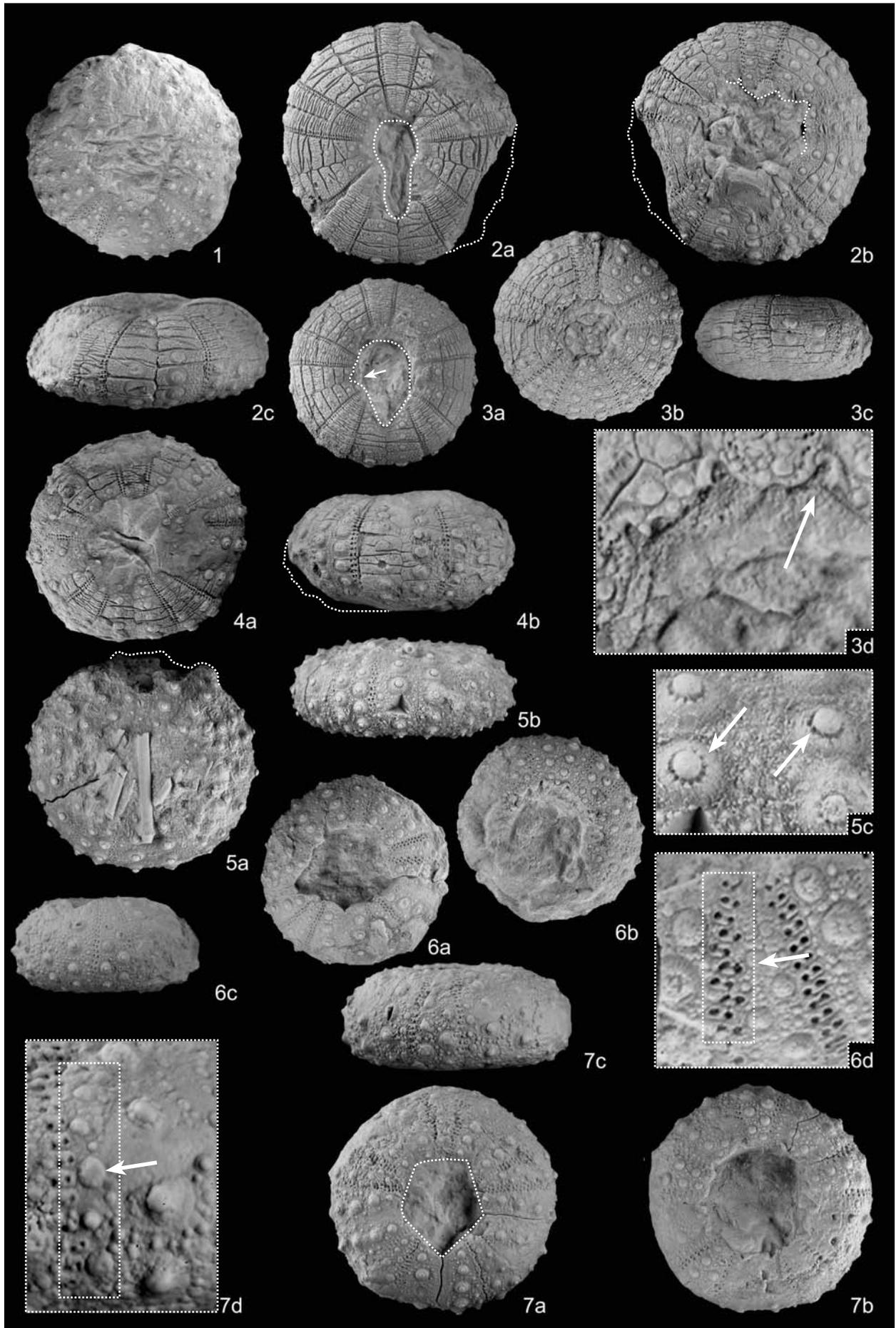
n=2	D	H	H/D	dp	dp/D	Wa	Wi	Wa/Wi
Range	26-33	11-14	0.42-	12	0.37-0.46	7-9	10-15	0.6-0.7
Mean	29.5	12.5	0.42	12	0.41	8	10	0.65

Description. Test medium-to large-sized, nearly rounded, test height about 42% of total diameter with strongly convex sides. Both adapical and adoral surfaces flattened to slightly convex. Large pentagonal apical disc not preserved. Ambulacral width about 24% of test diameter, 65% of interambulacral width, and slightly swollen. Poriferous zone narrower adorally, becoming wider adapically, biserial at ambitus and near apical disc but uniserial near peristome. Pores rounded, non-conjugated, and wide adapically. Interporiferous zone bearing two rows of perforated and crenulated primary tubercles. Interambulacral area with two internal rows of perforated and crenulated primary tubercles extending between the apical disc and peristome (bigger one near ambitus; see Pl. 1, Fig. 8d), whereas two external ones do not persist to the apical disc. Peristome rounded and large (about 41% of test diameter). Gill slits not preserved.

Temporal and spatial distribution. *Tetragramma variolare* is a widespread Cenomanian echinoid. It has been recorded from Europe, Africa, the Arabian Peninsula, and America. The main North-Tethyan occurrences are Spain (LAMBERT, 1919, 1922), France (NÉRAUDEAU & MOREAU, 1989); and England (SMITH et al., 1988; SMITH & WRIGHT, 1993). In the South Tethyan area, it occurs in the Cenomanian of Palestine (BLANCKENHORN, 1925), United Arab Emirates (ALI, 1990), Oman (SMITH et al., 1990), Algeria (NÉRAUDEAU et al., 1993), Saudi Arabia (NÉRAUDEAU et al., 1995), Nigeria (NÉRAUDEAU & COURVILLE, 1997), and Jordan (BANDEL & GEYS, 1985; BERNDT, 2003). In Brazil, it has been recorded from the Early Cenomanian by SMITH & BENGTON (1991). In Egypt, the species has been found in the Late Albian-Cenomanian of the Eastern Desert and Sinai (Fourtau, 1921; GEYS, 1989; ABDELHAMID & AZAB, 2003; EL QOT, 2006).

EXPLANATION OF PLATE 2

Fig. 1. *Tetragramma variolare* (BRONGNIART, 1822) from the middle carbonate member of the Cenomanian Halal Formation at Gebel Areif El-Naqa. Adapical view, x1.5; MU2009AEN.15.3. **Figs. 2-4.** *Heterodiadema libycum* (AGASSIZ & DESOR, 1846). 2-3. Specimens from the middle carbonate member of the Cenomanian Halal Formation at Gebel Areif El-Naqa. 2. a: Adapical view, x1.5, b: adoral view, x1.5, c: side view, x1.5; MU2009AEN.15.5. 3. a: Adapical view, x2, b: adoral view, x2, c: side view, x2, d: part of peristomal region, x10; MU2009AEN.15.6. 4. Specimen from the middle siliciclastic/carbonate member of the Cenomanian Galala Formation at Wadi Quseib. a: Adapical view, x1.5, b: side view, x1.5; MU2009WQ.8.3. **Figs. 5-6.** *Phyosoma abbatei* (GAUTHIER, 1898). 5. Specimen from the Upper Turonian Wata Formation at Wadi Quseib. a: Adapical view, x2, b: side view, x2, c: ambital interambulacrum, x6; MU2009WQE.67.1. - 6. Specimen from the lower member of the Lower Turonian Abu Qada Formation at Gebel Areif El-Naqa. a: Adapical view, x2, b: adoral view, x2, c: side view, x1.5, d: adapical ambulacrum, x8; MU2009AEN.22.1. **Fig. 7.** *Phyosoma sinaeum* (FOURTAU, 1914) from the Lower Turonian Abu Qada Formation at Wadi Quseib. a: Adapical view, x2.5, b: adoral view, x2.5, c: side view, x2.5, d: detail of ambital interambulacrum, x8; MU2009WQ.25.2.



Discussion. ALI (1990: 102) distinguished *Tetragramma brongniarti* (AGASSIZ) from *T. variolare* by its more elevated shape, less markedly diplopodous poriferous zones, and narrow peristome. Moreover, AGASSIZ (1840) had already pointed out that *T. brongniarti* differs in having smaller secondary interambulacral tubercles, larger tubercle bases, and smaller mamelons. SMITH & WRIGHT (1993: 237) discussed all differences between *T. variolare* and *T. brongniarti* and considered the latter species as synonym to *T. variolare*. GEYS (1989: 132) regarded the differences between *T. marticense* and *T. variolare* as small and considered *T. marticense* from France, Portugal, and Egypt as a synonym of the present species (for more detailed discussion, see SMITH & WRIGHT, 1993: 236).

Family Heterodiadematidae SMITH & WRIGHT, 1993

Genus *Heterodiadema* COTTEAU, 1846

Heterodiadema libycum (AGASSIZ & DESOR, 1846)

Pl. 2, Figs. 2-4; Text-fig. 4

- 1846 *Hemicidaris libyca* sp. nov. – AGASSIZ & DESOR: 338.
 1864 *Heterodiadema libycum* AGASSIZ & DESOR – COTTEAU: 522, pl. 1124.
 1921 *Heterodiadema libycum* AGASSIZ & DESOR – FOURTAU: 16.
 1925 *Heterodiadema libycum* AGASSIZ & DESOR – BLANCKENHORN: 85, pl. 7, fig. 1a-c.
 1963 *Heterodiadema libycum* AGASSIZ & DESOR – FAWZI: 5.
 1985 *Heterodiadema lybicum* (AGASSIZ & DESOR) – BANDEL & GEYS: 106, pl. 4, figs. 6-7; pl. 5, figs. 1, 2.
 1989 *Heterodiadema lybicum* (AGASSIZ & DESOR) – GEYS: 129, pl. 1, figs. 5-6.
 1990 *Heterodiadema lybica* (AGASSIZ & DESOR) – SMITH et al.: 43, figs. 8c-g, 9-10.
 1992 *Heterodiadema libycum* (AGASSIZ & DESOR) – ABDEL-GAWAD & ZALAT: pl. 3, fig. 11.
 1995 *Heterodiadema lybicum* (AGASSIZ & DESOR) – NÉRAUDEAU et al.: 406, fig. 3e.
 1995 *Heterodiadema buhaysensis* sp. nov. – SMITH: 133, pl. 2, figs. 1-3; text-figs. 10-11.
 1997 *Heterodiadema libycum* (AGASSIZ & DESOR) – NÉRAUDEAU & COURVILLE: 839, fig. 6/6.
 2001 *Heterodiadema libycum* (AGASSIZ & DESOR) – ABDELHAMID & EL QOT: 7, fig. 3L-N.
 ? 2001 *Heterodiadema buhaysensis* SMITH – ABDELHAMID & EL QOT: 6, pl. 3K.
 2002 *Heterodiadema lybicum* (AGASSIZ & DESOR) – AHMAD & AL-HAMMAD: 462, fig. 5/11-12.
 2003 *Heterodiadema libycum* (AGASSIZ & DESOR) – BERNDT: 78, fig. 3/1-2.
 2003 *Heterodiadema libycum* (AGASSIZ & DESOR) – ABDELHAMID & AZAB: 857, pl. 1, fig. Q.
 2006 *Heterodiadema libycum* (AGASSIZ & DESOR) – EL QOT: 132, pl. 30, figs. 6-9.
 ? 2006 *Heterodiadema buhaysensis* SMITH – EL QOT: 130, pl. 30, fig. 5a-c.
 2007 *Heterodiadema libycum* (AGASSIZ & DESOR) – ABDEL-GAWAD et al.: pl. 6, fig. 6.

Material and occurrence. 21 mostly complete specimens from the middle carbonate member of the Cenomanian Halal Formation, bed 15 (MU 2009AEN.15.5-25) at Gebel Areif El-Naqa; six specimens from the middle siliciclastic/carbonate member of the Cenomanian Galala Formation, bed 8 (MU2009WQ.8.3-8) at Wadi Quseib.

Measurements (in mm).

n=16	D	H	H/D	Ls	Ls/D
Range	17-37	8-18	0.36-0.55	6-9	0.22-0.40
	dp	dp/D	Wa	Wi	Wa/Wi
	7-12	0.37-0.50	5-9	7-13	0.54-0.75
Mean	D	H	H/D	Ls	Ls/D
	26	11.75	0.45	7.66	0.31
	dp	dp/D	Wa	Wi	Wa/Wi
	9.9	0.42	6.25	10	0.61

Description. Test small-to medium-sized, nearly rounded, its height about 45% of test diameter, with strongly convex sides. Adapical surface slightly convex to flat. Adoral surface flattened and slightly depressed around peristome. Apical disc large (about 31% of test diameter) and key-shaped, deeply penetrating into the posterior interambulacrum. Posterior prolongation U- or V-shaped (Pl. 2, Figs. 2a, 3a). Interambulacra 1 to 4 with only faint interradian notches. Greatest width of apical disc along this penetration about 42% of test diameter, while the transverse width is only about 30% of test diameter. Ambulacral width about 24% of test diameter, 61% of the interambulacral width at the ambitus, and slightly swollen. Poriferous zone narrow, straight, and uniserial. Pores rounded, nearly equal, and non-conjugated. Interporiferous zone bearing compound plates with two rows of perforated and crenulated primary tubercles adorally, which become imperforate with either little or no crenulations adapically. Some of these tubercles distinctly reduced in size above the ambitus and others reduced sharply closer to the apical disc. This applies also to the interambulacral tubercles (Pl. 2, Figs. 2c, 4b). Interambulacral area consisting of 12 simple and wide plates with two rows of strongly crenulated and perforated primary tubercles. Peristome circular in outline, and centric (about 42% of test diameter). Gill slits well developed (Pl. 2, Fig. 3d).

Temporal and spatial distribution. *Heterodiadema libycum* is a well known Cenomanian echinoid, especially abundant in North Africa and the Arabian Peninsula. It has been recorded from the Cenomanian of Palestine (BLANCKENHORN, 1925), Cenomanian-Turonian of Central Jordan (BANDEL & GEYS, 1985; AHMAD & AL-HAMMAD, 2002; BERNDT, 2003), Cenomanian of Oman (SMITH et al. 1990), Maastrichtian of Oman and United Arab Emirates (SMITH, 1995), Saudi Arabia (NÉRAUDEAU et al., 1993, 1995), and Nigeria (NÉRAUDEAU & COURVILLE, 1997). In Egypt, it is known from the Cenomanian of the Eastern Desert and Sinai (FOURTAU, 1921; GEYS, 1989; ABDELHAMID & AZAB, 2003).

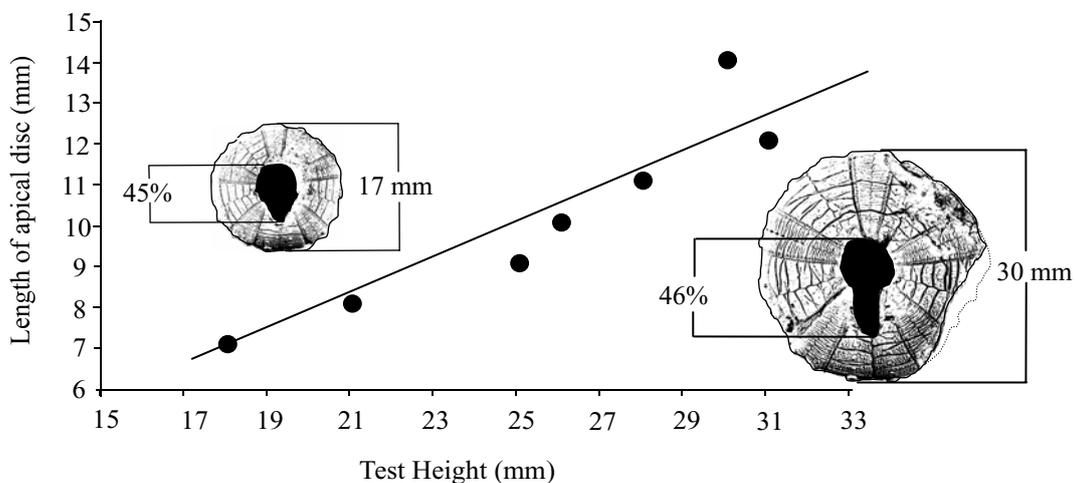
Discussion. The variability in *Heterodiadema libyicum* is mainly confined to the degree of reduction in size of the primary tubercles above the ambitus and degree of penetration of the apical disc in the posterior interambulacrum (ABDELHAMID & EL QOT, 2001; EL QOT, 2006). SMITH et al. (1990) noted that the abruptness in size reduction of the primary tubercles above the ambitus differs from population to population. For instance, in specimens from Oman, the change is extremely abrupt, whereas in other populations such as from Algeria, the change tends to be less abrupt and the tubercle size decreases gradually adapically. In addition, ADELHAMID & AZAB (2003) distinguished two forms of *H. libyicum* according to the general shape of the apical disc and the degree to which it penetrates into the posterior interambulacrum; the first population has been collected from Saint Paul, Wadi Dakhel, and W. Abu Qada and the specimens have an apical disc with straight to slightly convex sides and a V-shaped posterior prolongation of the apical disc, which penetrates 2-4 plates deep into the posterior interambulacrum. The second population has been collected from G. Gharamul and has an apical disc with highly convex sides towards the center, and a posterior prolongation which is U-shaped and penetrates 4-7 plates deep into the posterior interambulacrum. LAMBERT (1933) distinguished three varieties in addition to the typical form from Egypt. The var. *martini*, figured and described by COTTEAU (1864), has a narrow and elongated apical disc and has been collected from Egypt and Tunisia, the var. *batnense* COQUAND is of moderate size with well developed primary tubercles adapically and has been collected from Algeria, and the third var. *russoi* is characterized by its large size (D=50 mm, H=30 mm, H/D=0.60 mm) and by the primary tubercles being

less developed adapically. The last variety has been collected from Algeria and Morocco. LAMBERT (1933) noted also that the typical forms from Egypt are small-sized with a less prolonged apical disc posteriorly.

GEYS (1989: 129) agrees with FOURTAU (1914) and BANDEL & GEYS (1985) that *H. libyicum* seems to become larger in the course of its evolution.

SMITH (1995: 133, pl. 2, figs. 1-3) pointed out that his new species *H. buhaysensis* is most closely related to the Cenomanian *H. libyicum* in having the same form of ambulacral compounding and tuberculation style but differs in having fewer reduced tubercles, which become smaller distinctly closer to the apex, and in lacking the extreme prolongation of the apical disc into the posterior interambulacrum. The latter differences have been discussed as different varieties of *H. libyicum* by LAMBERT (1933), SMITH et al. (1990), and ABDELHAMID & AZAB (2003). Moreover, no photograph of the apical disc in SMITH's specimens documents its shorter prolongation into the posterior interambulacrum. The prolongation of the apical disc is due to the displacement of the periproct, which occurs relatively late in the ontogenetic sequence of the post-larva (SAUCÈDE et al., 2003). In addition, the degree of prolongation (eccentricity) is directly proportional to the size of specimens (Text-fig. 4). Therefore, *H. buhaysensis* is probably a variety of *H. libyicum*.

H. libyicum also resembles *H. ouremense* DE LORIO from the Cenomanian of Portugal with respect to shape of ambulacra, interambulacra, and apical disc, but the latter species differs in having a globular test. NÉRAUDEAU & COURVILLE (1997) suggested that *H. ouremense* probably is also a variety of *H. libyicum*.



Text-fig. 4. Relationship of test height and the length of apical disc of *Heterodiadema libyicum* (AGASSIZ & DESOR, 1846) from the Cenomanian of Gebel Areif El-Naqa.

Family Phymosomatidae POMEL, 1883Genus *Phymosoma* HAIME in D'ARCHIAC & HAIME, 1853*Phymosoma abbatei* (GAUTHIER, 1898)

Pl. 2, Figs. 5-6

- 1898 *Cyphosoma abbatei* sp. nov. – GAUTHIER in FOURTAU: 620, pl. 1, figs. 2-6.
 1906 *Coptosoma abbatei* GAUTHIER – GREGORY: 223.
 1914 *Cyphosoma abbatei* GAUTHIER – FOURTAU: 28.
 1998 *Phymosoma abbatei* (GAUTHIER) – EL-SHEIKH et al.: pl. 2, fig. B.
 1999 *Phymosoma abbatei* (GAUTHIER) – ABDELHAMID: pl. 2, fig. I; pl. 3, fig. A.
 2001 *Phymosoma abbatei* (GAUTHIER) – ABDALLAH et al.: pl. 3, fig. 12.
 2001 *Phymosoma abbatei* (GAUTHIER) – ABDELHAMID & EL QOT: 13, fig. 4J-K.
 2004a *Phymosoma abbatei* (GAUTHIER) – ABDEL-GAWAD et al.: pl. 10, figs. 1, 4.
 2006 *Phymosoma abbatei* (GAUTHIER) – EL QOT: 134, pl. 31, figs. 1-2, 4.

Material and occurrence. Five specimens from the lower member of the Abu Qada Formation (Lower Turonian), bed 22 (MU2009AEN.22.1-5) at Gebel Areif El-Naqa; 10 specimens from the Upper Turonian of the Wata Formation, beds 60, 67, and 71 (MU2009WQ.60.1-3; MU2009WQ.67.1-3; MU2009WQ.71.1-4) at Wadi Quseib.

Measurements (in mm).

n=11	D	H	H/D	Ls	Ls/D
Range	13-21	5-11	0.37-0.62	4-7	0.28-0.52
	dp	dp/D	Wa	Wi	Wa/Wi
	5-8	0.33-0.53	3-6	5-9	0.54-0.84
Mean	D	H	H/D	Ls	Ls/D
	17	7.88	0.46	6.27	0.37
	dp	dp/D	Wa	Wi	Wa/Wi
	6.80	0.42	4.31	6.38	0.67

Description. Test small-sized, rounded, its height about 46% of test diameter, with strongly convex sides. Adapical surface flattened to slightly convex with spine fragments in a few specimens (Pl. 2, Fig. 5a). Adoral surface flattened and not sunken around peristome. Apical disc large (28% to 52% of test diameter) and pentagonal in outline without any plating remains. Ambulacral areas wide near the ambitus (about 30% of test diameter) and narrower adapically than peristome. Poriferous zone narrow, biserial in some poriferous zones (Pl. 2, Fig. 6d) near the apical disc, becoming uniserial near peristome. Pores nearly rounded, equal-sized, and isolated. Interporiferous zone carrying two rows of imperforated and crenulated primary tubercles as large as in interambulacral area (Pl. 2, Fig. 5c). Peristome semi-rounded, centric, and large (about 37% of test diameter). Gill slits well developed.

Temporal and spatial distribution. *Phymosoma abbatei* has been recorded from the Turonian of Egypt by GREGORY (1906); EL-SHEIKH et al. (1998); ABDELHAMID

& EL QOT, 2001); ABDEL-GAWAD et al. (2004a); and EL QOT (2006).

Discussion. GREGORY (1906) referred the present species to the genus *Coptosoma* according to the uniserial arrangement of the pore pairs. According to FOURTAU (1914) the uniserial arrangement of the poriferous zone of *Cyphosoma abbatei* is restricted to specimens with a diameter of less than 16 mm. However, the poriferous zone in the present material is biserial adapically in some poriferous zones with a diameter of less than 15 mm.

Phymosoma major COQUAND (1862: 256, pl. 27, figs. 16-18) from Algeria differs from the present species in having four rows of primary tubercles in the interambulacral area and in being larger (D=39 mm, H=17 mm; H/D=0.43 mm).

Phymosoma sinaeum (FOURTAU, 1914)

Pl. 2, Fig. 7

1914 *Cyphosoma sinaeum* sp. nov. – FOURTAU: pl. 3, fig. 2.

Material and occurrence. Three specimens from the Lower Turonian Abu Qada Formation, bed 25 (MU2009WQ.25.2-4) at Wadi Quseib.

Measurements (in mm).

n=3	D	H	H/D	Ls	Ls/D
Range	16-21	7-10	0.42-0.50	6-8	0.35-0.40
	dp	dp/D	Wa	Wi	Wa/Wi
	6-8	0.40-0.50	4-6	6-9	0.64-0.70
Mean	D	H	H/D	Ls	Ls/D
	17.59	8.07	0.45	6.78	0.38
	dp	dp/D	Wa	Wi	Wa/Wi
	7.38	0.45	4.80	7.71	0.63

Description. Test small-sized and rounded. Height about 45% of test diameter with rounded ambitus. Both adapical and adoral surfaces flattened without depression around peristome. Apical disc large (about 38% of test diameter) and pentagonal in outline without any plating remains (Pl. 2, Fig. 7a). Ambulacral area wide near ambitus and narrower adapically than peristome. Poriferous zone narrow and biserial above ambitus to apical disc. Pores nearly rounded, equal-sized, and isolated. Interporiferous zone with two rows of imperforated and crenulated primary tubercles. Interambulacral area carrying two rows of imperforated and crenulated primary tubercles, which are better developed marginally and have internal and external secondary tubercles (Pl. 2, Fig. 7d). At ambitus and near peristome, each tubercle is surrounded by a circle of mamelonated granules. Peristome centric, semi-rounded, and wide (about 45% of test diameter). Gill slits well developed.

Temporal and spatial distribution. *Phymosoma sinaeum* has been recorded from the Turonian of Gebel Um Raiying, Egypt by FOURTAU (1914).

Discussion. The present species differs from *Phymosoma abbatei* (GAUTHIER) in having internal and external rows of secondary tubercles in each interambulacrum (Pl. 2, Fig. 7d) with biserial poriferous zones above the ambitus. In contrast, *Ph. thevestense* (PÉRON & GAUTHIER) from the Turonian of Algeria lacks secondary tubercles in interambulacra with wider ambulacra adapically.

Genus *Rachiosoma* POMEL, 1883

Rachiosoma geysi ABDELHAMID & EL QOT, 2001

Pl. 3, Figs. 1-2

- 1985 *Rachiosoma major* (COQUAND) – BANDEL & GEYS: 110, pl. 7, figs. 6-7; pl. 8, figs. 1-2.
 2001 *Rachiosoma geysi* sp. nov. – ABDELHAMID & EL QOT: 14, fig. 5B-C.
 2004a *Rachiosoma geysi* ABDELHAMID & EL QOT – ABDEL-GAWAD et al.: pl. 10, fig. 2.
 2006 *Rachiosoma geysi* ABDELHAMID & EL QOT – EL QOT: 137, pl. 31, figs. 6a-b, 7, 9.

Material and occurrence. Five specimens from the Wata Formation (Upper Turonian), bed 71 (MU2009WQ.71.5-9) at Wadi Quseib.

Measurements (in mm).

n=4	D	H	H/D	Ls	Ls/D
Range	20-33	11-14	0.43-0.54	6-7	0.20-0.22
	dp	dp/D	Wa	Wi	Wa/Wi
	6-8	0.25-0.32	4-7	7-13	0.43-0.65
Mean	D	H	H/D	Ls	Ls/D
	26.15	12.12	0.50	6.34	0.21
	dp	dp/D	Wa	Wi	Wa/Wi
	7	0.29	5.45	10	0.56

Description. Test small-to medium-sized, wheel-shaped, rounded in outline, its height about 50% of test diameter. Adapical surface relatively high and slightly convex with rounded ambitus. Adoral surface flattened and slightly depressed around peristome. Apical disc pentagonal and medium-sized (about 21% of test diameter). Ambulacra slightly swollen ambitally, its width about 24% of test diameter and 56% of the interambulacra at the ambitus. Poriferous zone uniserial and feebly undulating. Pores rounded, equal-sized, isolated, and arranged in arcs of three pore pairs around peristome. Interporiferous zone carrying two rows of imperforated, crenulated primary tubercles. In addition, two rows of granules exist around the perradial suture. Interambulacral area wide (7-13 mm) with four rows of well-developed, imperforated, and crenulated primary tubercles (Pl. 3, Fig. 1c). The internal rows are non-confluent and slightly larger than those of the external ones. Peristome slightly sunken, rounded, its width ranging from 25% to 32% of test diameter. Gill slits well developed.

Temporal and spatial distribution. *Rachiosoma geysi* has been recorded from the Coniacian of Jordan (BANDEL & GEYS, 1985) and in Egypt from the Turonian of Sinai

by ABDELHAMID & EL QOT (2001); ABDEL-GAWAD et al. (2004a); and EL QOT (2006). The stratigraphic range of this species is from Turonian to Coniacian.

Discussion. The present species can be easily distinguished from other *Rachiosoma* species by having uniserial poriferous zones and four rows of imperforated and crenulated primary tubercles on each interambulacrum (Pl. 3, Figs. 1c, 2). BANDEL & GEYS (1985) described the poriferous zones of *Phymosoma major* (COQUAND, 1862) in ten specimens from the Coniacian of Jordan as uniserial and referred them to the genus *Rachiosoma*. They argued that *Ph. major* is uniserial and that COQUAND (1862) did not describe the poriferous zone of this species. However, COQUAND stated that the pores are "bigemine". Moreover, his figures show a biserial poriferous zone on the adapical surface (COQUAND, 1862: pl. 25, figs. 16, 18). BANDEL & GEYS also mentioned that COTTEAU (1864) indicated that *Ph. major* has simple poriferous zones. However, COTTEAU (1864) pointed out that the simple arrangement of pores exists only in very small individuals. In the main description of the species he stated that the poriferous zones are adapically biserial. For these reasons, ABDELHAMID & EL QOT (2001) considered the Jordanian material to belong to their new species *Rachiosoma geysi*.

Rachiosoma irregulare FOURTAU, 1921

Pl. 3, Fig. 3

- 1921 *Rachiosoma irregulare* sp. nov. – FOURTAU: 39, pl. 5, figs. 3-4.
 1932 *Rachiosoma irregulare* FOURTAU – LAMBERT: 191.
 2001 *Rachiosoma irregulare* FOURTAU – ABDELHAMID & EL QOT: 18, fig. 5D-E.
 2004a *Rachiosoma irregulare* FOURTAU – ABDEL-GAWAD et al.: pl. 10, figs. 3,5.
 2006 *Rachiosoma irregulare* FOURTAU – EL QOT: 137, pl. 31, fig. 10 a, b.

Material and occurrence. A single specimen from the Wata Formation (Upper Turonian), bed 71 (MU2009WQ. 71.10) at Wadi Quseib.

Measurements (in mm).

n=1	D	H	H/D	Ls	Ls/D
	26	11	0.42	8	0.31
	dp	dp/D	Wa	Wi	Wa/Wi
	11	0.42	7	10	0.70

Description. Test medium-sized, rounded, its height about 42% of test diameter. Adapical surface slightly convex with strongly rounded ambitus. Adoral surface flattened and slightly depressed around peristome. Apical disc pentagonal and medium-sized (31% of test diameter) without plating remains. Ambulacral area wide (27% of test diameter and 70% of interambulacral width). Poriferous zone uniserial, straight, and narrow. Pores well rounded, equal-sized, and non-conjugated.

Interporiferous zone carrying two rows of imperforated and crenulated primary tubercles, which are separated by fine granules. Interambulacral area moderately wide with two rows of imperforated and crenulated primary tubercles, which are well developed ambilaterally, and separated from the neighbouring one by well-developed fine granules (Pl. 3, Fig. 3d). Adradial and interrational extrascrobicular surfaces wide and occupied by two rows of small granules. Peristome rounded and large (42% of test diameter). Gill slits moderately well developed.

Temporal and spatial distribution. *Rachiosoma irregulare* has been recorded from the Turonian of Gebel Um Kécheiba (FOURTAU, 1921), G. El-Minsherah (ABDELHAMID & EL QOT, 2001), and G. Ekma (ABDEL-GAWAD et al., 2004a; EL QOT, 2006).

Discussion. *Rachiosoma irregulare* differs from *R. geysi* by having two rows of well-developed crenulated and imperforated primary tubercles in each interambulacrum (Pl. 3, Fig. 3d). *R. rectilineatum* (PERON & GAUTHIER) of BANDEL & GEYS (1985: 111, pl. 8, figs. 3-7; pl. 9, fig. 1) from the Coniacian of Algeria and of GEYS (1992: 147, pl. 2, figs. 8-9) from the Santonian of Wadi Qena are similar to the present species in having two rows of crenulated and imperforated primary tubercles in each interambulacrum, but differ in having a regular series of small secondary tubercles (two secondary tubercles for each primary) and well-developed ambulacral tubercles adapically.

Cohort Irregularia LATREILLE, 1825

Order Holectypoida DUNCAN, 1889

Suborder Holectypina DUNCAN, 1889

Family Holectypidae LAMBERT, 1900

Subfamily Coenholectypinae SMITH & WRIGHT, 1999

Genus *Coenholectypus* POMEL, 1883

Coenholectypus larteti (COTTEAU, 1869)

Pl. 3, Figs. 4-6

- 1869 *Holectypus Larteti* sp. nov. – COTTEAU: 537.
 1914 *Holectypus Larteti* COTTEAU – FOURTAU: 44, pl. 3, fig. 8.
 1914 *Holectypus Larteti* COTTEAU race *sinaea* – FOURTAU: 46, pl. 4, figs. 1-4.
 1914 *Holectypus Larteti* COTTEAU var. *dowsoni* var. nov. – FOURTAU: 47.
 1921 *Holectypus Larteti* COTTEAU race *sinaea* var. nov. – FOURTAU: 55.
 1925 *Holectypus Larteti* COTTEAU – BLANCKENHORN: 90, pl. 7, figs. 10-11.
 1925 *Holectypus larteti* COTTEAU var. *major* var. nov. – BLANCKENHORN: 91, pl. 7, fig. 12a-d.
 1963 *Holectypus larteti* COTTEAU – FAWZI: 9, pl. 1, fig. 1.
 ? 1989 *Holectypus (Caenholectypus) larteti* (COTTEAU) – ALI: 401, fig. 5/10.
 1990 *Coenholectypus larteti* (COTTEAU) – SMITH et al.: 57, fig. 14d-f; text-figs. 17-18.
 1999 *Caenholectypus larteti* (COTTEAU) – ABDELHAMID: pl. 3, fig. D.
 2001 *Caenholectypus larteti* (COTTEAU) – ABDELHAMID & EL QOT: 21, fig. 6A.
 2003 *Caenholectypus larteti* (COTTEAU) – ABDELHAMID & AZAB: 864, pl. 4, figs. C-D.
 2006 *Coenholectypus larteti* (COTTEAU) – EL QOT: 143, pl. 32, fig. 11a-b.

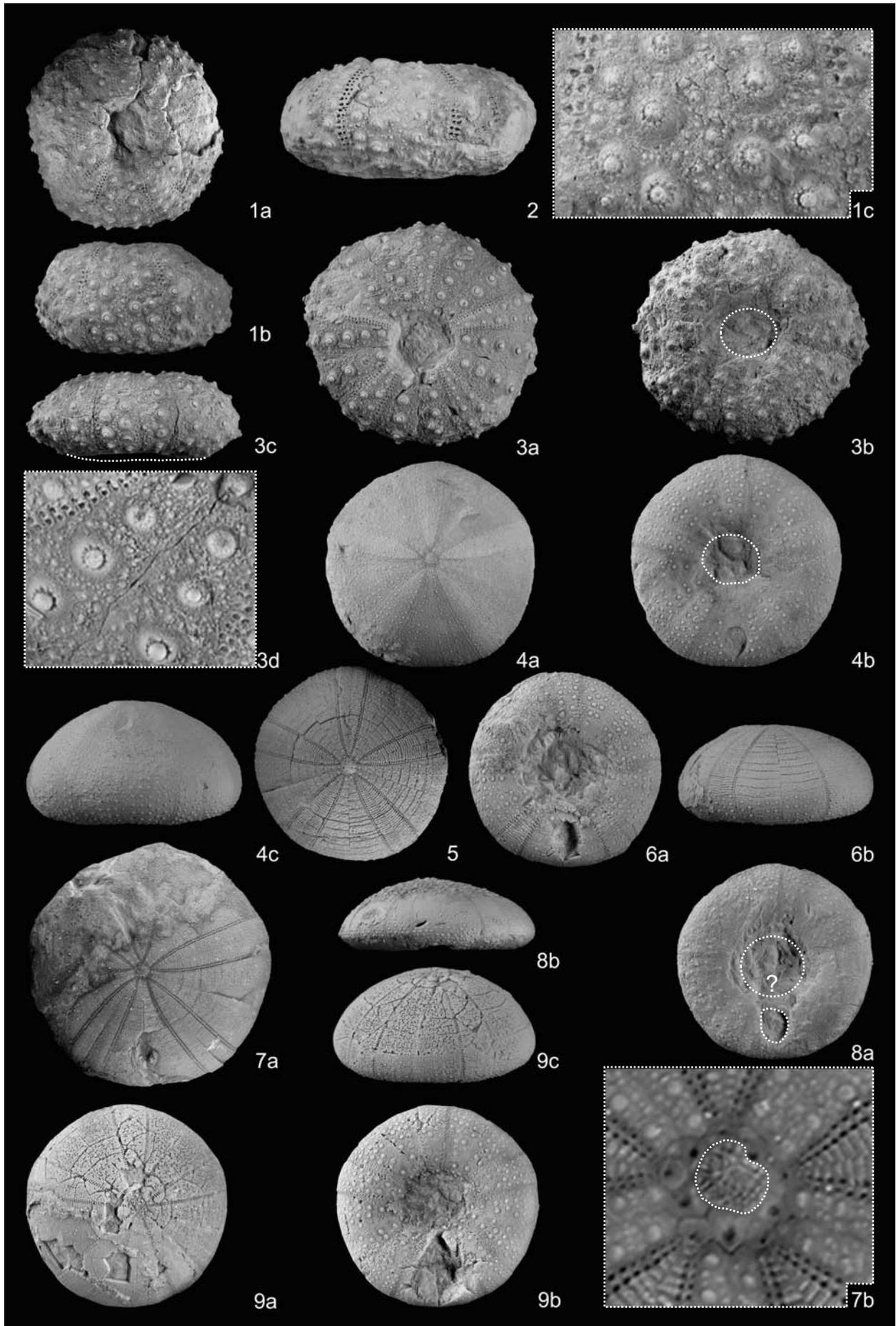
Material and occurrence. 23 specimens from the middle carbonate member of the Cenomanian Halal Formation, bed 15 (MU2009 AEN.15.26-47) at Gebel Areif El-Naqa; six specimens from the middle siliciclastic/carbonate member of the Cenomanian Galala Formation, beds 8, 12, 23 (MU2009WQ. 8.9; MU2009WQ.12.1-2; MU2009 WQ.23.22-24) at Wadi Quseib.

Measurements (in mm).

n=20	D	H	H/D	Lk	Lk/D
Range	13-28	6-15	0.39-0.60	3-5	0.17-0.22
	dp	dp/D	Wa	Wi	Wa/Wi
	4-6	0.16-0.26	3-5	6-13	0.37-0.50
Mean	D	H	H/D	Lk	Lk/D
	19.10	9.57	0.49	3.80	0.20
	dp	dp/D	Wa	Wi	Wa/Wi
	6.33	0.22	3.75	8.62	0.44

EXPLANATION OF PLATE 3

Figs. 1-2. *Rachiosoma geysi* ABDELHAMID & EL QOT, 2001 from the Upper Turonian Wata Formation at Wadi Quseib. 1. a: Adapical view, x1.5, b: side view, x1.5, c: ambital interambulacrum, x5; MU2009WQ.71.5. – 2. Side view, x1.5; MU2009WQ.71.6. **Fig. 3.** *Rachiosoma irregulare* FOURTAU, 1921 from the Upper Turonian Wata Formation at Wadi Quseib. a: Adapical view, x1.5, b: adoral view, x1.5, c: side view, x1.5, d: detail of interambulacrum, x5; MU2009WQ.71.10. **Figs. 4-6.** *Coenholectypus larteti* (COTTEAU, 1869). 4. From the middle siliciclastic/carbonate member of the Cenomanian Galala Formation at Wadi Quseib. a: Adapical view, x1.5, b: adoral view, x1.5, c: side view, x1.5; MU2009WQ.8.9. 5-6. From the middle carbonate member of the Cenomanian Halal Formation at Gebel Areif El-Naqa. 5. Adapical view, x2; MU2009AEN.15.26. 6. a: adoral view, x2, b: side view, x2; MU-2009AEN.15.27. **Figs. 7-8.** *Coenholectypus portentosus* COQUAND, 1876 from the lower marly and middle carbonate members of the Upper Albian-Cenomanian Halal Formation at Gebel Areif El-Naqa. 7. a: Adapical view, x1.5, b: detail of apical disc, x10; MU2009AEN.9.1. – 8. a: Adoral view, x1, b: side view, x1; MU2009AEN.15.48. **Fig. 9.** *Coenholectypus turonensis* (DESOR, 1847) from the Lower Turonian Abu Qada Formation at Wadi Quseib. a: Adapical view, x1.5, b: adoral view, x1.5, c: side view, x1.5; MU2009WQ.25.5.



Description. Test small-to medium-sized and circular to sub-pentagonal. Test height ranges from 39% to 49% of total diameter. Adapical surface strongly convex (low dome-shaped) with strongly rounded ambitus. Adoral surface flattened and slightly concave around peristome. Apical disc small (about 11% of test diameter) and carrying five gonopores; ocular pores are not seen. Ambulacral area flush to feebly swollen, lancet-shaped, and reaching about 44% of interambulacral width ambitally. Poriferous zone narrow, slightly convex to straight, and uniserial. Pore pairs small, circular, closer together adorally, wider adapically, and non-conjugated. Interporiferous zone with four rows of primary tubercles per plate marginally and 2-3 adapically. Ambulacral plate simple and narrow. Interambulacral plates twice the width of ambulacral ones and carrying 10 tubercles marginally and two adapically. The biggest tubercles occur on the adoral side close to the margin. Both ambulacral and interambulacral primary tubercles imperforated and crenulated. Peristome circular and small (range: 16% to 22% of test diameter). Periproct inframarginal, small, oval to drop-shaped, elongated, and nearer to the ambitus than peristome (Pl. 3, Fig. 6a).

Temporal and spatial distribution. *Coenholectypus larteti* has been recorded from the Cenomanian of Palestine (BLANCKENHORN, 1925), Oman (SMITH et al., 1990), and the Maastrichtian of United Arab Emirates (ALI, 1989). In Egypt, it is known from the Cenomanian of Wadi Um Mitla and Gebel Yelleg (FOURTAU, 1921), G. El-Minsherah (FAWZI, 1963), G. El-Hamra (ABDELHAMID & EL QOT, 2001), Saint Paul and G. Musabba Salama (ABDELHAMID, 1999; ABDELHAMID & AZAB, 2003), and G. Yelleg (EL QOT, 2006). Stratigraphically, *C. larteti* has a wide range, from the Cenomanian to the Maastrichtian.

Discussion. The genus *Coenholectypus* differs from *Holectypus* DESOR (1842) mainly in having a perforate genital plate 5, which is imperforate in *Holectypus*. DUTHAM et al. (1966: U444) noted that *Coenholectypus* and *Caenholectypus* are synonyms with the first one having a priority.

Many species of the genus *Coenholectypus* can be distinguished according to the size and position of the periproct, the size of the peristome, and the outline of the test.

Coenholectypus larteti differs from other *Coenholectypus* species recorded in the present study by its dome-shaped, rounded ambitus, and small peristome. In addition, its periproct is small and nearer to the ambitus than to the peristome.

FOURTAU (1914) differentiated his varieties (see synonymy list) according to test height and size of peristome and periproct. In agreement with SMITH et al. (1990)

and EL QOT (2006), all varieties of *C. larteti* (e.g. the varieties of FOURTAU, 1914-1921 and BLANCKENHORN, 1925) are placed within the range of variation of *C. larteti*.

C. excisus (DESOR, 1847) differs in having a large marginal periproct, which extends from near the peristome up to a third to half the distance between apical disc and ambitus. Therefore, the periproct of *Holectypus excisus* (DESOR, 1847) figured by ABDEL-GAWAD et al. (2004b) from the Cenomanian of Gebel El-Fallig is completely inframarginal and large with a wide and depressed peristome. For these reasons, their specimen is more similar to *C. larteti* than to *C. excisus*.

C. inflatus (COTTEAU & GAUTHIER) of SMITH (1995: 178, pl. 18, figs. 7-11) from Oman differs from the present species by having a larger peristome and a periproct that extends much closer to the peristome than the ambitus and its tubercles are well developed adorally.

Coenholectypus portentosus (COQUAND, 1876)

Pl. 3, Figs. 7-8

1876 *Holectypus portentosus* sp. nov. – COQUAND in COTTEAU et al.: 30, pl. 2, figs. 9-11.

1912 *Holectypus portentosus* COQUAND – FOURTAU: 46, pl. 12, fig. 6.

1921 *Holectypus portentosus* COQUAND – FOURTAU: 56.

1925 *Holectypus portentosus* COQUAND – BLANCKENHORN: 89, pl. 7, fig. 8a-b.

1990 *Holectypus (Coenholectypus) portentosus* COQUAND – ALI: 109, fig. 5/4-6.

Material and occurrence. Two specimens from the lower marly and middle carbonate members of the Halal Formation (Upper Albian-Cenomanian), beds 9 and 15 (MU2009AEN.9.1; MU2009AEN.15.48) at Gebel Areif El-Naqa.

Measurements (in mm).

n=2	D	H	H/D	Lk	Lk/D
Range	31-33	11-12	0.35-0.36	5-7	0.16-0.21
	dp	dp/D	Wa	Wi	Wa/Wi
	9-10	0.29-0.30	5-6	13-15	0.38-0.40
Mean	D	H	H/D	Lk	Lk/D
	32	11.50	0.35	6	0.19
	dp	dp/D	Wa	Wi	Wa/Wi
	8	0.29	5.5	14	0.39

Description. Test medium-sized, circular, its height about 35% of total test diameter (low conical-shaped). Adapical surface convex with sharp ambitus (Pl. 3, Fig. 8b). Adoral surface flattened and strongly concave around peristome. Apical disc small (7% of the test diameter), elevated, and yielding five genital plates with five gonopores and five ocular plates with five ocular pores. Madreporite well developed and separating the posterior gonopores 1 and 4, while the posterior gonopore 5 and the ocular pores are still behind the madreporite (Pl. 3, Fig. 7b). Ambulacral area lancet-shaped, flush to slightly swollen, reaching about 39% of inter-

ambulacral width, and about 18% of total test diameter. Poriferous zone narrow, straight, and uniserial. Pores small, circular, isolated, close together near ambitus, and less close on the adapical and adoral surfaces. Interporiferous zone carrying six primary tubercles marginally and 2-3 adapically. Ambulacral plates simple and narrow. Interambulacral area with about 16-18 primary tubercles marginally and two adapically. Both ambulacral and interambulacral primary tubercles imperforated, crenulated, and more developed below ambitus and adorally. Periproct small (about 19% of test diameter), oval, and inframarginal. Peristome centric, rounded, and medium-sized (about 30% of test diameter).

Temporal and spatial distribution. *Coenholectypus portentosus* has been recorded from the Cenomanian of Palestine (BLANCKENHORN, 1925) and United Arab Emirates (ALI, 1990). In Egypt, it occurs in the Aptian of Gebel Mandhour (FOURTAU, 1921).

ALI (1990: 109) mentioned that the species has been recorded also from the Aptian of Lebanon, and Algeria, the Aptian-Albian of Syria, and the Cenomanian of Algeria, France, Syria, and Portugal.

Discussion. *Coenholectypus portentosus* differs from other *Coenholectypus* species by its circular outline, very low conical test, sharp ambitus, and moderately-sized periproct that extends from near the peristome to near the posterior margin. The present species resembles *C. cenomanensis* (GUÉRANGER) in having the same shape of ambulacra and peristome, but differs in having a sharp ambitus and smaller periproct.

Coenholectypus turonensis (DESOR, 1847)

Pl. 3, Fig. 9

- 1847 *Holectypus turonensis* sp. nov. – DESOR in AGASSIZ & DESOR: 146.
 1912 *Holectypus turonensis* DESOR – FOURTAU: 162.
 1914 *Holectypus turonensis* DESOR – FOURTAU: 48.
 1921 *Holectypus turonensis* DESOR – FOURTAU: 57.
 2004a *Coenholectypus turonensis* (DESOR) – ABDEL-GAWAD et al.: pl. 10, figs. 7, 9.
 2006 *Coenholectypus turonensis* (DESOR) – EL QOT: 144, pl. 32, figs. 12-14.
 2007 *Coenholectypus turonensis* (DESOR) – ABDEL-GAWAD et al.: pl. 6, fig. 7.

Material and occurrence. Three specimens from the Abu Qada Formation (Lower Turonian), bed 25 (MU2009WQ.25.5-7) of the Wadi Quseib section.

Measurements (in mm).

n=3	D	H	H/D	dp
Range	21-32	9-14	0.43-0.45	6-7
	dp/D	Wa	Wi	Wa/Wi
	0.22-0.28	4-7	12-13	0.33-0.53

Mean	D	H	H/D	dp
	26.50	11.50	0.44	6.50
	dp/D	Wa	Wi	Wa/Wi
	0.25	5	12.50	0.43

Description. Test medium-sized, circular in outline, its height about 44% of test diameter. Adapical surface dome-shaped with rounded ambitus. Adoral surface flat and strongly concave around peristome. Apical disc medium-sized with five well-rounded gonopores. Madreporite well developed. Ambulacral width about 20% of test diameter and 43% of interambulacral width. Poriferous zone narrow, straight, and uniserial. Pores well-rounded, equal-sized, and isolated. Interporiferous zone yielding four rows of imperforated and crenulated primary tubercles, well developed adorally. Interambulacral area wide with 12-14 rows of primary tubercles. Periproct drop-shaped, large (about 31% of test diameter), and occupying the distance between the peristome and posterior margin (Pl. 3, Fig. 9b). Peristome circular and relatively small (about 25% of test diameter). Gill slits well developed.

Temporal and spatial distribution. *Coenholectypus turonensis* has been recorded from the Turonian of Gebel Dhalfa and G. Halal (FOURTAU, 1921), Gebel Ekma, the East Themed area, and G. Yelleg (ABDEL-GAWAD et al., 2004a; EL QOT, 2006).

Discussion. According to EL QOT (2006: 146), *Coenholectypus turonensis* differs from *C. serialis* (DESHAYES, 1847) in being higher and highly concave around the peristome. The two species have been recorded from the Turonian and their stratigraphic range is extended to the Santonian. According to COTTEAU et al. (1881), *C. turonensis* is confined to the Turonian and *C. serialis* to the Santonian.

Suborder Pygasterina DURHAM & MELVILLE, 1957

Family Anorthopygidae WAGNER & DURHAM, 1966

Genus *Anorthopygus* COTTEAU, 1869

Anorthopygus orbicularis (GRATELOUP, 1836)

Pl. 4, Fig. 1

- 1836 *Nucleolites orbicularis* sp. nov. – GRATELOUP: 180, pl. 2, fig. 21.
 1878 *Anorthopygus orbicularis* (GRATELOUP) – COTTEAU et al.: 175.
 ? 1921 *Anorthopygus atavus* sp. nov. – FOURTAU: 53, pl. 2, fig. 5.
 ? 1990 *Anorthopygus arabicus* sp. nov. – ALI: 111, fig. 7/1-5.
 1999 *Anorthopygus orbicularis* (GRATELOUP) – SMITH & WRIGHT: 362, pl. 115, figs. 3-6, 7-9; text-fig. 136.
 2003 *Anorthopygus orbicularis* (GRATELOUP) – ABDELHAMID & AZAB: 866, pl. 4, fig. k.

Material and occurrence. A single well preserved specimen from the middle siliciclastic/carbonate member of the Galala Formation (Cenomanian), bed 8 (MU2009WQ.8.10) at Wadi Quseib.

Measurements (in mm).

n=1	D	H	H/D	Ls	Ls/D	dp
	33	14	0.42	4	0.12	10
	dp/D	Lk	Wk	Wa	Wi	Wa/Wi
	0.30	7.54	5.35	5	15	0.33

Description. Test large, wheel-shaped, rounded in outline, its height about 42% of test diameter. Adapical surface broad and flat with rounded ambitus. Adoral surface nearly flattened and slightly depressed around peristome. Apical disc ethmolytic (Pl. 4, Fig. 1d), nearly central, consisting of five genital plates with five gonopores and five ocular plates. Madreporite large and separating the posterior ocular plates as well as the posterior genital plates. Ambulacral area lancet-shaped, moderately swollen ambitally, and wide near ambitus (16% of test diameter and 33% of interambulacral width) but relatively narrow throughout. Poriferous zone narrow, straight, and uniserial. Pores well-rounded, equal-sized, and isolated. Interporiferous zone carrying 2-6 rows of imperforated and crenulated primary tubercles, which are well developed adorally. Interambulacral area wide (45% of test diameter) with simple and wide plates, and yielding 8-12 rows of perforated and crenulated primary tubercles with wide and deep areole. The external rows of primary tubercles reach the apical disc and peristome. Periproct opening immediately above the ambitus. It is oblique towards the anterior right and almost as wide as long. Peristome central, medium-sized (30% of test diameter), rounded, and situated in slightly deep depression.

Temporal and spatial distribution. *Anorthopygus orbicularis* has been recorded from the Cenomanian of United Arab Emirates (ALI, 1990) and England (SMITH & WRIGHT, 1999). In Egypt, it is known from the Albian of Gebel Mandhour (FOURTAU, 1921) and G. Manzour

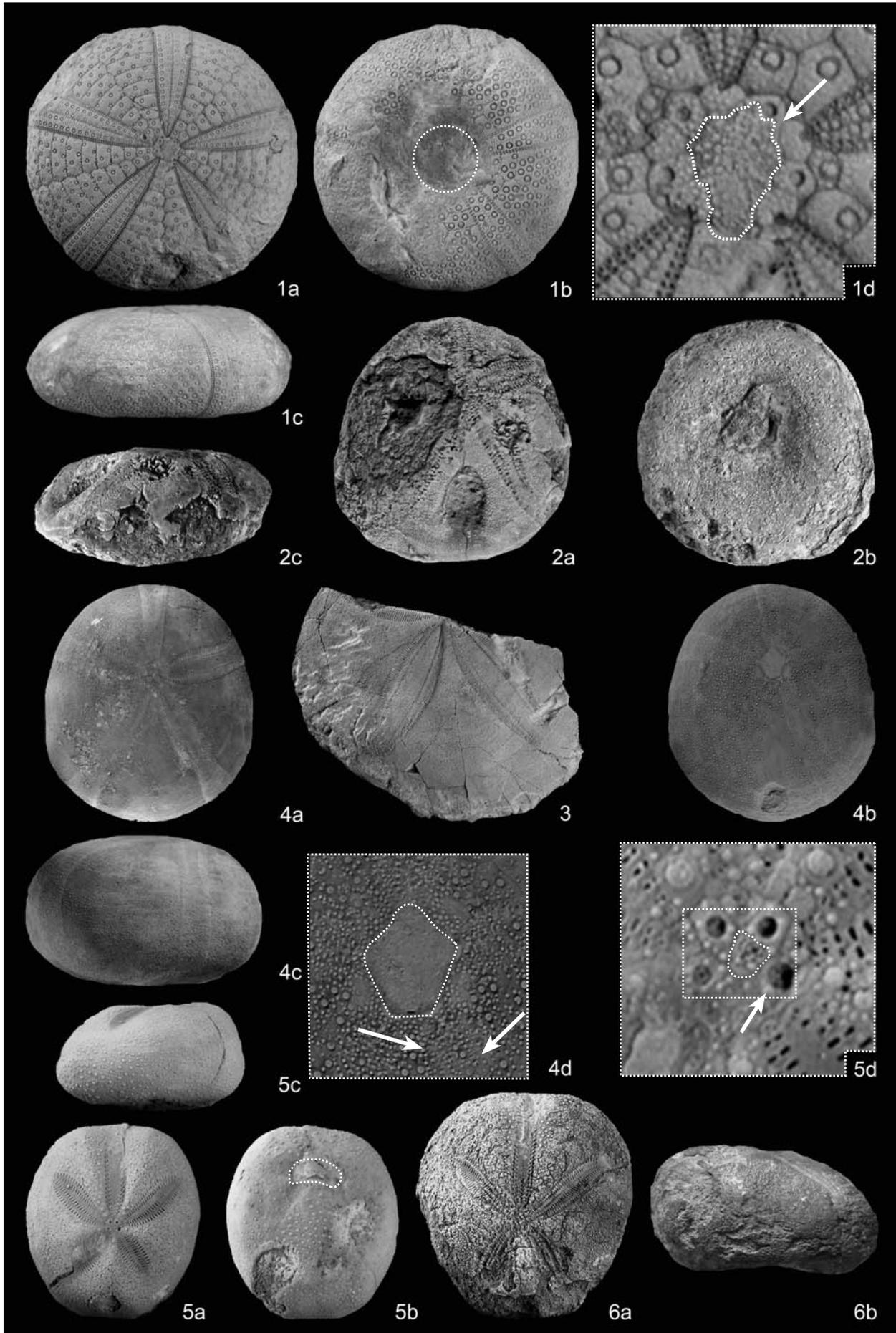
(ABDELHAMID & AZAB, 2003). Stratigraphically, *A. orbicularis* ranges from the Albian to the Cenomanian.

Discussion. FOURTAU (1921) distinguished his new species *Anorthopygus atavus* from *A. orbicularis* by having a regular periproct ambitally (nearer to ambitus than to apical disc) and by its ocular plate 4 reaching the madreporite. SMITH & WRIGHT (1999) noted that FOURTAU's species is very similar to *A. orbicularis* in shape but has a slightly different apical disc, with ocular 4 inserted and completely separating genital plates 3 and 4. However, LAMBERT (1932) after having examined the French specimens of *A. orbicularis* noted that the ocular plate 4 in some forms extends the madreporite and that the periproct is more regular. Moreover, ABDELHAMID & AZAB (2003) pointed out a more regular periproct on some specimens of *A. orbicularis* from Portugal but that the periproct in some other specimens from Sarthe lies nearer to the posterior margin than to the apical disc. The present material closely resembles FOURTAU's species in shape, size, and position of periproct but the slightly different apical disc makes the author doubt whether *A. atavus* is a synonym of *A. orbicularis*.

ALI (1990) pointed out that his new species *A. arabicus* is most closely related to *A. atavus* FOURTAU, but differs in having a narrower ambulacral area (12-15.4% of test diameter) and a larger apical disc and periproct (maximum height 25.7-29.6% and maximum width 18-21.3% of test diameter). SMITH & WRIGHT (1999) noted that the periproct of *A. orbicularis* occupies slightly more than 25% of the test diameter and that the width of ambulacral areas of some specimens (pl. 115, figs. 3-6) is relatively narrow (about 13% of test diameter). For these reasons, *A. arabicus* ALI may be a junior synonym of the present species. *A. michelini* COTTEAU & TRIGER (1860) differs from *A. orbicularis* by having a weakly subconical test (for a more extensive discussion, see SMITH & WRIGHT, 1999: 363).

EXPLANATION OF PLATE 4

Fig. 1. *Anorthopygus orbicularis* (GRATELOUP, 1836) from the middle siliciclastic/carbonate member of the Cenomanian Galala Formation at Wadi Quseib. a: Adapical view, x1.5, b: adoral view, x1.5, c: side view, x1.5, d: detail of the apical disc, x10; MU2009WQ.8.10. **Fig. 2.** *Petalobrissus* cf. *pygmaeus* (FOURTAU, 1921) from the Lower Turonian Abu Qada Formation at Wadi Quseib. a: Adapical view, x3, b: adoral view, x3, c: side view, x3; MU 2009WQ.46.1. **Fig. 3.** *Pygurus* cf. *subproductus* FOURTAU, 1921 from the lower marly member of the Upper Albian-Cenomanian Halal Formation at Gebel Areif El-Naqa, adapical view, x1.5; MU2009AEN.12.1. **Fig. 4.** *Gentilia syriensis* KIER, 1962 from the upper carbonate member of the Cenomanian Galala Formation at Wadi Quseib. a: Adapical view, x1.5, b: adoral view, x1.5, c: side view, x1.5, d: peristomal region, x5; MU2009WQ.23.25. **Figs. 5-6.** *Hemiaster (Hemiaster) syriacus* (CONRAD, 1852). 5. From the middle siliciclastic/carbonate member of the Cenomanian Galala Formation at Wadi Quseib. a: Adapical view, x2, b: adoral view, x2, c: side view, x2, d: detail of apical disc, x15; MU2009WQ.21.1. 6. From the middle carbonate member of the Cenomanian Halal Formation at Gebel Areif El-Naqa. a: Adapical view, x1.5, b: side view, x1.5; MU2009AEN.15.49.



Cohort Neognathostomata SMITH, 1981**Order Cassiduloidea CLAUS, 1880****Family Nucleolitidae AGASSIZ & DESOR, 1847**Genus *Petalobrissus* LAMBERT, 1916*Petalobrissus* cf. *pygmaeus* (FOURTAU, 1921)

Pl. 4, Fig. 2

- cf. 1921 *Echinobrissus pygmaeus* sp. nov. – FOURTAU: 67, pl. 9, fig. 5.
- cf. 1932 *Clitopygus pygmaeus* FOURTAU – LAMBERT: 193.
- cf. 2001 *Petalobrissus pygmaeus* (FOURTAU) – ABDELHAMID & EL QOT: 22, fig. 6G.
- cf. 2006 *Petalobrissus pygmaeus* (FOURTAU) – EL QOT: 147, pl. 33, figs. 5-6.

Material and occurrence. Three specimens, two of them incomplete, from the Abu Qada Formation (Lower Turonian), bed 46 (MU2009WQ. 46.1-3) at Wadi Quseib.

Measurements (in mm).

n=1	L	W	H	W/L	H/L	LI
	19	17	9	0.89	0.47	10
	LII	LIII	NI	LK	WK	
	9	?6	30	5	4	

Description. Test small and oval in outline. Height about 47% of total diameter and maximum height at apical disc. Adapical surface convex to low dome-shaped. Adoral surface strongly concave with depressed peristome. Both anterior and posterior margins regularly rounded. Ambitus sharp. Apical disc tetrabasal, eccentric anteriorly with four gonopores. Ambulacral areas petaloid and narrow (about 12% of test diameter) with narrow poriferous zone. Pores rounded to oval, unequal, and non-conjugated. Interporiferous zone slightly wider than one poriferous zone and carrying fine granules. Periproct oval, large, and supramarginal.

Temporal and spatial distribution. *Petalobrissus pygmaeus* has been recorded from the Turonian of Gebel Dhalfa (FOURTAU, 1921), G. El-Minsherah (ABDELHAMID & EL QOT, 2001), and G. Ekma, East Themed, and G. Yelleg (EL QOT, 2006).

Discussion. The genus *Petalobrissus* is characterized by the presence of single pores in ambulacral plates outside the petals and by the possession of buccal pores (ABDELHAMID & EL QOT, 2001: 23). The present material is poorly preserved but it is closely similar to *P. pygmaeus* as figured by FOURTAU (1921) with respect to shape and size of petals and also the position and size of periproct. According to EL QOT (2006), *P. pygmaeus* differs from *P. humei* (FOURTAU, 1906) in having a less round outline and lower test. *P. waltheri* (GAUTHIER, 1900) has a wider poriferous zone with a different petal system (relationship among petals).

Family Faujasiidae LAMBERT, 1905

Subfamily Faujasiinae LAMBERT, 1905

Genus *Pygurus* AGASSIZ, 1839*Pygurus* cf. *subproductus* FOURTAU, 1921

Pl. 4, Fig. 3

- cf. 1921 *Pygurus subproductus* sp. nov. – FOURTAU: 72, pl. 10, fig. 6.
- cf. 1990 *Pygurus (Pygurus) cf. subproductus* FOURTAU – ALI: 113, fig. 7/6.

Material and occurrence. A single incomplete specimen from the lower marly member of the Halal Formation (Upper Albian-Cenomanian), bed 12 (MU2009AEN.12.1) at Gebel Areif El-Naqa.

Measurements (in mm).

n=1	D	H	H/D	Wa	Wi	Wa/Wi
	34	6	0.17	6	16	0.37

Description. Test large-sized, compressed, its height about 17% of total test diameter. Adapical surface slightly convex. Adoral surface slightly concave. Posterior margin rounded and more prolonged. Ambulacral area moderately large (about 37% of interambulacral width), subpetaloid, lancet-shaped, and flush to feebly swollen. Poriferous zone wide and uniserial. Pores rounded, unequal, and conjugated. The outer pores slit-shaped, the inner ones, in contrast, rounded. Interporiferous zone slightly less than double the width of one poriferous zone. Interambulacral area wide and slightly raised. Tubercles of interambulacra small and numerous adapically and slightly larger adorally. Both peristome and periproct not preserved.

Temporal and spatial distribution. *Pygurus subproductus* has been recorded from the Cenomanian of United Arab Emirates (ALI, 1990), and in Egypt from the Albian of Gebel Abu Diab (FOURTAU, 1921).

Discussion. The present material closely resembles *Pygurus subproductus* figured by FOURTAU (1921) in shape and size of poriferous and interporiferous zones of the ambulacral area and the prolongation of the posterior margin but the specimen is not complete. FOURTAU distinguished *P. productus* AGASSIZ from his new species by having a shorter posterior prolongation and by being slightly smaller than *P. subproductus*. ALI (1990) noted that his material differs from FOURTAU's species by having a broad inflation along the interradiial suture of the posterior interambulacrum 5.

Family Archiaciidae COTTEAU & TRIGER, 1869 [after DURHAM et al., 1966]Genus *Gentilia* LAMBERT, 1918

Gentilia syriensis KIER, 1962

Pl. 4, Fig. 4

1962 *Gentilia syriensis* sp. nov. – KIER: 156, pl. 23, figs. 5-11, text-figs. 129-131.1995 *Gentilia syriensis* KIER – NÉRAUDEAU et al.: 415, fig. 5f.

Material and occurrence. A single specimen from the upper carbonate member of the Cenomanian Galala Formation, bed 23 (MU2009WQ.23.25) at Wadi Quseib.

Measurements (in mm).

n=1	D	H	H/D	Ls	Ls/D	dp
	28	18	0.64	4	0.14	5
	dp/D	Lk	Lk/D	Wa	Wi	Wa/Wi
	0.18	4	0.14	5	11	0.45

Description. Test medium-sized, ovate, globular, its height being 64% of test diameter. Both anterior and posterior borders rounded. Widest part of test lying about two-thirds the distance from the anterior. Adapical surface broad and slightly convex with rounded ambitus. Adoral surface flat with slight depression around peristome. Apical disc tetrabasal, lying anteriorly, and consisting of four large gonopores, but plating not seen. Ambulacral area petaloid (aborally), flush, the largest width close to the apex (18% of test diameter and 45% of interambulacral width), and open distally. Poriferous zone narrow, straight, and uniserial. Outer pores distinctly slit-like, but inner ones rounded and isolated. Ambulacrum III short and widely open. Interambulacral area wide (39% of test diameter) and slightly swollen with simple and wide plates, and yielding small granules. Periproct ovate-shaped, small (14% of test diameter), and occupying the distance between the peristome and posterior margin (inframarginal). Peristome pentagonal, very eccentric anteriorly (35% of test length from the anterior end), and relatively small (about 18% of test diameter) with well-rounded paired phyllodal pores (Pl. 4, Fig. 4d).

Temporal and spatial distribution. *Gentilia syriensis* was first described by KIER (1962) from the Cenomanian of Syria. It has been also recorded from the Cenomanian of Saudi Arabia by NÉRAUDEAU et al. (1995). This is the first record of the species from Egypt.

Order Spatangoida CLAUS, 1876**Family Hemiasteridae CLARK, 1917**Genus *Hemiaster* AGASSIZ, in AGASSIZ & DESOR, 1847Subgenus *Hemiaster* AGASSIZ, in AGASSIZ & DESOR, 1847*Hemiaster (Hemiaster) syriacus* (CONRAD, 1852)

Pl. 4, Figs. 5-6

1852 *Holaster syriacus* sp. nov. – CONRAD in LYNCH: 212, pl. 1, fig. 2.1925 *Hemiaster syriacus* CONRAD – BLANCKENHORN: 103, pl. 8, figs. 33-35.1990 *Hemiaster syriacus* (CONRAD) – SMITH et al.: 61, figs. 19a-b, 20.? 1995 *Mecaster orbignyanus* (DESOR) – NÉRAUDEAU et al.: 419, fig. 6c.2001 *Hemiaster syriacus* (CONRAD) – ABDELHAMID & EL QOT: 28, fig. 7L.2003 *Hemiaster syriacus* (CONRAD) – ABDELHAMID & AZAB: 872, pl. 5, figs. R, P.2003 *Hemiaster (Mecaster) syriacus* (CONRAD) – BERNDT: 84, fig. 4/1a-c.2006 *Hemiaster (Hemiaster) syriacus* (CONRAD) – EL QOT: 150, pl. 34, fig. 7.

Material and occurrence. 23 specimens from the lower marly and middle carbonate members of the Halal Formation (Upper Albian-Cenomanian), beds 6, 13, and 15 (MU2006AEN.6.1-5; MU2009AEN.13.1; MU2009AEN.15.49-66) at Gebel Areif El-Naqa; Six specimens from the middle siliciclastic/carbonate member of the Cenomanian Galala Formation, bed, 21 (MU2009WQ.21.1-6) at Wadi Quseib.

Measurements (in mm).

n=13

Range

L	W	H	W/L	H/L	LI	LII
14-38	12-35	9-19	0.84-1	0.50-0.67	3-12	4-16
LIII	NI	NII	NIII	LK	WK	
6-17	15-30	23-35	15-24	3-7	2-5	

Mean

L	W	H	W/L	H/L	LI	LII
20	18.38	12	0.91	0.60	7	8.77
LIII	NI	NII	NIII	LK	WK	
11.15	19.18	29.27	18.0	4.12	2.88	

Description. Test small- to medium-sized, oval in outline, maximum height near the posterior end attaining about 60% of total test diameter. Adapical surface flattened to slightly convex and gradually sloping anteriorly. Adoral surface flattened. Greatest width slightly anterior of apical disc. Anterior margin almost rounded without central sulcus. Posterior margin nearly straight and vertically rounded. Apical disc large, quadrate, slightly eccentric posteriorly, and lying about 58% of the anterior-posterior distance from the anterior margin. Posterior gonopores slightly wider than the anterior ones (Pl. 4, Fig. 5d). Petals more or less straight, shallow, and rose-shaped. Anterior pairs petaloid and extending for about 62% of the distance from the apex to the ambitus (about 1.5 times longer as the posterior one). Posterior petals petaloid, shorter, and less divergent than the anterior ones (extending for about 48% of the distance from apex to ambitus). Poriferous zones wide (the width of two poriferous zones is about 95% of petal width). Pores slit-shaped, equal-sized, and conjugated. Frontal ambulacrum non-petaloid, narrow, and shallower than the anterior and posterior petals with nearly parallel sides. Poriferous zone narrow with oval, non-conjugated, and oblique pores. Periproct oval, small,

and situated high on the test (about 72% of test height above the base). Peristome small (20% of total test height), semi-lunar, situated nearly one-third (17%) of the test length from the anterior end, and surrounded by well developed phyllodal pores. Peripetalous fasciole well developed.

Temporal and spatial distribution. *Hemiaster (Hemiaster) syriacus* has been recorded from the Cenomanian of Syria (CONRAD, 1852), Palestine (BLANCKENHORN, 1925), Oman (SMITH et al., 1990), Saudi Arabia (NÉRAUDEAU et al., 1995), and Jordan (BERNDT, 2003). In Egypt, it has been documented from the Cenomanian of Gebel El-Hamra (ABDELHAMID & EL QOT, 2001), Saint Paul, Wadi Dakhil, and G. Gharamul (ABDELHAMID & AZAB, 2003), and G. Ekma and the East Themed area (EL QOT, 2006).

Discussion. *Hemiaster orbignyanus* DESOR, 1857 from the Cenomanian of Saudi Arabia of NÉRAUDEAU et al. (1995) closely resembles the present species in shape and size of petals and periproct. SMITH et al. (1990) considered *H. orbignyanus* as a synonym of *H. syriacus*. BLANCKENHORN (1925) pointed out that *H. orbignyanus* has very unequal petals like *H. syriacus* but that its petals are very narrow. *H. orbignyanus* has been originally described from the Turonian of France. According to ABDELHAMID & EL QOT (2001: 28) and EL QOT (2006: 152), the specimens described from the Middle East as *H. orbignyanus* are thought to belong to *H. syriacus*, whereas *H. orbignyanus* sensu stricto is confined to the Turonian of France.

SMITH et al. (1990) noted that *H. lusitanicus* DE LORIO (1888: 100, pl. 19, figs. 1-7) and *H. subtilis* DE LORIO (1888: 106, pl. 21, figs. 1-3) from the Cenomanian of Portugal are very similar to *H. syriacus* and considered them as synonyms of *H. syriacus* with some doubts.

Hemiaster (Hemiaster) gabrielis

PERON & GAUTHIER, 1878

Pl. 5, Figs. 1-2

- 1878 *Hemiaster Gabrielis* sp. nov. – PERON & GAUTHIER in COTTEAU et al.: 116, pl. 4, figs. 9-12.
 1914 *Hemiaster Gabrielis* PERON & GAUTHIER var. *aegyptiaca* var. nov. – FOURTAU: 74, pl. 6, fig. 7.
 1921 *Hemiaster Gabrielis* PERON & GAUTHIER var. *aegyptiaca* var. nov. – FOURTAU: 87.
 1932 *Hemiaster Gabrielis* PERON & GAUTHIER – LAMBERT: 125.
 1998 *Hemiaster gabrielis* PERON & GAUTHIER – EL-SHEIKH et al.: pl. 1E.
 1999 *Hemiaster gabrielis* PERON & GAUTHIER – ABDELHAMID: pl. 2, fig. B.
 2001 *Hemiaster gabrielis* PERON & GAUTHIER – ABDELHAMID & EL QOT: 25, fig. 7E.
 2003 *Hemiaster gabrielis* PERON & GAUTHIER – ABDELHAMID & AZAB: 871, pl. 5, figs. J-K.
 2004a *Hemiaster (Hemiaster) gabrielis* PERON & GAUTHIER – ABDEL-GAWAD et al.: pl. 10, figs. 10-11.
 2006 *Hemiaster (Hemiaster) gabrielis* PERON & GAUTHIER – EL QOT: 149, pl. 34, figs. 4-5.

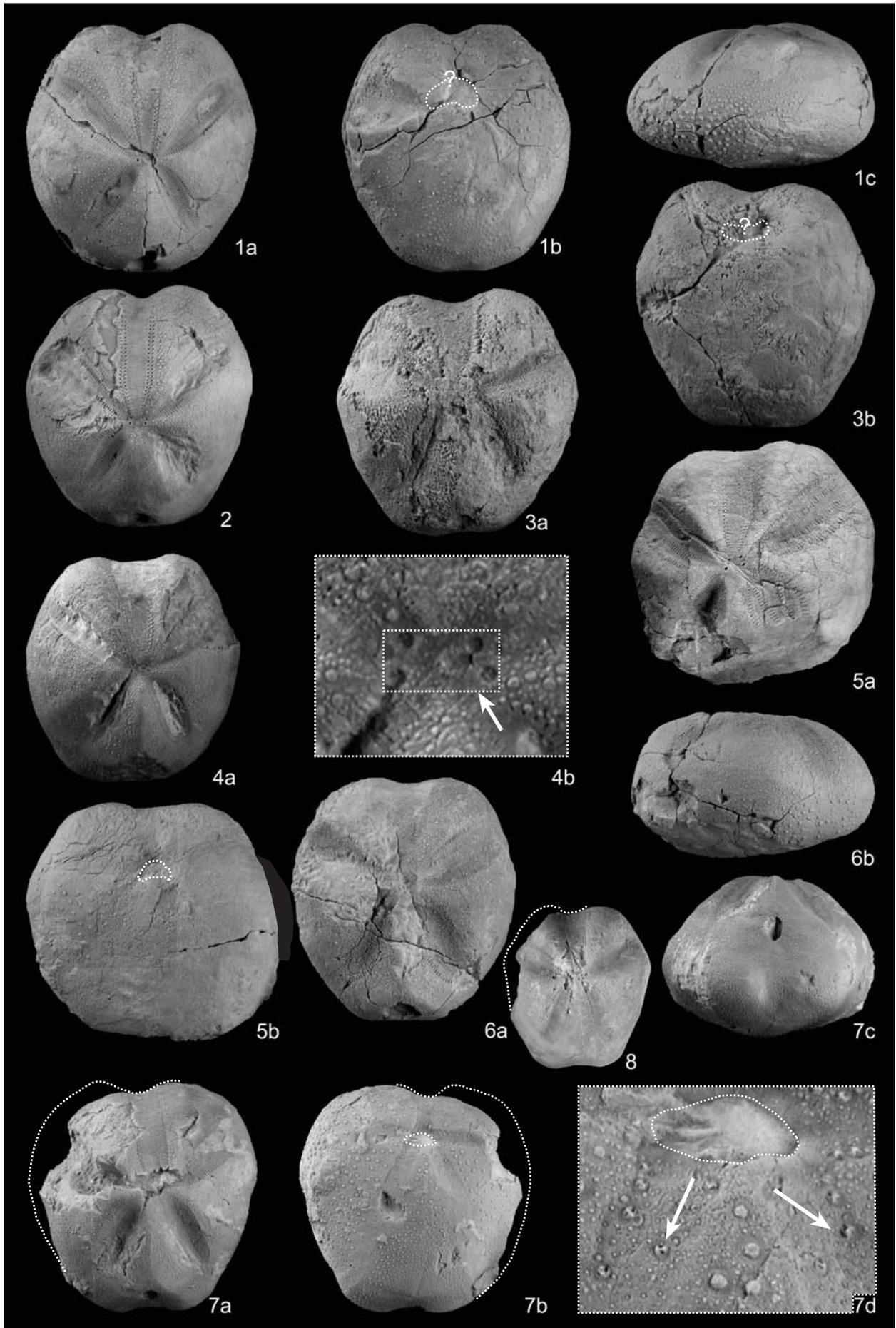
Material and occurrence. 77 specimens from the lower marly member of the Halal Formation (Upper Albian-Cenomanian), beds 1, 6, 7, and 9 (MU2009AEN.1.1-33; MU2009AEN.6.6-27; MU2009AEN.7.1-2; MU2009AEN.9.2-23) at Areif El-Naqa.

Measurements (in mm).

n=29							
Range							
L	W	H	W/L	H/L	LI	LII	
15-30	14-25	8-20	0.83-1.00	0.47-0.76	4-10	6-15	
LIII	NI	NII	NIII	LK	WK		
8-17	16-31	23-43	10-25	2-7	2-4		
Mean							
L	W	H	W/L	H/L	LI	LII	
19.72	18.24	11.86	0.89	0.59	6.89	9.31	
LIII	NI	NII	NIII	LK	WK		
11.89	23.31	30.62	18.36	3.16	2.40		

EXPLANATION OF PLATE 5

Figs. 1-2. *Hemiaster (Hemiaster) gabrielis* PERON & GAUTHIER, 1878 from the lower marly member of the Upper Albian-Cenomanian Halal Formation at Gebel Areif El-Naqa. 1. a: Adapical view, x1.5, b: adoral view, x1.5, c: side view, x1.5; MU2009AEN.6.6. – 2. Adapical view, x1.5; MU2009AEN.1.1. **Figs. 3-4.** *Hemiaster (Mecaster)ourneli* (DESHAYES, 1847) from the Upper Turonian Wata Formation at Gebel Areif El-Naqa. 3. a: Adapical view, x1.5, b: adoral view, x1.5; MU2009AEN.31.2. – 4. a: adapical view, x1.5, b: detail of apical disc, x8; MU2009AEN.31.3. **Fig. 5.** *Hemiaster (Mecaster) cf. newtoni* FOURTAU, 1914 from the middle siliciclastic/carbonate member of the Cenomanian Galala Formation at Wadi Quseib. a: Adapical view, x1.5, b: adoral view, x1.5; MU2009WQ.8.11. **Fig. 6.** *Hemiaster (Mecaster) pseudofourneli* PÉRON & GAUTHIER, 1878 from the middle siliciclastic/carbonate member of the Cenomanian Galala Formation at Wadi Quseib. a: Adapical view, x1.5, b: adoral view, x1.5; MU2009WQ.8.12. **Figs. 7-8.** *Hemiaster (Mecaster) heberti* (COQUAND, 1862) *turonensis* FOURTAU, 1921. 7. Specimen from the Upper Turonian Wata Formation at Wadi Quseib. a: Adapical view, x1, b: adoral view, x1, c: posterior view, x1, d: ambulacra groove with well-developed phyllodal pores, x5; MU2009WQ.67.4. – 8. Specimen from the Upper Turonian Wata Formation at Gebel Areif El-Naqa. Adapical view, x1; MU2009AEN.31.9.



Description. Test small-to medium-sized, heart-shaped, inflated, and posteriorly higher than anteriorly. Greatest width slightly anteriorly of apical disc, its height about 59% of test diameter. Anterior margin straight with moderately deep sulcus. Posterior margin rounded and oblique to subvertical. Adapical and adoral surfaces slightly convex and gradually sloping anteriorly. Apical disc slightly eccentric posteriorly (about 58% from the anterior margin) and large with four well developed gonopores. Madreporite well developed and separating gonopores 1 and 4. Anterior and posterior petals more or less straight, petaloid, moderately deep, and arranged in cross-like fashion. Length of anterior pairs about 1.5 times that of the posterior ones and extending from the apex to or nearly to the ambitus. Posterior pair shorter than anterior ones and covering only slightly more than half the distance from the apex to the ambitus. Poriferous zones of both anterior and posterior petals large with non-conjugated slit-pores. Frontal ambulacrum non-petaloid, deep, and narrow with nearly parallel poriferous zones. Pores round and non-conjugated. Peristome semi-rounded to semi-lunar, lying 30% of the length from the anterior end and surrounded by well developed phyllodal pores. Periproct medium-sized, circular to slightly ovate, and at the top of the posterior margin (above ambitus). Peripetalous fasciole well developed.

Temporal and spatial distribution. *Hemiaster (Hemiaster) gabrielis* has been recorded from the Cenomanian of Algeria (PERON & GAUTHIER, 1878), and Morocco (LAMBERT, 1932). In Egypt it is known from the Cenomanian of Sinai and the Eastern Desert by FOURTAU (1914, 1921), ABDELHAMID (1999), ABDELHAMID & AZAB (2003), ABDEL-GAWAD et al. (2004a), and EL QOT (2006).

Discussion. BLANCKENHORN (1925) and SMITH et al. (1990) regarded *Hemiaster gabrielis* from the Cenomanian of Algeria and *H. gabrielis* var. *aegyptiaca* FOURTAU (1914) from the Cenomanian of Sinai as synonyms of *H. syriacus*. The author agrees with EL QOT (2006) that *H. gabrielis* and *H. syriacus* are two different species. The more sinuous anterior margin, more depressed petals, rounded posterior, and the nearly centric apical disc of *H. gabrielis* suggest that it a separate species.

SMITH et al. (1990: 64) agreed with FOURTAU (1914: 75) that *H. lusitanicus* and *H. subtilis* are identical with the present species. COTTEAU et al. (1878) erected *H. gabrielis*, *H. saadensis*, and *H. zitteli* from the Cenomanian of Algeria. According to EL QOT (2006: 150), *H. zitteli* is a junior synonym of *H. gabrielis*, but *H. saadensis* differs in having a more elongated and flattened test.

Subgenus *Mecaster* POMEL, 1883

Hemiaster (Mecaster)ourneli (DESHAYES, 1847)

Pl. 5, Figs. 3, 4

- 1847 *Hemiasterourneli* sp. nov. – DESHAYES in AGASSIZ & DESOR: 123.
 1898 *Hemiasterourneli* DESHAYES – FOURTAU: 631.
 1912 *Hemiasterourneli* DESHAYES – FOURTAU: 168.
 1921 *Hemiasterourneli* DESHAYES – FOURTAU: 87.
 1925 *Hemiasterourneli* DESHAYES – BLANCKENHORN: 106, pl. 8, fig. 37a-b.
 1991 *Mecasterourneli* (DESHAYES) – SMITH & BENGTON: 61, pl. 14, figs. A-M; pl. 15, figs. A-L; pl. 16, figs. E, F; text-figs. 45K, L, 48B, 50.
 1997 *Mecaster* aff. *ourneli* (DESHAYES) – NÉRAUDEAU & COURVILLE: 842, fig. 6/12.
 1998 *Hemiasterourneli* DESHAYES – EL-SHEIKH et al.: pl. 2, fig. D.
 2001 *Hemiasterourneli* DESHAYES – ABDELHAMID & EL QOT: 25, fig. 7C-D.
 2002 *Hemiasterourneli* DESHAYES – KORA et al.: pl. 4, fig. 13.
 2004a *Hemiaster (Mecaster)ourneli* DESHAYES – ABDEL-GAWAD et al.: pl. 10, figs. 12-13.
 2006 *Hemiaster (Mecaster)ourneli* DESHAYES – EL QOT: 152, pl. 34, figs. 2-3.
 2007 *Hemiaster (Mecaster)ourneli* DESHAYES – ABDEL-GAWAD et al.: pl. 4, figs. 9-10.

Material and occurrence. Seven specimens from the Wata Formation (Upper Turonian), bed 31 (MU2009AEN.31.2-8) at Gebel Areif El-Naqa and 14 specimens from the Turonian Abu Qada and Wata formations, beds 25, 71 (MU2009WQ.25.6-13; MU2009WQ.71.11-16) of Wadi Quseib section.

Measurements (in mm).

n=12

Range

L	W	H	W/L	H/L	LI	LII
15-30	14-29	8-20	0.83-1	0.53-0.69	5-14	8-15
LIII	NI	NII	NIII	LK	WK	
8-20	18-30	22-38	14-31	2-6	2-4	

Mean

L	W	H	W/L	H/L	LI	LII
24.58	22.75	15.66	0.92	0.63	9.16	12.25
LIII	NI	NII	NIII	LK	WK	
15.50	24.73	28.82	21	3.55	2.36	

Description. Test small-to medium-sized, subhexagonal; height about 63% of test diameter. Adapical surface strongly convex, adoral surface slightly convex. Maximum width slightly anterior of apical disc and slightly narrower posteriorly. Anterior margin sulcate. Apical disc large, centric to slightly eccentric anteriorly, and situated about 47% of the anterior-posterior distance from the anterior margin, laterally elongated, the pairs of gonopores on either side being close together (Pl. 5, Fig. 4b). Frontal ambulacrum non-petaloid, wide, deep, and covered by more regularly arranged and dense granules. Poriferous zone narrow with equal, oblique and non-conjugated pores. Both anterior and posterior paired petals petaloid, slightly depressed, and wide. Anterior

paired petals longer and more divergent than the posterior ones. Poriferous zones equal and wide (the two poriferous zones occupy about 78% of petal width) with slit-shaped, conjugated, and equal-sized pores. Peristome large, lunular, lying 26% nearly of the test length from the anterior end. Periproct medium-sized, oval to rounded, and lying at top of the posterior margin.

Temporal and spatial distribution. *Hemiaster (Mecaster) fourneli* has been recorded from the Santonian of Palestine (BLANCKENHORN, 1925), Turonian-Coniacian of Brazil (SMITH & BENGSTON, 1991), and the late Middle Turonian of Nigeria (NÉRAUDEAU & COURVILLE, 1997). According to PETITOT (1961) the species is relatively common in the Upper Turonian to Campanian of North Africa and most abundant in the Coniacian to Santonian. In Egypt, the species is known from the Santonian of Gebel Raha, G. El-Fallig, and G. Yelleg (FOURTAU, 1921), the Coniacian-Santonian of Wadi Sudr, W. Matulla (KORA et al., 2002), G. El-Hamra and G. El-Minsherah (EL-SHEIKH et al., 1998; ABDELHAMID & EL QOT, 2001), and of G. Ekma and the East Themed area (ABDEL-GAWAD et al., 2004a; EL QOT, 2006).

Discussion. Some authors treated *Mecaster* as a subgenus of *Hemiaster*. SMITH & BENGSTON (1991) regarded *Mecaster* as a separate genus on account of its subequal petals and its laterally elongated apical disc, in which the madreporite separates genital plates 1 and 4. In *Hemiaster* the posterior genital plates are not separated by the madreporite and all four genital plates are subequal in size. In addition, the posterior petals are truncated in comparison to the anterior pairs and the apical disc lies posterior of the center. According to DURHAM & WAGNER (1966: U559, figs. 442/1, 443/1) *Hemiaster (Mecaster)* is relatively low, subhexagonal, and possesses subequal petals with wide frontal ambulacrum (with anterior sulcus).

COQUAND (1880) distinguished two varieties in *Hemiaster fourneli*, var. *ambiguous*, which is characterized by its nearly orbicular outline, and var. *refanensis*, which is elongated, polygonal, and narrow posteriorly. COTTEAU et al. (1881) distinguished three varieties, an elongated one, a relatively short test, and a third variety with a more obliquely truncated posterior margin.

SMITH & BENGSTON (1991) distinguished that *H. batnensis* from *Mecaster fourneli* by its slightly rounded form and relatively greater number of pores in the frontal ambulacrum between the apex and fasciole. Moreover, the apical disc in the two species also differs; in *M. fourneli* it is laterally elongated and the pairs of gonopores on either side are close together (Pl. 5, Fig. 4b). The tuberculation in the frontal ambulacrum is denser

and more regularly arranged into horizontal rows in *M. fourneli* than in *H. (M.) batnensis* (SMITH & BENGSTON, 1991: 59, fig. 48a, b).

H. pseudofourneli PERON & GAUTHIER differs from *H. (M.) fourneli* by its longer and deeper posterior paired petals and more anteriorly displaced apical disc. *H. (M.) pseudofourneli* has been recorded from the Cenomanian of North Africa and the Middle East, whereas *H. fourneli* ranges from the Turonian to Campanian, but occurs predominantly in the Coniacian-Santonian.

According to SMITH & BENGSTON (1991: 62), *Mecaster texanum* (ROEMER) from the Santonian-Campanian of the United States differs in having a smaller peristome, more elongated apical disc, and a large madreporite, which separates the posterior ocular plates widely. In addition, *M. messai* (PERON & GAUTHIER) has a much wider frontal ambulacrum.

Hemiaster (Mecaster) cf. newtoni FOURTAU, 1914

Pl. 5, Fig. 5

- cf. 1914 *Hemiaster Newtoni* sp. nov. – FOURTAU: 79, pl. 7, figs. 4-5.
 cf. 1921 *Hemiaster Newtoni* FOURTAU – FOURTAU: 92
 cf. 2001 *Hemiaster newtoni* FOURTAU – ABDELHAMID & EL QOT: 26, fig. 7I.
 cf. 2003 *Hemiaster newtoni* FOURTAU – ABDELHAMID – AZAB: 872, pl. 5, figs. L, M.

Material and occurrence. A single deformed specimen from the middle siliciclastic/carbonate member of the Cenomanian Galala Formation, bed 8 (MU2009WQ. 8.11) at the Wadi Quseib.

Measurements (in mm).

n=1	L	W	H	W/L	H/L	LI
	?33	31	24	0.94	0.73	14
	LII	LIII	NI	NII	NIII	
	17	19	?20	41	38	

Description. Test large-sized, polygonal in outline, inflated, posteriorly higher than anteriorly (about 73% of test diameter). Greatest width slightly anterior of apical disc. Adapical surface slightly convex. Adoral surface feebly convex with moderately deep anterior sinus. Apical disc large (much broader than long), quadrate, and nearly central with four gonopores, which are closer on both sides. Madreporite well developed. Frontal ambulacrum non-petaloid and in moderately deep sulcus that continues to the peristome. Pores oval, oblique, and non-conjugated. Interporiferous zone wide and covered with numerous fine granules. Both anterior and posterior petals very wide and deep. Poriferous zone wide (the two poriferous zones represent about 95% of petal width) with slit-shaped, non-conjugated, and equal-sized pores. Peristome moderately large, semi-lunar, and situated at about 22% of test length from the anterior end. Periproct not preserved.

Temporal and spatial distribution. *Hemiaster (Mecaster) newtoni* has been recorded from the Cenomanian of Qalaat El Karam and Gebel Um Asagil (FOURTAU, 1921), G. El-Hamra (ABDELHAMID & EL QOT, 2001), and G. Gharamul (ABDELHAMID & AZAB, 2003).

Discussion. The present material is not complete but closely resembles *Hemiaster newtoni* which has been described and figured by FOURTAU (1914). It can be easily distinguished from other *Hemiaster* species recorded in the present study by its higher test, wide and strongly depressed petals, and more angular outline. According to ABDELHAMID & EL QOT (2001) *Hemiaster newtoni* differs from *H. latigrunda* PÉRON & GAUTHIER from the Turonian of Algeria by having deeper petals, a higher test, and larger peristome.

Hemiaster (Mecaster) pseudofourneli

PÉRON & GAUTHIER, 1878

Pl. 5, Fig. 6

- 1878 *Hemiaster pseudofourneli* sp. nov. – PÉRON & GAUTHIER: 113, pl. 4, figs. 5-8.
 1914 *Hemiaster pseudofourneli* PÉRON & GAUTHIER – FOURTAU: 82, 109.
 1963 *Hemiaster pseudofourneli* PÉRON & GAUTHIER – FAWZI: 14.
 1981 *Hemiaster pseudofourneli* PÉRON & GAUTHIER – AMARD et al.: 106, pl. 16, figs. 24-27.
 1995 *Mecaster pseudofourneli* (PÉRON & GAUTHIER) – NÉRAUDEAU et al.: 418, fig. 6d-e; text-fig. 7.
 2001 *Hemiaster pseudofourneli* PÉRON & GAUTHIER – ABDELHAMID & EL QOT: 28, fig. 7j-k.
 2001 *Hemiaster pseudofourneli* PÉRON & GAUTHIER – KORA et al.: pl. 3, fig. 9.
 2002 *Mecaster pseudofourneli* (PÉRON & GAUTHIER) – AHMAD & AL-HAMMAD: 459, fig. 5/1-4, 6, 8.
 2003 *Hemiaster pseudofourneli* PÉRON & GAUTHIER – ABDELHAMID & AZAB: 872, pl. 5, figs. N-O.
 ? 2004b *Hemiaster cubicus* DESOR – ABDEL-GAWAD et al.: pl. 6, fig. 4.

Material and occurrence. Three specimens from the middle siliciclastic/carbonate member of the Cenomanian Galala Formation, bed 8 (MU 2009WQ.8.12-14) at Wadi Quseib.

Measurements (in mm).

n=2

Range	L	W	H	W/L	H/L	LI
	27-31	23-28	19-20	0.85-0.90	0.64-0.67	10-14
	LII	LIII	NI	NII	LK	WK
	13-14	16-16	16-22	25-30	4-5	3-4
Mean	L	W	H	W/L	H/L	LI
	29	25.5	19.5	0.87	0.65	12
	LII	LIII	NI	NII	LK	WK
	13.5	16	19	27.5	4.5	3.5

Description. Test medium-sized, subhexagonal to oval, its height about 65% of test diameter. Both adapical and adoral surfaces convex. Greatest width slightly anterior of apical disc. Posterior margin straight. Anterior margin moderately sulcate. Apical disc large, excentric

anteriorly, situated about 43% of test length from the anterior margin. The four gonopores well developed and close together on either side. Frontal ambulacrum non-petaloid, wide, and deep. Poriferous zone small and narrow. Pores equal, oblique, and non-conjugated. Both anterior and posterior paired petals petaloid, slightly depressed, and wide. Anterior paired petals nearly equal and more divergent than the posterior ones. Poriferous zones equal and wide (the two poriferous zones account for about 80% of petal width). Pores slit-shaped, conjugated, and equal-sized. Periproct medium-sized, slightly elongated vertically, and lying at the top of the posterior margin. Peristome not preserved. Peripetalous fasciole well developed.

Temporal and spatial distribution. *Hemiaster (Mecaster) pseudofourneli* has been recorded from the Cenomanian-Turonian of Algeria (AMARD et al., 1981), Cenomanian of Saudi Arabia (NÉRAUDEAU et al., 1995), and Jordan (AHMAD & AL-HAMMAD, 2002). In Egypt, it is known from the Cenomanian of Gebel El-Minsherah (FAWZI, 1963), G. El-Hamra (ABDELHAMID & EL QOT, 2001), G. El-Fallig (ABDEL-GAWAD et al., 2004b), Wadi Abu Qada (KORA et al., 2001), and G. Gharamul and W. Dakhil (ABDELHAMID & AZAB, 2003).

H. (M.) pseudofourneli is a well known Cenomanian species reported from southwestern Europe, western Africa, Middle-East, and Brazil (AHMAD & AL-HAMMAD, 2002).

Discussion. *Hemiaster (Mecaster) pseudofournel* differs from *H. (M.) newtoni* by having narrower and equal-sized petals and a lower test. *H. cubicus* (DESOR, 1847) is characterized by an extremely eccentric peristome very close to the anterior margin, a small periproct, and a deep anterior sulcus. The periproct of *H. cubicus* of ABDEL-GAWAD et al. (2004b) from the Cenomanian of Gebel El-Fallig (Sinai), which is not close to the anterior margin, may therefore be belong to *H. pseudofourneli* rather than to *H. cubicus*.

Hemiaster (Mecaster) heberti (COQUAND, 1862)

turonensis FOURTAU, 1921

Pl. 5, Figs. 7, 8

- 1921 *Hemiaster Heberti* mutatio *Turonensis* FOURTAU: 89, pl. 11, figs. 1-10.
 1999 *Hemiaster heberti* (COQUAND) *turonensis* FOURTAU – ABDELHAMID: pl. 1, figs. A-D, J, K-L; pl. 2, figs. D-E, F, G-H, J-K.
 2001 *Hemiaster heberti* (COQUAND) *turonensis* FOURTAU – ABDELHAMID & EL QOT: 26, fig. 7G-H.
 2004a *Hemiaster (Mecaster) heberti* (COQUAND) *turonensis* FOURTAU – ABDEL-GAWAD et al.: pl. 10, fig. 14a-b.
 2006 *Hemiaster (Mecaster) heberti* (COQUAND) *turonensis* FOURTAU – EL QOT: 153, pl. 34, fig. 6a-b.

2007 *Hemiaster (Mecaster) heberti* (COQUAND) *turonensis*
FOURTAU – ABDEL-GAWAD et al.: pl. 6, fig. 11.

Material and occurrence. Four specimens from the lower member of the Turonian Abu Qada and Wata formations, beds 23 and 31 (MU2009 AEN.23.1-3; MU2009AEN.31.9) at Gebel Areif El-Naqa; and 19 specimens from the same formations, beds 25, 67, 71 (MU2009 WQ.25.14-23; MU2009WQ.67.4-6; MU2009WQ.71.17-22) at Wadi Quseib.

Measurements (in mm).

n=15

Range

L	W	H	W/L	H/L	LI	LII
16-41	13-38	8-30	0.81-0.94	0.50-0.72	9-25	7-28
LIII	NI	NII	NIII	LK	WK	
9-34	19-40	25-45	13-20	2-5	2-5	

Mean

L	W	H	W/L	H/L	LI	LII
23.13	21	14.13	0.90	0.60	9.60	11.60
LIII	NI	NII	NIII	LK	WK	
14	27	32	17.14	3.42	2.70	

Description. Test small-to large-sized, polygonal, its maximum height about 60% of posterior test diameter. Adapical surface convex. Adoral surface slightly convex with slight depression around peristome. Posterior margin straight with shallow sulcus below periproct. Anterior margin rounded with slight depression centrally. Apical disc large and centric to slightly eccentric anteriorly. Madreporite well developed and separating the two posterior gonopores. Frontal ambulacrum non-petaloid, ovate, narrower and shallower than the anterior and posterior petals. Poriferous zone narrow. Pores

oblique, ovate to short, slit-shaped, and equal. Interporiferous zone wide and covered with dense, small granules. Paired petals petaloid, large, wide, and depressed. Posterior petals slightly shorter and less divergent than anterior ones. Poriferous zones wide, equal, and slightly convergent near apical disc. Pores slit-shaped and slightly conjugated. Peristome medium-sized, sub-rounded, situated nearly one-third (29%) of test length from the anterior end, and surrounded by well developed phyllodal pores (Pl. 5, Fig. 7d). Periproct large, oval, and placed at the top of the posterior margin (Pl. 5, Fig. 7c).

Temporal and spatial distribution. *Hemiaster (Mecaster) heberti turonensis* has been recorded from the Lower Turonian of Sinai, e.g. Gebel Libni (FOURTAU, 1921), G. El-Hamra, and G. Minsherah (ABDELHAMID & EL QOT, 2001), Wadi Dakhel, W. Abu Qada (ABDELHAMID, 1999), and of G. Ekma, East Themed area, and G. Yelleg (ABDEL-GAWAD et al., 2004a; EL QOT, 2006).

DISCUSSION. ABDELHAMID & EL QOT (2001) raised the rank of FOURTAU's "mutatio" to a subspecies, which differs from *H. heberti* sensu stricto by a higher test and wider and more developed petals. According to them the species differs from *Hemiaster latigrunda* PERON & GAUTHIER (1880) by having shallower paired petals and frontal ambulacrum. The latter species does not have a deeply excavated anterior margin.

4 Palaeoecological and taphonomic remarks

Echinoids are a conspicuous and an important element of Upper Cretaceous faunas and can be good palaeo-environmental indicators, because they are often highly facies restricted (SMITH et al., 1988; SMITH & BENGTON, 1991).

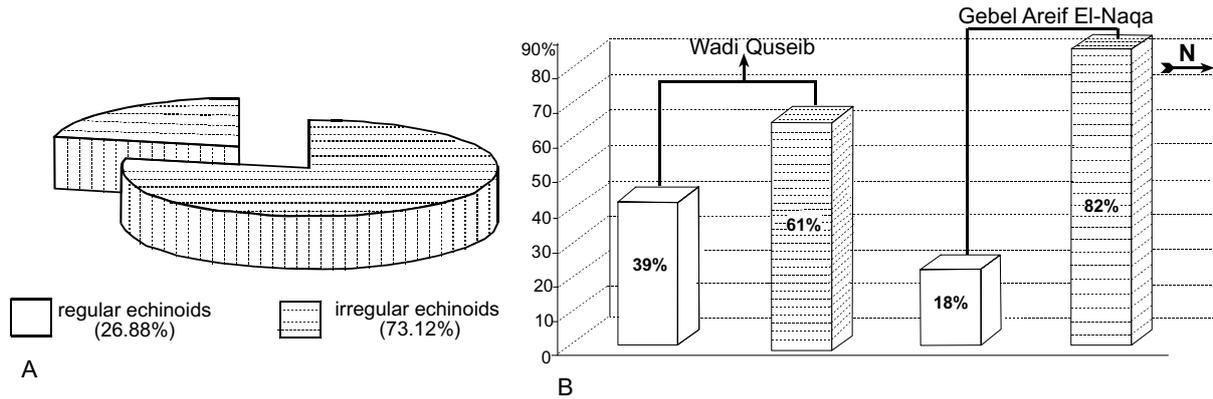
The detailed study of skeletal characters can provide information concerning the general life habits, substrate relationships, feeding mechanism, and respiration of different taxa. According to SMITH (1984), each taxon has a preferred habit and life style that is partially reflected by, and can be deduced from, the skeletal characters. Moreover, the nature of substrate plays an important role in the change of skeletal morphology (BARRAS, 2008). These skeletal characters include (1) general test morphology; (2) peristome with surrounding phyllodal pores; (3) size of periproct; (4) tubercle morphology and density; and (5) tube feet morphology deduced from ambulacral pores.

Twenty-six echinoid species were collected from the studied sections (20 species from the Wadi Quseib section, 12 species from Gebel Areif El-Naqa), of which

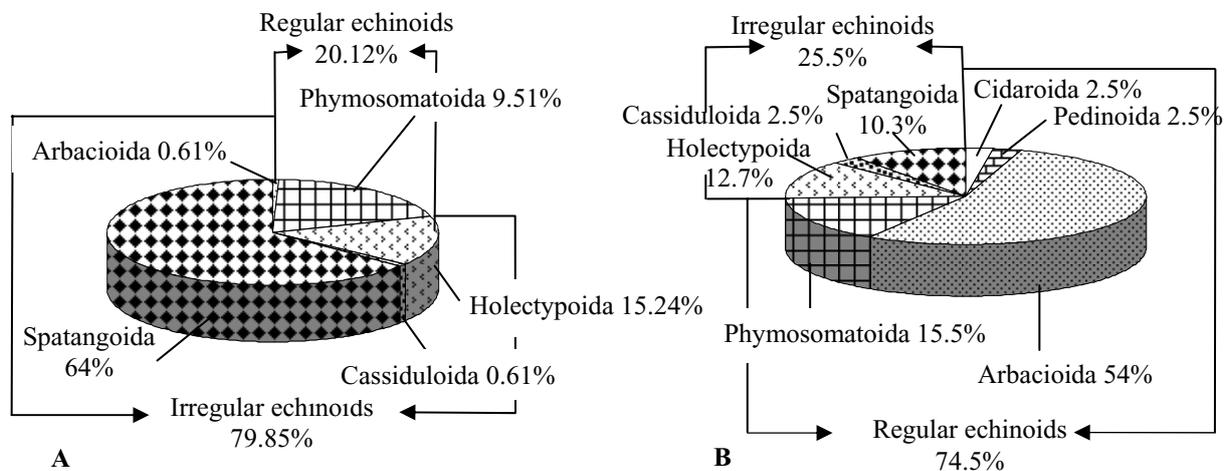
26.88% are regular echinoids and 73.12% irregular echinoids (Text-fig. 5A).

From the Areif El-Naqa section, 18% of the species are regular echinoids and 82% irregular ones, whereas at the Wadi Quseib section, 39% of the species are regular and 61% irregular echinoids (Text-fig. 5B).

The echinoids occur in two different facies: a marly facies and a facies consisting mainly of reefal carbonates. The marly facies is glauconitic, only moderately cemented, and fossiliferous (e.g. oysters and gastropods). The marly facies is dominated by burrowing and ploughing irregular echinoids (79.85% of the total numbers of individuals of the Areif El-Naqa section), regular echinoids being rare (Text-fig. 6A). The carbonate facies consists of hard limestone, rich in rudists, *Chondrodonta*, corals, and sponges (e.g., *Chondrodonta* rudstone) and is dominated by epifaunal grazing regular echinoids (74.5% of the total numbers of individuals in Wadi Quseib), irregular is being rare (25.5%) (Text-fig. 6B).



Text-fig. 5. Distribution of regular and irregular echinoid species (in %) in the Wadi Quseib and Areif El-Naqa sections.



Text-fig. 6. Relative abundance of echinoids, A. Marly facies of Gebel Areif El-Naqa. B. Reefal carbonate facies of Wadi Quseib.

4.1 Irregular echinoids

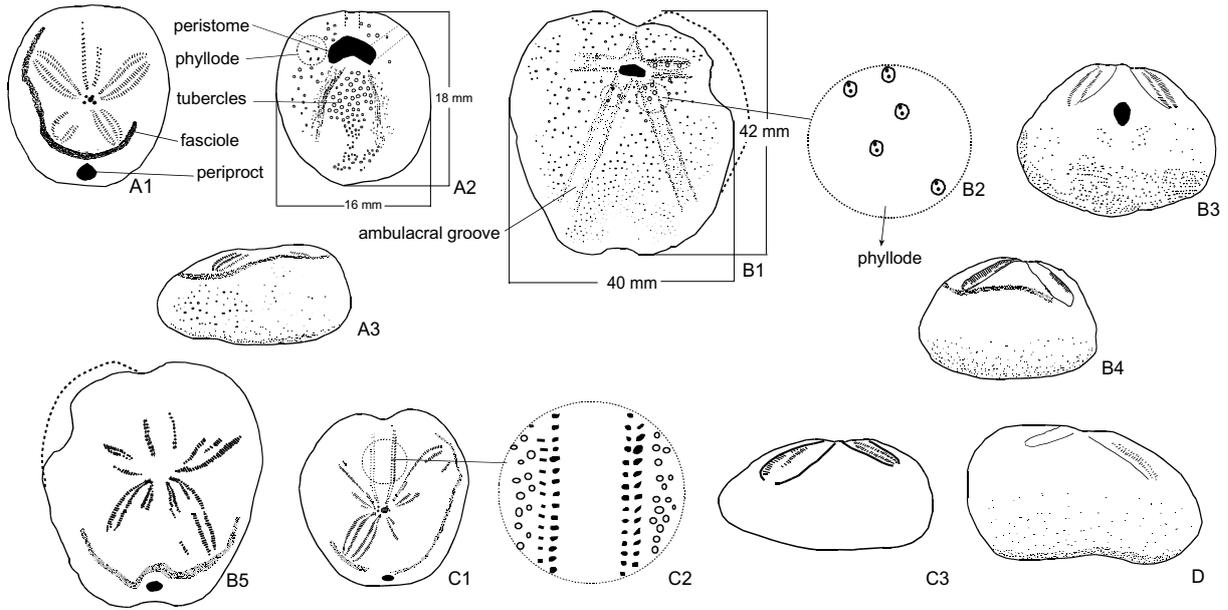
Today, irregular echinoids are quantitatively abundant, taxonomically diverse, and environmentally widespread (BARRAS, 2008). Irregular echinoids are deposit-feeders that live within the sediment and are exclusively microphagous being able to ingest only small nutrient-bearing particles (DE RIDDER & LAWRENCE, 1982; SMITH, 1995). This feeding behaviour implies a specialization of the body form and appendages for feeding and moving on or inside soft sediments (KIER, 1974; SMITH, 1981; KANAZAWA, 1992; TELFORD & MOOI, 1996). In most general sense, it was the development of a dense coating of fine spines and the posterior migration of the periproct in the earliest irregular echinoid that enabled the group to exploit infaunal niches which regular echinoids cannot (SMITH, 1978).

Spatangoida

Five species of *Hemiaster* have been identified (10,3% from Wadi Quseib and 64% from Gebel Areif El-Naqa; Text-fig. 6A, B), and most of them have been collected

from the marly facies. Most of these species of *Hemiaster* have wedge-shaped tests e.g. *Hemiaster* (*H.*) *syriacus*, but others are globular in outline e.g. *H. (Mecaster) heberti turonensis* (Text-fig. 7B3-4). They have relatively deep and petaloid petals, well developed non-conjugated ambulacral pores as well as peristomal pores (phyllodal pores), and lack a real frontal sulcus. The pores of ambulacrum III are separated and circular, and are almost certainly associated with adapically funnel-building tube-feet (SMITH, 1980; SMITH et al., 1988).

Many authors e.g., SMITH & BENGTON (1991), SMITH (1995), and BARRAS (2008) pointed out that many spatangoids are infaunal deposit-feeders, burrowing relatively deeply within the sediment (of different sand-grades), and picking up suitable particles from the floor of the burrow by the penicillate tube-feet around the peristome (phyllodal pores). These feet (podia) are soft tissues and do not fossilize. However, each foot is associated with a single pore or with pore-pairs on the echinoid test (Text-fig. 7B2). KIER (1974) has noted an evolutionary trend in irregular echinoids for oral pores



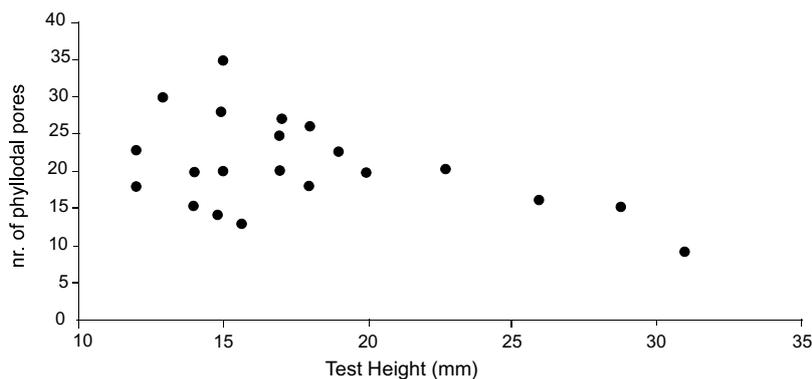
Text-fig. 7. Some morphological characters of *Hemiaster* species. A, D. *Hemiaster* (*H.*) *syriacus* (CONRAD, 1852); B. *H.* (*Mecaster*) *heberti* (COQUAND, 1862) *turonensis* FOURTAU, 1921; C. *Hemiaster* (*Hemiaster*) *gabrielis* PERON & GAUTHIER, 1878.

to change from double to single pores. Moreover, the lack of the frontal groove in some species such as *H. (H.) syriacus* (Pl. 4, Figs. 5-6) indicates that all food particles were derived from within the sediment and not from the sediment-water interface. In this case, phyllode tubes pick up the food particles from the sediment and transfer them to the mouth (SMITH, 1980). The presence of such tube feet is a good indicator that the organism lived infaunally and that the surface sediment is low in organic matter.

The number of phyllodal pores in some *Hemiaster* species such as *H. (H.) gabrielis* slightly decreases with increasing test height (Text-fig. 8). They are well-developed, circular, single to paired isopores. The penicillate tube foot in spatangoids is ideally suited for picking up very small, mud-sized particles, and each tube foot can pick up a disc-full of fine sediment particles by mucous adhesion (SMITH, 1980; BARRAS, 2008). Moreover, the large number of podia within the phyllo-

des increases the rate at which the echinoid can feed (BARRAS, 2008). According to JAGT (2000), the presence of frontal well-developed pores (in ambulacrum III) indicates that the species lived in relatively poorly permeable, rather fine-grained sediment. It appears that the presence of well-developed ambulacrum III pores as well as phyllodal pores are adaptations for feeding in muddy sediments.

The ambulacral pores (anterior and posterior petals) are slit-shaped, non-conjugated, and of relatively equal size. The shape of an ambulacral pore obviously matches the shape of the base of the tube foot (SMITH, 1980). According to this author not all isopores and anisopores bear tube feet that play an important role in gaseous exchange. If the pores are well separated and elongated with respect to the inner structure of the test, they have a primary or secondary respiratory function, whereas the tube feet associated with closely spaced pores, which show little or no divergence, play no significant part in



Text-fig. 8. Relationship of test height with the number of phyllodal pores in *Hemiaster* (*Hemiaster*) *gabrielis* PERON & GAUTHIER, 1878 from the Upper Albian-Cenomanian Halal Formation at Gebel Areif El-Naqa.

gaseous exchange across the test. The deep anterior and posterior petals improve the protection of these respiratory tube feet when organism adapted an infaunal mode of life (VILLIER et al., 2004). The latter author also pointed out that the pores of the frontal ambulacrum are likely to be associated with tube feet used in burrowing or food transport.

The outline (profile) of the echinoid test is known to be sensitive to environmental variations (NÉRAUDEAU, 1995). In several Cretaceous *Hemiaster* the shape of the test is related to the grain size of the sediment (more gibbous in finer-grained sediment), to the depth of burrowing, and to water depth (SMITH & PAUL, 1985; NÉRAUDEAU & MOREAU, 1989). Thus, species of *Hemiaster* are adapted to living on and within a wide range of sediment types (MCNAMARA, 1987). Spatangoids are common in fine-grained silt or mud as well as in sandy sediments (TELFORD & MOOI, 1996). According to SMITH et al. (1988), the wedge-shaped profile of *H. (H.) bufo* (BRONGNIART, 1822) and *H. nasutulus* (SORIGNET, 1850), suggests that they were excellent burrowers, well adapted for moving through more compact layers. This applies also to species such as *H. (H.) syriacus*, *H. (M.) journali*, and *H. (M.) pseudournali*. The heart-shaped test of *H. (M.) heberti turonensis* indicates that they lived infaunally, within relatively poorly permeable, rather fine-grained sediment (SMITH, 1995).

The increase in test height in spatangoids most likely caused water to flow over the test and on to respiratory tube feet-bearing petals at a faster rate (MCNAMARA, 1987). It is here suggested that the different *Hemiaster* species lived semi-infaunally (until the ambitus) or shallow infaunally (slightly above the ambitus) in marly facies (Table 1).

Fascioles are dense bands of small, modified spines that are found only in spatangoids and holasteroids (NÉRAUDEAU et al., 1998; BARRAS, 2008) (Text-figs. 7A1, B5, C1). Mud-dwelling spatangoids use mucus-lined spines as a barrier and have mucus-producing spines concentrated in fascioles, which are visible as bands of minute tubercles on a naked test (JAGT, 2000). Their presence is a strong indication that the echinoid lives infaunally, as fascioles have important roles in respiration, maintaining burrow cleanliness, and ensuring a successful protection of the respiratory feet through a mucus envelop (KROH, 2003; SMITH & STOCKLEY, 2005; BARRAS, 2008). In the present specimens, spines within fascioles produced currents that drew water into the burrow for respiration, especially in low-permeable sediments. In conclusion, the presence of an apical fasciole, building tube-feet, and of a dense and effective spine canopy enables the species to burrow into any type of sediment including mud (SMITH et al., 1988).

The type of spine and its layout on the test are clearly

correlated with the mode of life (SMITH, 1980). Spines of echinoids are outer body appendages mainly involved in the passive and active defense of echinoids (DUBIOS & AMEYE, 2001). The size and density of tubercles (base of spines) on the both oral and aboral surfaces differ in shape, size, and density. In the present material the tubercles on the oral surface (oral spines) are coarser than on the opposite surface. They were used to excavate the sediment so that the animal sinks shallowly into the substrate. The anterior spines (in front of the mouth) are used for forward motion and for loosening grains from the front side of the animal, while the numerous and strong spines posterior of the mouth are used to push the animal within the moderately hard marly sediments (Text-fig. 7A2).

In summary, four significant features, i.e. change in tubercle density, well-developed phylloidal pores as well as ambulacrum III pores, change of test shape, and presence of a peripetalous fasciole provide strong evidence for adaptations to inhabiting relatively poorly permeable sediment (marly facies) as semi-infaunal organisms (until the ambitus or slightly above the ambitus).

Cassiduloida

Petalobrissus cf. *pygmaeus* and *Gentilia syriensis* are the representative of this order. *P. cf. pygmaeus* has a small, depressed test and a depressed, large peristome (irregular outline without slit) with small tubercles. It has been interpreted as an infaunal bulk sediments swallower (SMITH et al., 1995; JAGT, 2000) because the substrate is generally low in organic matter. In this case organisms have to process vast quantities of sediment to obtain sufficient nutrition by moving through unconsolidated medium sand (SMITH, 1995; BARRAS, 2008). According to the latter author the depressed form of *Petalobrissus* is a good indicator that the echinoid moved through loose sediments. Moreover, the numerous small tubercles (base of spines) permit oxygenate water to flow around the animal (JAGT, 2000). The presence of a depression around the peristome suggests that food particles, after having been collected from the substrate, were quickly moved towards the mouth (TELFORD & MOOI, 1996).

Holectypoida

The genus *Coenholectypus* is represented by three species, *C. larteti*, *C. portentosus*, and *C. turonensis*, while the genus *Anorthopygus* is represented by a single species, *A. orbicularis*. Most of the *Coenholectypus* species have a low ambitus, broad base, and low-domed apical surface. The periproct is variable in shape, size, and degree of migration. It can be large and drop-shaped (about 31% of test diameter) as in *C. turonensis*, and small, inframarginal, and ovate as in *C. larteti*.

Table 1. Life habits and feeding modes of echinoids from the Upper Cretaceous of eastern Sinai.

	Species	Life habit	Feeding mode
1	<i>Sinaecidaris cf. gauthieri</i>	epifaunal	grazing/omnivorous
2	<i>Micropedina olisiponensis</i>	epifaunal (mobile)	?herbivorous/ carnivorous
3	<i>Orthopsis ovata</i>	epifaunal (mobile)	herbivorous
4	<i>Goniopygus menardi</i>	epifaunal (mobile)	?herbivorous/ carnivorous
5	<i>Goniopygus cf. peroni</i>	epifaunal (mobile)	?herbivorous/ carnivorous
6	<i>Codiopsis</i> sp.	epifaunal	omnivorous
7	<i>Pedinopsis desori</i>	epifaunal	?herbivorous
8	<i>Tetragramma variolare</i>	epifaunal (mobile)	?herbivorous/ carnivorous
9	<i>Heterodiadema libycum</i>	epifaunal (mobile)	omnivorous
10	<i>Phymosoma abbati</i>	epifaunal (mobile)	herbivorous
11	<i>Rachiosoma geysi</i>	epifaunal	herbivorous
12	<i>Coenholectypus larteti</i>	shallow infaunal to semi-infaunal/?epifaunal	deposit- feeding
13	<i>Coenholectypus portentosus</i>	shallow infaunal	deposit- feeding
14	<i>Coenholectypus turonensis</i>	shallow infaunal	deposit- feeding
15	<i>Anorthopygus orbicularis</i>	semi-infaunal	deposit- feeding
16	<i>Petalobrissus cf. pygmaeus</i>	infaunal (mobile)	deposit- feeding
17	<i>Pygurus cf. subproductus</i>	infaunal	?deposit- feeding
18	<i>Gentilia syriensis</i>	infaunal	?deposit- feeding
19	<i>Hemiaster (Hemiaster) syriacus</i>	shallow infaunal	deposit- feeding
20	<i>Hemiaster (H.) gabrielis</i>	shallow infaunal	deposit- feeding
21	<i>Hemiaster (Mecaster) fourneli</i>	shallow infaunal	deposit- feeding
22	<i>Hemiaster (M.) newtoni</i>	shallow infaunal	deposit- feeding
23	<i>Hemiaster (M.) pseudofourneli</i>	shallow infaunal	deposit- feeding
24	<i>Hemiaster (M.) heberti turonensis</i>	shallow infaunal	deposit- feeding

In the hard, fossiliferous *Chondrodonta* rudstone, bed 8, of the Cenomanian Galala Formation at Wadi Quseib, *C. larteti* is, on average, larger and higher (with numerous oral tubercles) than its representatives from the marls (lower marly member) of the Upper Albian-Cenomanian Halal Formation at the Areif El-Naqa section (Text-fig. 9A-B). SMITH (1995) thought that the highly inflated *C. inflatus* (COTTEAU & GAUTHIER, 1895) may have reverted to a primary epifaunal mode of life below the fair-weather wave-base. According to NEJBERT (2007), test height decreases with increasing clay or

sand content in the substrate. This interpretation is generally accepted, and NÉRAUDEAU & MOREAU (1989) noted that *C. excisus* is small and flattened in fine-grained sandstone and becomes large and flattened in reefal limestone, while *C. cenomanensis* becomes globular and large in limestone facies. Therefore, the high domal test of *C. larteti* from Wadi Quseib might be a sign of an epifaunal mode of life. SMITH (1981, 1984) interpreted the reduction in size and the increase in number of tubercles as an adaptation of the first irregular echinoids to an infaunal mobile life-style in soft bottom

environments. A broad and flat base, low profile, low ambitus, and a domed apical surface of the genus *Coenholectypus*, has been interpreted as an adaptation for more efficient locomotion and probably enhanced the stability on unconsolidated sediment and against stronger currents and/or wave action (SMITH, 1984; SMITH et al., 1988; RADWAŃSKA, 2005).

Anorthopygus orbicularis differs in having an almost circular outline (wheel-shaped test), deep and wide scrobicule (areole), and very inconspicuous petalodia (Pl. 4, Fig. 1). The presence of a deep scrobicule indicates that the species burrowed within the sediment by using strong spines with strong muscles (NÉRAUDEAU & MOREAU, 1989). The circular outline and rounded ambitus of *A. orbicularis* are similar to other *Holectypus*-species which indicate that individuals of this species presumably did not burrow deeply but lived semi-infaunal (Table 1). The present authors suggest that the strong flattening of the oral surface of *A. orbicularis* has greatly increased the number of tube feet in contact with the bottom. Also the scrobicule of tubercles is deep. These features indicate that the species could inhabit high-energy environments.

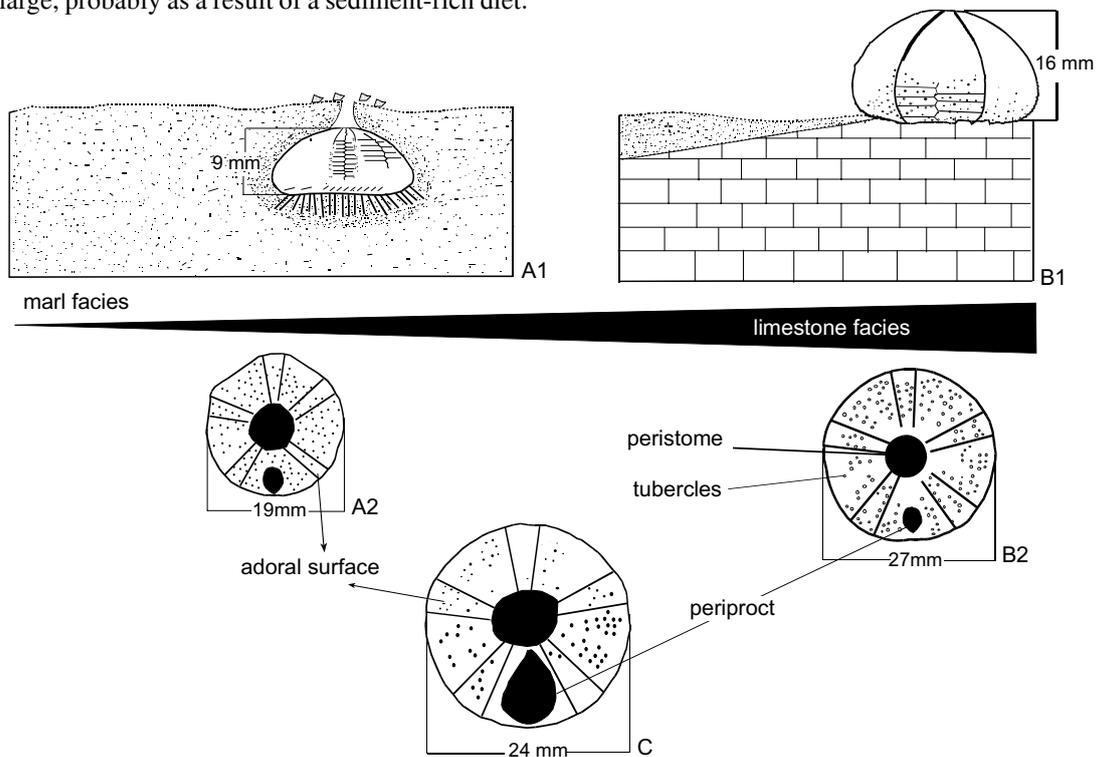
Periproct migration (out of the apical system) is also of adaptative significance (SAUCÈDE et al., 2007). It has been constrained, initiated or fostered by environmental factors (SMITH, 1984). The large periproct of *C. turonensis* (Text-fig. 9C) indicates that the volume of faecal material was great and that ingested particles were relatively large, probably as a result of a sediment-rich diet.

4.2 Regular echinoids

According to SMITH (1984, 1995), SMITH et al. (1988, 1995), JAGT (2000), and (SAUCÈDE et al., 2003) all regular echinoids without exception are epifaunal and wander over the sea floor in search of food as grazers and browsers. In comparison with irregular echinoids, they are generally much less adapted to the type of sediments on which they live, although it is possible to infer which species were adapted to shallow-water rocky bottoms.

Spines of regular echinoids are separated classically into three size classes: primary (large-sized, also called radioles), secondary (medium-sized), and tertiary (small-sized, also called miliary) (DUBOIS & AMEYE, 2001).

These spines (tubercles) play an important role in both regular and irregular echinoids. In regular echinoids, spines are used to for defense against predators (often associated with poison sacs in deep-sea forms), for preventing structural damage (STRATHMANN, 1981; JAGT, 2000), and for locomotion. While irregular echinoids use their spines for burrowing within the sediment. Therefore, most irregular echinoids avoid predators by living within the sediment, and their aboral surface is covered with fine, hair-like granules, which are used to support the wall of the burrow. In contrast, the aboral surface of most of regular echinoids has well-developed tubercles (large spines), which are used for defense and for locomotion.

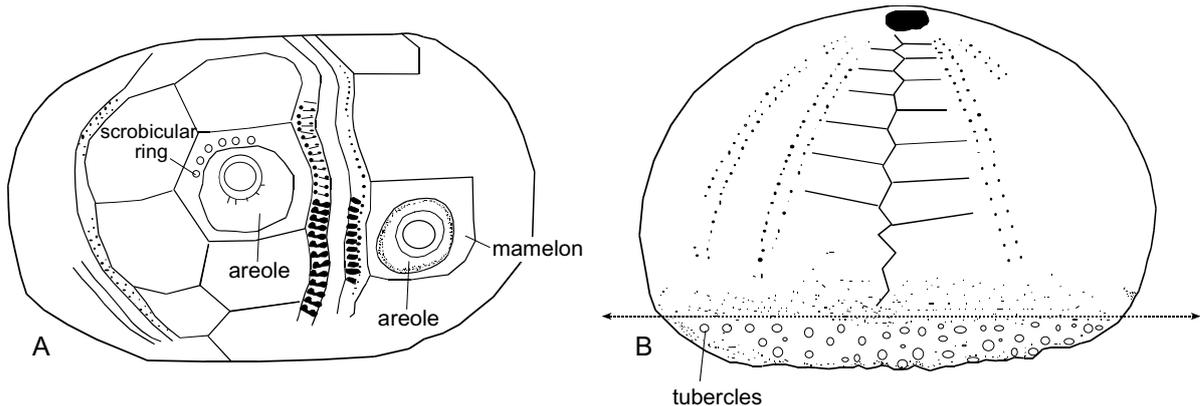


Text-fig. 9. A, B. Relationship between test height of *Coenholectypus larteti* (COTTEAU, 1869) and sediment type. C. *C. turonensis* (DESOR, 1847) with large periproct.

Cidaroida

Cidaroida are epifaunal, omnivorous, grazing on encrusting organisms (animal and plants). They move on the bottom with the help of spines without any directional preference (BIRKELAND, 1989; SMITH, 1995; RADWAŃSKA, 2005).

Only one species of this group, *Sinaecidaris* cf. *gauthieri*, has been identified. This species is characterized by having two rows of large and weakly crenulated primary tubercles with conjugated pores.



Text-fig. 10. A. *Sinaecidaris* cf. *gauthieri* FOURTAU, 1921 with wide areoles. B. Concentration of the primary tubercles around the peristomal area and below the ambitus (dotted line) of *Codiopsis* sp.

Phymosomatoida

Seven species belonging to this group have been identified, *Pedinopsis desori*, *Tetragramma variolare*, *Heterodiadema libycum*, *Phymosoma abbatei*, *Ph. sinaeum*, *Rachiosoma geysi*, and *R. irregulare*.

T. variolare has a flat oral surface (wheel-shaped profile) and its ambulacral pores become slightly larger and more closely packed adorally and biserial adapically with numerous and strong tubercles. According to SMITH et al. (1988), the flattened wheel-shaped profile of *T. variolare* presumably provided increased stability on sediments where tube feet could not provide anchorage in currents. The biserial arrangement on the aboral side of the test, such as in *T. variolare*, might have balanced their lower efficiency (RADWAŃSKA, 2005). The numerous spines are used for locomotion. As the aboral area is devoid of large spines, *Tetragramma* may have used its aboral tube feet to cover itself with loose material for camouflage (SMITH et al., 1988).

The different species of *Phymosoma* have a depressed profile, slight phyllode, well-developed tubercles and often have increased densities of aboral pore-pairs, (e.g., *Ph. abbatei*) where tube-feet possibly were specialized for gaseous exchange. According to SMITH (1995), the genera *Phymosoma* and *Orthopsis* (Order Orthopsida) are equivalent to modern genera such as *Lytechinus* or *Temnopleurus*, which live in and around hard substrate

Large spines of cidaroids are used to deter predators, while the conjugated pores indicate that the species clearly lives in shallow waters (SMITH et al., 1988; SMITH, 1995). The size of the areole indicates the strength of muscles and hence how active/powerful a species is. The present authors suggest that the presence of a wide areole indicates that the spines were large and strong (with strong muscles) for defence against predators and turbulent currents (Text-fig. 10A).

in reasonably well-protected habitats but not subjected to strong currents. They are predominantly grazers, feeding on encrusting or boring algae or plants. The uniform tubercles of members of the order Phymosomatoida, which are attached to sharply pointed spines of equal length, were used for defence (RADWAŃSKA, 2005).

Arbacioida

The genus *Codiopsis* is characterized by a flat oral surface, numerous and coarse tubercles adorally, and dense aboral pore-pairs with a nearly naked aboral surface. The broad and flat base with numerous and large tubercles (not continuing above the ambitus, Text-fig. 10B) is a feature characteristic of present-day echinoids living on rocky surfaces within the zone of active wave surge, where they feed on encrusting algae and other organisms (SMITH, 1995; SMITH et al., 1995). The aboral pore-pairs are indicative of specialized respiratory tube-feet. The additional tube feet of *Codiopsis* provided adhesion in turbulent environments where they grazed/rasped rock surfaces and fed on filamentous or fleshy algae (JAGT, 2000). The naked aboral side, which helped to channel the water and wash the test, did, however, not offer protection against predators (RADWAŃSKA, 2005). The present authors suggest that the large and strong oral tubercles were necessary for firmly attaching the echinoid on hard substrate in agitated and turbulent

waters as it occurs commonly during early transgression (lower part of the Cenomanian Galala Formation).

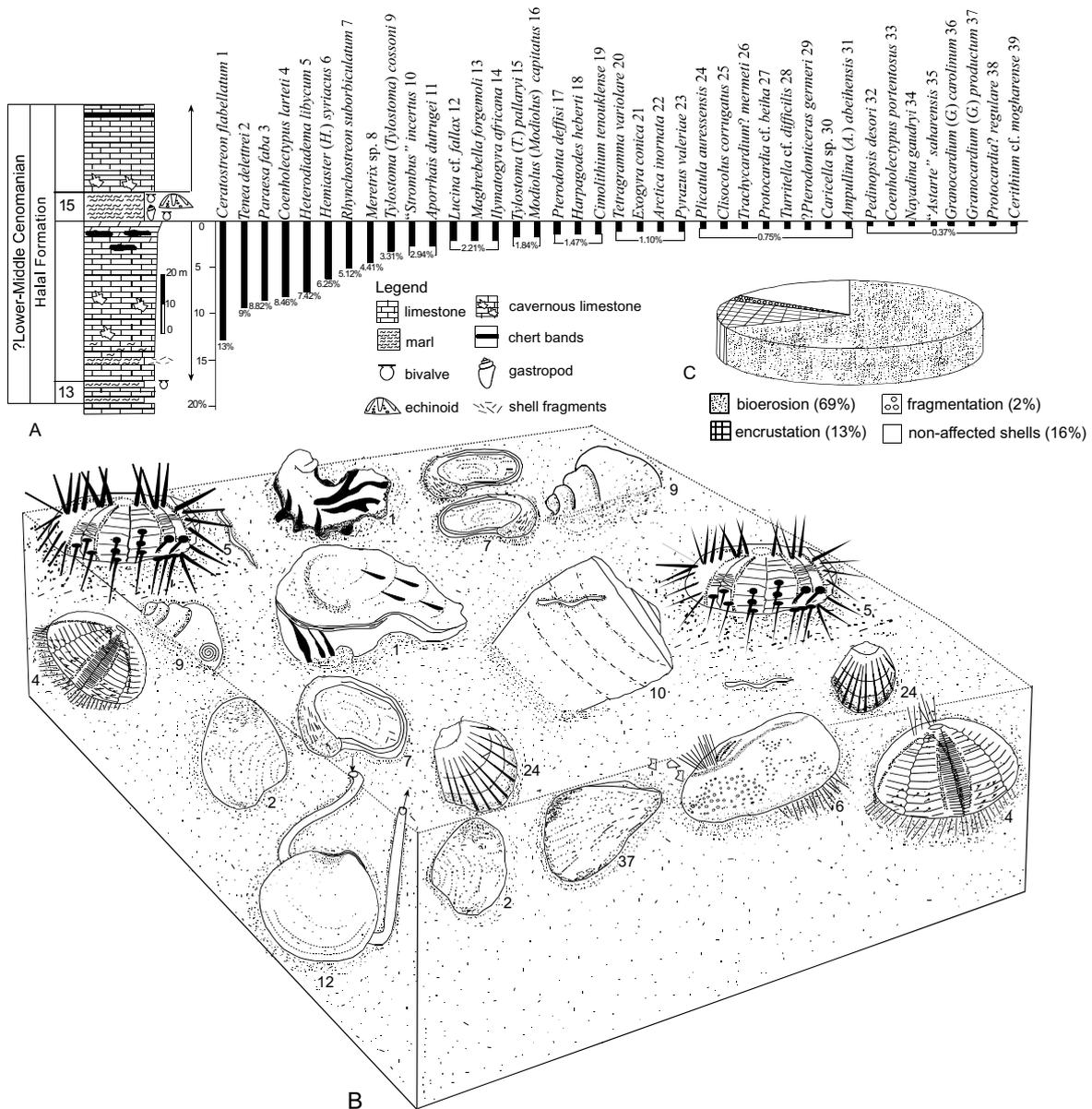
The genus *Goniopygus* has a depressed profile without a broad flat oral surface, and well-developed pore-pairs. SMITH (1995) and JAGT (2000) suggested that the pre-

sence of well-developed aboral respiratory tube-feet (pore-pairs) indicate a relatively high metabolic rate and that the echinoid therefore lived as epifaunal grazers in shallow, warm waters and probably not in fully exposed habitats.

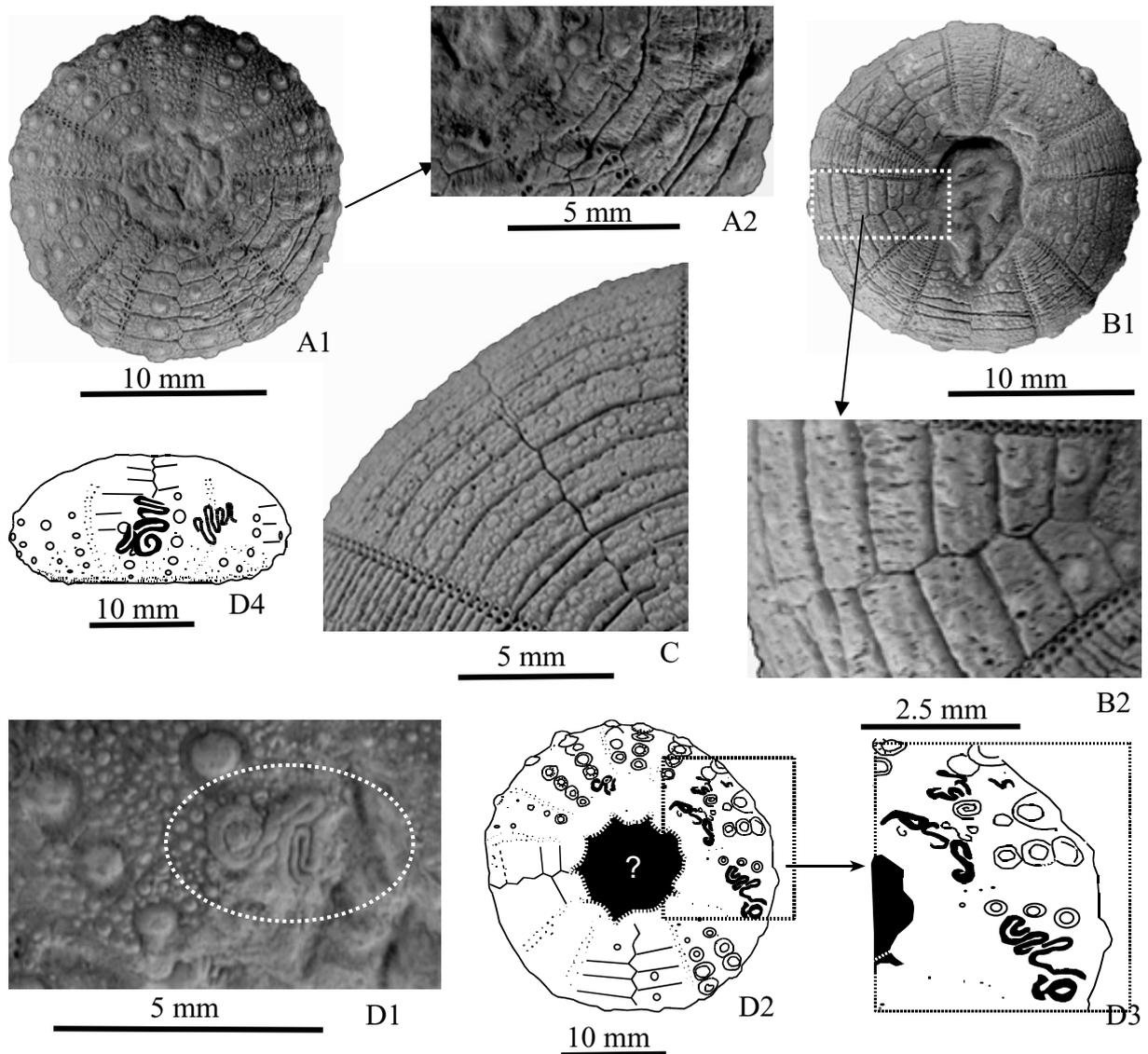
5 Taphonomic and syncological features

Some of the echinoid tests (e.g., *Heterodiadema libycum* and *Coenholectypus larteti*) and oyster shells (e.g. *Ceratostreon flabellatum*) from the middle carbonate member of the Cenomanian Halal Formation at Gebel Areif El-Naqa have been highly bioeroded (69%) and encrusted (13%) (Text-fig. 11C).

In the Wadi Quseib section, *C. turonensis* and *Hemiaster (Hemiaster) syriacus* exhibit also signs of bioerosion. However, other echinoid species, e.g. *H. (H.) gabrielis* (78 individuals) from the lower marly member of the Areif El-Naqa section lack any sign of bioerosion. This suggests that they were not exhumed after death.



Text-fig. 11. A, B. Relative abundance of the various taxa and reconstruction of the *Ceratostreon flabellatum* – *Tenea delectrei* assemblage. C. Pie diagram of the dominant taphonomic features (in %) in this assemblage.



Text-fig. 12. A, B. *Heterodiadema libycum* (AGASSIZ & DESOR, 1846) with microborings (B2) and scratch marks of grazing gastropods (A2). C. *Coenholectypus larteti* (COTTEAU, 1869) with microborings (?*Entobia*). D. *H. libycum* encrusted with *Serpula* (*Cycloserpula*) sp. All material has been collected from the middle carbonate member of the Upper Albian-Cenomanian Halal Formation at Gebel Areif El-Naqa.

The middle 10 m of the middle carbonate member of the Cenomanian Halal Formation at Gebel Areif El-Naqa (bed 15) contain a highly diverse fauna dominated by the epifaunal oyster *Ceratostreon flabellatum*, the infaunal bivalve *Paraesa faba*, and the epifaunal echinoid *Heterodiadema libycum* (Text-figs. 11A, B).

Bivalves dominate the assemblage with 54.3%, followed by echinoids 26%, and gastropods (19%). Epifaunal (47%) and infaunal (53%) mode of life is nearly equally represented. Nearly all infaunal bivalves are preserved as internal moulds of articulated specimens. Epifaunal oysters occur single-valved or articulated and are generally preserved with their shell. Most of the oyster species such as *Ceratostreon flabellatum* and *Rhynchostreon suborbiculatum* exhibit micro-and

macro-borings. As oyster shells are generally quite thick, borings are widely distributed in their shells. Most common are small, round, and closely spaced chambers of the ichnogenus *Entobia* BRONN, 1837. This ichnogenus is a product of clionid sponges which are restricted to fully lithified calcareous substrates (e.g., BROMLEY & D'ALESSANDRO, 1984). A few oysters exhibit small pouch-shaped borings with comma-shaped apertures made by acrothoracican barnacles (e.g., LAMBERS & BOEKSCHOTEN, 1986). These borings extend obliquely from the upper surface of *C. flabellatum*. The same species carries also club-shaped chambers which belong to the ichnogenus *Gastrochaenolites* LEYMARIE, 1842. This boring is produced by bivalves (BROMLEY, 2004).

Both infaunal and epifaunal echinoids are mostly well preserved. Most of the tests of epifaunal echinoids exhibit scratch marks of other organisms along the ambitus and oral surface with other small pores (Text-fig. 12A, C). Such marks were possibly left by grazing gastropods. A common epibiont on echinoid tests (e.g. on *H. libycum*) is the serpulid *Serpula (Cycloserpula)* sp. (Text-fig. 12D). All gastropods are preserved as internal moulds and are encrusted by serpulids.

Discussion

The *Ceratostreon flabellatum*–*Tenea delettrei* assemblage of bed 15 at Gebel Areif El-Naqa is characterized by a high species richness and evenness and was subjected to a low degree of environmental stress. The dominance of shallow infaunal bivalves (e.g., *Paraesa faba*), stenohaline echinoids (e.g., *H. (H.) syriacus*), and deep infaunal bivalves points to well oxygenated, fully marine conditions. According to STENZEL (1971), BOTTJER (1981), and DHONDT et al. (1999), exogyre oysters such as *Ceratostreon*, *Ilymatogyra*, and *Rhynchostreon* lived in shallow to very shallow waters (i.e., in middle shelf environments; 25-50 m in depth). The epibenthos consists of thick-shelled oysters and spinose plicatulids, which were well adapted to withstand the predation pressure by crabs, drilling gastropods, etc. Large and heavy gastropods such as „*Strombus*“ *incertus* and *Tylostoma cossoni* indicate a certain stability of the substrate.

The oyster shells in this assemblage are well preserved but mostly disarticulated (68% left valves, 11% right valves, 21% articulated valves). They are heavily bored (*Entobia*, less commonly *Gastrochaenolites*). The degree of disarticulation is a reliable means of determining the relative amount of reworking after death (BOUCOT et al., 1958). Consequently, the oysters in the *Ceratostreon flabellatum* – *Tenea delettrei* assemblage rarely occur in situ, but commonly have been transported for a short distance (i.e., they are parautochthonous) under a moderately high energy regime.

Boring organisms are widespread in most marine facies and are primary agents of shell destructions (e.g., DRISCOLL, 1970; BERTLING, 1992; CUTLER & FLESSA, 1995;

RUBERTI, 1997). The presence of the ichnogenus *Entobia* indicates favorable condition for their existence. Moreover, a low sedimentation rate gives bioeroders the chance to affect the oyster prior to final burial, because when sediments input is high, a large amount of energy is required to clear blocked canals and tissues (KRAUTTER 1998; EL-HEDENY & EL-SABBACH 2007). In addition, the abundance of clionid sponges decreases with increasing water depth (HOBBIE et al., 1972).

As the morphology of echinoids is closely related to the environment, they are excellent tools for reconstructing palaeoenvironments (KROH & NEBELSICK, 2003). Thus, SMITH & BENGTON (1991) noted that the poorly developed petals of the genus *Mecaster* (as in *Hemiaster (H.) syriacus*) indicate that relatively warm water conditions prevailed. The greater abundance of irregular echinoids such as *Coenholectypus larteti* and *H. (H.) syriacus* indicate quiet-water environments (NEJBERT, 2007). *Heterodiadema libycum* and *Tetragramma variolare* are good indicators of moderately shallow platform environments (NÉRAUDEAU & COURVILLE, 1997).

Some echinoid tests, e.g., *H. libycum* and *C. larteti* exhibit scratch marks possibly produced by grazing gastropods. These bioeroders started their action after the death of the echinoids, because the echinoid tests were covered, during their life-times with tissue so that no bioeroding activity was possible. Also the presence of serpulid worms on the adoral surface of the echinoid *H. libycum* clearly indicates post-mortem encrustation.

In the Wadi Quseib section, regular echinoids dominate (74.5%, Text-fig. 6B). According to NEJBERT (2007), most regular echinoids prefer nearshore, rocky substrate. A broad/flat base and numerous, large oral tube feet as for example in *Codiopsis* indicate rocky surface forms (JAGT, 2000). The large interambulacral spines of *Sinaecidaris* served to deter predators and to cope with turbulent currents (Text-fig. 13). Stenohaline, epifaunal echinoids as well as corals and sponges indicate euhaline conditions. The nearly complete lack of infauna in this association might be due to a very firm substrate. The high degree of fragmentation of *Chondrodonta* and rudists possibly indicate high water energy (Text-fig. 13).

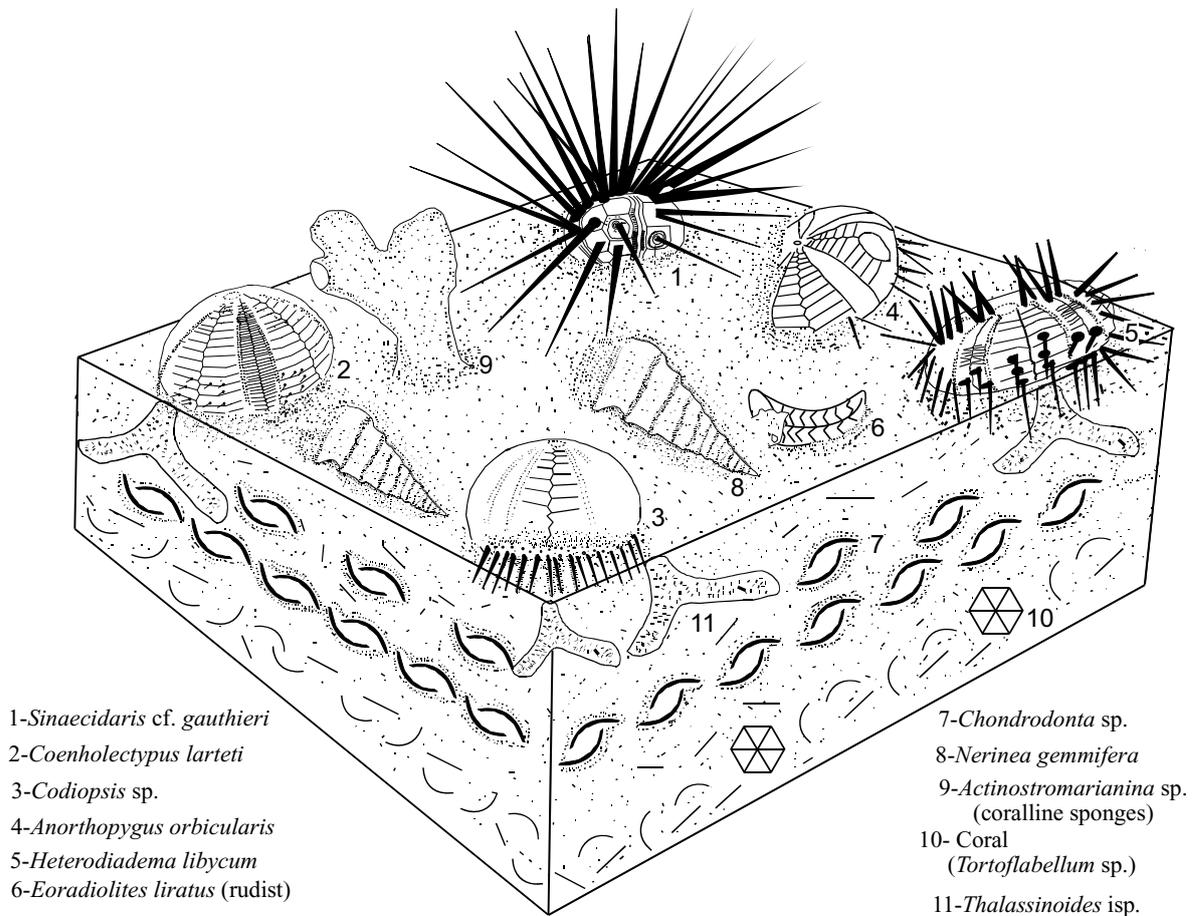
6 Conclusions

(1) The Cenomanian-Turonian rocks of the Areif El-Naqa and Wadi Quseib sections yield two assemblages of echinoids, most of them well preserved, and associated with other macrobenthic faunal elements (such as oysters, gastropods, and corals).

(2) Twenty-six echinoid species (20 species from the Wadi Quseib section, 12 species from Gebel Areif El-Naqa) belonging to sixteen genera, fourteen families,

and eight orders have been systematically described. 26.88% of these taxa are regular echinoids and 73.12% irregular echinoids.

(3) The echinoids occur in two different facies: a marly facies and a reefal carbonate facies. The marly facies is dominated by burrowing and ploughing irregular echinoids with rare regular echinoids, while the reefal carbonate facies (*Chondrodonta* rudstone) is dominated by



Text-fig. 13. Reconstruction of the *Chondrodonta* sp.-*Nerinea gemmifera* assemblage.

epifaunal, grazing regular echinoids.

(4) Four significant trends features have been identified, which provide strong evidence for morphological adaptations of *Hemiaster* to inhabiting relatively poorly permeable sediments (marl facies). They are an increase in tubercle density, well-developed phylloidal pores as well as ambulacrum III pores, a change of the test shape, and presence of a peripetalous fasciole. Therefore, the different species of *Hemiaster* probably lived semi-epifaunally (until the ambitus) or shallow burrowers.

(5) The domal shape of *Coenholectypus larteti* from

the reefal carbonate facies of Wadi Quseib indicates an epifaunal mode of life. In the marly facies at Gebel Areif El-Naqa, the echinoid may have lived shallow infaunally.

(6) In the middle carbonate member of the Halal Formation at Gebel Areif El-Naqa, most echinoids and oysters are affected by epi- and endobionts such as clionid sponges and serpulids, which indicate a shallow, relatively high-energy marine environment with a low sediment accumulation rate.

7 Acknowledgments

Prof. Dr. ANDREW B. SMITH, London, kindly identified some specimens. We would like to express our sincere thanks to Dr. MICHAEL HEINZE, Erlangen, for useful dis-

cussions. Great thanks are also due to Mrs. H. SCHÖNIG, Würzburg, who carried out the photographic work.

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