

Costinuculana magharensis n. gen. n. sp. (Bivalvia, Nuculanidae) from the Middle Jurassic of Gebel Maghara, North Sinai, Egypt

Wagih S. Ayoub-Hannaa,^{1,2} Ahmad A. Abdelhady,³ and Franz T. Fürsich²

¹Geology Department, Faculty of Science, Minufiya University, El-Minufiya, Shibin El Kom, Egypt (wagih_hannaa@yahoo.com)

²FG Paläoumwelt, Geozentrum Nordbayern der Friedrich-Alexander Universität Erlangen-Nürnberg, Loewenichstrasse 28, D-91054 Erlangen, Germany (franz.fuersich@fau.de)

³Geology Department, Faculty of Science, Minia University, 61519 Minia, Egypt (alhady2003@yahoo.com)

Abstract.—The nuculanid bivalve *Costinuculana magharensis* new genus new species is described from the middle to upper Bathonian Kehailia Formation of Gebel Maghara, North Sinai, Egypt. *Costinuculana* differs from other genera of the family Nuculanidae by the presence of opisthocline ribs along the rostrum. These ribs are variable in shape and size, straight to folded posteriorly, bifurcate ventrally and occasionally postero-dorsally, and cover an area ~45% of the total valve length from the posterior end. The life position of *C. magharensis* n. gen. n. sp. is reconstructed on the basis of a functional interpretation of its morphology and by comparison with closely related Recent forms. The asymmetrical commarginal ribs facilitated the burrowing process. The posterior oblique ribs are asymmetrical in cross-section with a steeply concave side in the burrowing direction and slightly convex side in the opposite direction. They probably kept the bivalve in a stable position once the desired depth had been reached. The thick oblique ribs probably also increased the strength of the rostrum and offered resistance against durophagous predators, being presumably partly exposed above the sediment-water interface. Based on the associated fauna, *Costinuculana* n. gen. lived in a low-energy environment characterized by a fine-grained, soft substrate.

Introduction

Gebel Maghara is a dome-like structure covering ~400 km² in the northern Sinai, 50 km south of the Mediterranean coast (Fig. 1). It comprises the thickest and most complete Jurassic outcrop in northern Sinai (1800 m; Al Far, 1966; Keeley, 1994). The Middle–Upper Jurassic succession of Gebel Maghara is well known for its rich and diverse macrobenthic fauna such as brachiopods, bivalves, gastropods, ammonites, and corals. This fauna has been repeatedly studied from a taxonomic point of view (e.g., brachiopods: Farag, 1957, 1959; Farag and Gatinaud, 1960a, b; Feldman, 1987; Hegab, 1989, 1991; Feldman et al., 1991, 2012; bivalves and gastropods: Douvillé, 1916, 1925; Hirsch, 1980; and ammonites: Arkell et al., 1952; Parnes, 1988). The most-recent studies dealing with the stratigraphy and paleoecology are given by Abdelhady (2014) and Abdelhady and Fürsich (2014, 2015a, b, c).

The purpose of this paper is: (1) to describe the new bivalve taxon *Costinuculana magharensis* n. gen. n. sp. (order Nuculanida) from the Bathonian of Gebel Maghara and to compare it with similar taxa of the family Nuculanidae; (2) to interpret the function of its oblique ribs, which cover an area up to ~45% of total valve length from the posterior end and to reconstruct its autecology; and (3) to determine its paleo-environmental setting on the basis of facies relationships and associated faunal elements.

Geologic setting

The Jurassic succession of Gebel Maghara represents a sequential development of continental and marine sediments, starting in the Early Jurassic (Toarcian) and lasting until the Kimmeridgian (Fig. 2). It represents a wide variety of continental, deltaic, nearshore-siliciclastic, and carbonate-shelf environments (Al Far, 1966; Picard and Hirsch, 1987), and contains a rich macrofauna. The marine strata are represented by the Rajabiah, Bir Maghara, and Masajid formations, whereas the continental sediments include the Mashabba, Shusha, and Safa formations. The nuculanid specimens have been collected from the middle to upper Bathonian Kehailia Formation (Fig. 2). This formation represents the lower member of Al Far's (1966) Masajid Formation (Kehailia Member). The Kehailia Formation unconformably overlies the lower Bathonian Safa Formation and underlies the Callovian Arousiah Formation (Fig. 2). It consists of yellow, highly fossiliferous marly silts and marls with thin, yellow glauconitic limestone intercalations and occasional sandstone interbeds. For more details about litho- and biostratigraphy see Abdelhady (2014) and Abdelhady and Fürsich (2015a, b, c).

Materials and methods

The present study is based on 10 specimens with preserved shells that were collected from the middle to upper Bathonian

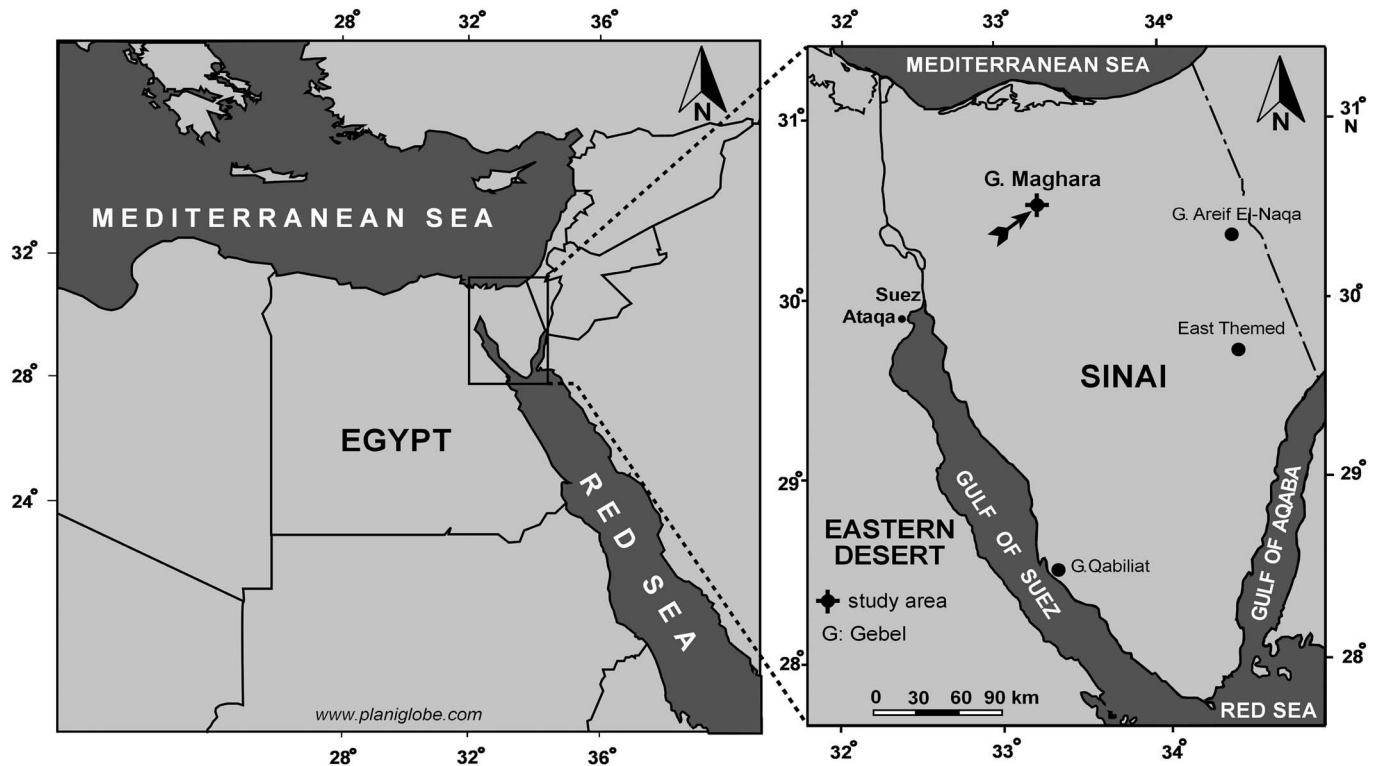


Figure 1. Locality map.

Kehailia Formation. The preservation of the specimens is of varying quality; especially the posterior ends are mostly broken off. Except for a single left valve, they are preserved as articulated shells. They were prepared mechanically and carefully cleaned. For photography, they were whitened with magnesium oxide to accentuate finer ornamental details.

Linear measurements (taken with a Vernier caliper) are in millimeters. Orientation of measurements is shown in Figure 3.1 and 3.2. Abbreviations for dimensions are as follows: L = length, H = height, I = inflation of articulated specimens, D = distance from the anterior end to umbo (umbonal distance), nr = number of ribs along rostrum.

Repositories and institutional abbreviations.—The specimens are housed in the collections of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich under the prefix BSPG 2014 V.

Systematic paleontology

The systematic classification of the bivalves follows that of Carter et al. (2011). The morphological terminology follows the glossary of Cox (1969) in the *Treatise on Invertebrate Paleontology*.

Class Bivalvia Linnaeus, 1758

Subclass Protobranchia Pelseneer, 1889 (= Palaeotaxodonta Korobkov, 1954)

Superorder Nuculaniformii Carter, Campbell, and Campbell, 2000

Order Nuculanida Carter, Campbell, and Campbell, 2000

Superfamily Nuculanoidea Adams and Adams, 1858 (Gray, 1854)

Family Nuculanidae Adams and Adams, 1858 (Gray, 1854)

Subfamily Veteranellinae Chen, Liu and Lan, 1983

Remarks.—Chen et al. (1983) relocated eleven nuculanid genera, including two new genera, to the new subfamily Veteranellinae. These genera are *Veteranella* Patte, 1926; *Glyptoleda* Fletcher, 1945; *Nucundata* Waterhouse, 1965; *Girtyana* Elias, 1956; *Teinonuculana* Zhang in Zhang, Wang, and Zhou, 1977; *Ledoides* Chen, Wen, and Lan in Gu et al., 1976; *Xiaoshuiculana* Chen, in Chen, Liu, and Lan, 1983; *Eleganuculana* Chen and Yang, 1983; *Indoculana* Kanjilal and Singh, 1973; *Costatoleda* Roth von Telegd, 1914; *Hilgardia* Harris and Palmer, 1946; *Qiongzhouina* Lan in Chen, Liu, and Lan, 1983; and *Zealeda* Marwick, 1924. These taxa are all strongly ornamented with one or more type of ribs (concentric, radial, and/or oblique). Based on the latter important taxonomic character, we place the new genus *Costinuculana* in the subfamily Veteranellinae. For more details and comparison among some of the above-mentioned genera, see below.

Genus *Costinuculana* new genus

Type species.—*Costinuculana magharensis* n. gen. n. sp. from the middle Bathonian (Middle Jurassic) of Gebel Maghara, North Sinai, Egypt.

Diagnosis.—Small, elongated, rostrate nuculanid, with posteriorly directed umbones. Rostrum with well-developed oblique ribs, variable in shape and size, asymmetrical in cross-section, straight to convex posteriorly, bifurcated ventrally and occasionally postero-dorsally, separated by wide and deep interspaces; escutcheon wide, moderately deep, and well ornamented with fine riblets, delimited by blunt ridges running from umbones to postero-dorsal margin; lunule narrow, lanceolate, sharply demarcated.

Age		Al Far (1966)		Abdelhady & Fürsich (2015a)	
Kimmeridgian	early	Masajid Fm.	Arousiah Mb.	Masajid Fm.	
	Oxfordian			late	Tauriat Fm.
middle					
early					
Callovian	late			Arousiah Fm.	
	middle				
	early				
Bathonian	late			Kehailia Mb.	Kehailia Fm.
	middle				
	early			Safa Fm.	Safa Fm.
Bajocian	late	Bir Maghara	Bir Maghara	Bir Maghara Fm.	
	early				Mowerib Mb.
			Mahl Mb.	Mahl Fm.	
Aalenian		Shusha Fm.		Shusha Fm.	
Toarcian				Ragabiah Fm.	


 position of *Costinuculana magharensis* n. gen. n. sp. Fm. formation Mb. member

Figure 2. Chronostratigraphic correction chart of the Jurassic formations of Gebel Maghara, Sinai, Egypt (modified after Abdelhady and Fürsich, 2015a).

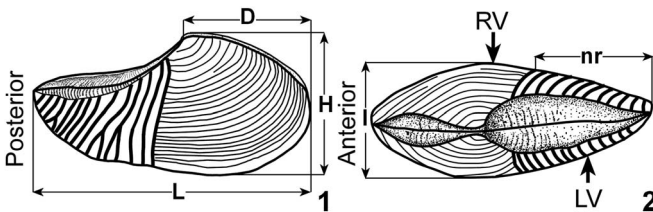


Figure 3. Measured parameters and orientation of *Costinuculana magharensis* n. gen. n. sp.: (1) lateral view of right valve; (2) dorsal view of articulated valves. Abbreviations: L = length, H = height, I = inflation of articulated specimen, D = distance from the anterior end to umbo, nr = number of oblique ribs along rostrum, RV = right valve, LV = left valve.

Etymology.—Combination of *costa* (Latin) = rib, and the genus *Nuculana*, referring to the oblique ribs along rostrum.

Occurrence.—The material of the new genus has been collected from the middle Bathonian ammonite *Clydomphalites clydocromphalus* Zone.

Remarks.—The significant taxonomic characters of *Costinuculana* n. gen. are not present in the majority of Jurassic nuculanid species that have been identified and described from different localities (e.g., Pandey and Singh, 1981; Fürsich, 1982;

Aberhan, 1994, 1998; Jaitly et al., 1995; Sha et al., 1998). The main diagnostic feature distinguishing *Costinuculana* from other genera of the family Nuculanidae (e.g., *Nuculana* Link, 1807) is the presence of well-developed oblique ribs on the posterior part of the flank, which cover an area up to ~45% of total valve length from posterior end (Fig. 4.1–4.9). The genus *Ryderia* Wilton, 1830 (type species: *Leda renevieri* Oppel, 1856, p. 215) is similar to the new genus in having an elongated-rostrate shell, a strongly rounded anterior margin, and small and opisthogyrate beaks, but differs in having a narrower and much more elongated rostrum, a narrow and smooth escutcheon, fine and closely spaced commarginal ribs, in lacking posterior oblique ribs, and in being much more compressed than the present material. The commarginal ribs of *Glyptoleda* Fletcher, 1945 are folded and sub-vertically deflected towards the posterior part of the flank, but the ornamentation style completely differs from that of *Costinuculana*. In addition, *Glyptoleda* differs in being much larger than the present genus (L = ~45 mm as opposed to 12.35 mm on average for *C. magharensis* n. sp.) and is of Permian origin. Chen et al. (1983) erected two genera, *Xiaoshuiculana* Chen in Chen et al. and *Qiongzhouunia* Lan in Chen et al. from the Upper Triassic and Pliocene of China, respectively. The genus *Xiaoshuiculana* differs from *Costinuculana* n. gen. in having only radial ribs that cover the entire valves and in being shorter. The genus *Qiongzhouunia* resembles *Costinuculana* n. gen. in having an elongated-rostrate shell and a well-developed umbonal posterior ridge, but differs also in the style of ornamentation. It is ornamented with faint concentric ribs on the flank and with delicate, weak growth lines on the posterior slope (see Chen et al., 1983, p. 619, fig. 1). The reticulate ornamentation and short rostrum distinguishes *Indoculana* Kanjilal and Singh (1973) from the Callovian of the Kachchh Basin, India, from *Costinuculana* n. gen. *Ledoides* Wen and Lan in Gu et al., 1976 from the Upper Triassic of China differs in having three different kinds of ribs: concentric ribs on the umbonal area, a reticulate pattern on the anterior part, and oblique radial ribs on the posterior part. In addition, *Ledoides* has a narrow and shorter rostrum. The subgenus (*Gonionucula*) Hautmann and Aghababalou in Hautmann et al. (2011, p. 22–24, figs. 2, 3) from the Norian–Rhaetian (Late Triassic) of Iran differs in having chevron-like ribs on the central part of the flank and an additional set of steeply opisthoclinal to nearly vertical ribs arranged in a narrow stripe on the posterior part of the flank. The latter authors stated that their new subgenus differs from the genus *Acila* Adams and Adams, 1858 in having an additional set of opisthoclinal ribs on the posterior part. Apart from its ornamentation, the genus *Acila* differs from *Costinuculana* n. gen. in being less elongated (not rostrate), larger, and in having a wide and strongly rounded anterior margin.

Pandey and Singh (1981, p. 1296, text-fig. 1) erected a new species “*Indoculana*” *sadharaensis* from the lower Callovian of Gora Dongar, India on the basis of the presence of faint radial riblets along the posterior part of flank. Jaitly et al. (1995, p. 160) regarded the different types of surface ornament just as intraspecific variations of *Nuculana* (*Praesaccella*) *calloviensis* (Kanjilal and Singh, 1973). The second feature regarded by Pandey and Singh (1981) as diagnostic feature of “*I.*” *sadharaensis*, is the presence of transverse threads in the escutcheon. Jaitly et al. (1995, p. 160, pl. 2, figs. 13, 14) observed

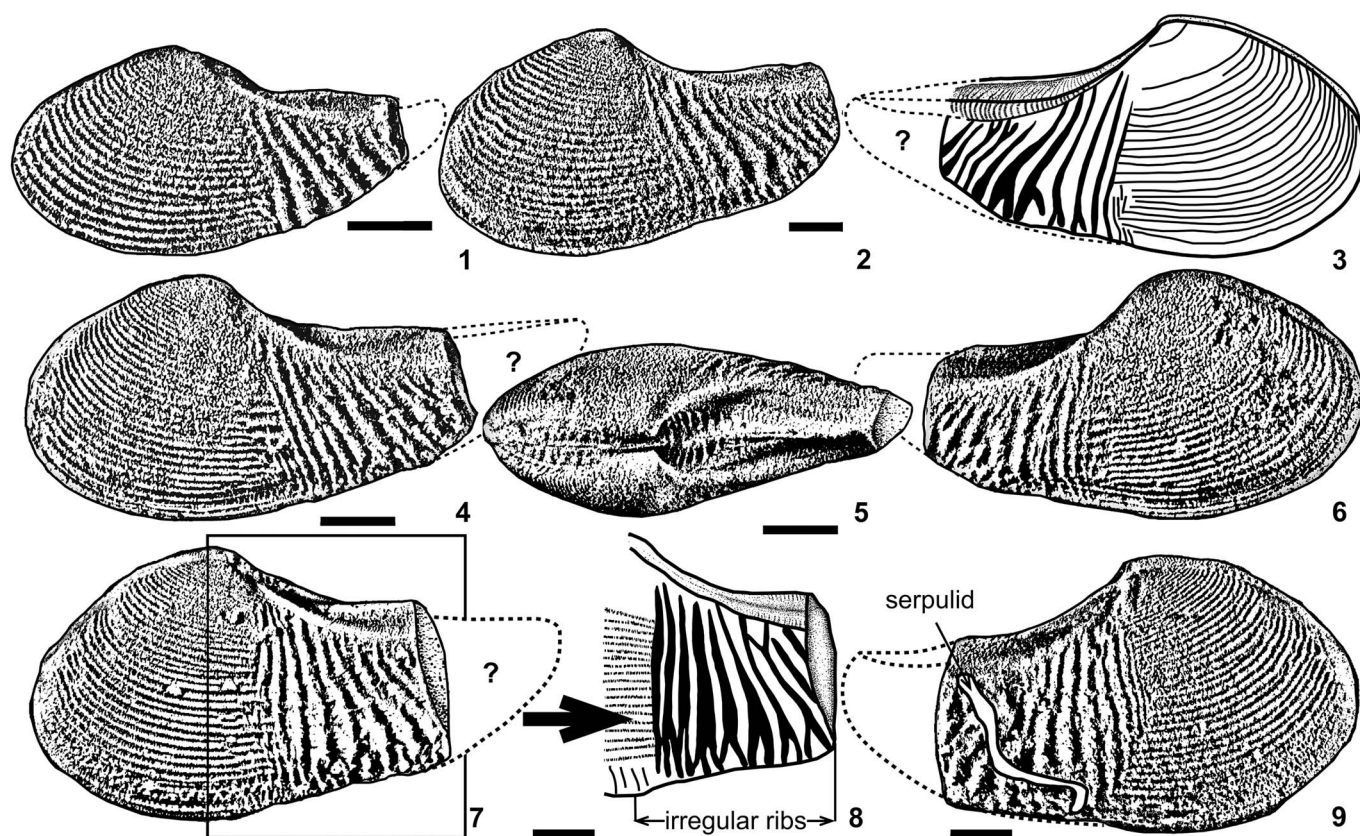


Figure 4. Modified photographs (1, 2, 5–7, 9) and sketches (3, 8) showing the variation of opisthocone ribs of articulated specimens of *Costinuculana magharensis* n. gen. n. sp. from the middle to upper Bathonian Kehailia Formation of Gebel Maghara: (1, 2, 4, 7) side view of left valves showing straight and arched ribs with rounded crests; (1) BSPG2014V I3b; (2) BSPG2014V I3a; (4) BSPG2014V I4b; (7) BSPG2014V 1, holotype; (3, 6, 9) right valves showing bifurcated ribs close to the ventral and postero-dorsal margin; (3) BSPG2014V I3a; (6) BSPG2014V I4b; (9) BSPG2014V 1; (5) dorsal view showing the oblique angle between ribs and postero-dorsal margin; BSPG2014V I4b; (8) sketch of posterior part of Figure 4.7 showing the irregular ribs, bifurcated close to the ventral margin and occasionally towards postero-dorsal margin. Scale bar = 2 mm.

the same transverse threads in *N. (P.) calloviensis*, which are therefore of no specific significance. In addition, “*L.*” *sadharaensis* differs from *C. magharensis* n. sp. in having a rapidly narrowing and short rostrum, less-developed postero-dorsal ridge, faint radial and commarginal ribs, and in being less inflated. *N. (P.) calloviensis* (Kanjilal and Singh, 1973), as figured and described by Jaitly et al. (1995), from the Callovian of Kachchh differs in having a reticulate ornamentation, which covers the entire valve, a less-elongated rostrum, and in being less inflated and smaller than the present species. The valve of *Ryderia texturata* (Terquem and Piette, 1865), described and figured by Hodges (2000, p. 45, pl. 3, figs. 5, 8–11, 13–17) and Aberhan et al. (2011, p. 70, pl. 1, fig. 7) from the Lower Jurassic of southwestern England and the Herforder Liasmulde, Germany, respectively, carries faint vertical threads in the posterior part of the flank, which start slightly below the postero-dorsal ridge and do not reach the ventral margin. The ribbing style of *C. magharensis* n. sp. is, indeed, completely different from that of the German material. In addition, *R. texturata* differs in having a very narrow and strongly elongated rostrum, strongly convex anterior and ventral margins, and in being larger ($L = \sim 42$ mm as opposed to 14.3 mm on average) and quite compressed.

Hautmann et al. (2011, p. 22, figs. 2–4) erected the new subgenus and species *Trigonucula (Gonionucula) aciloides*

from the Upper Triassic of Iran based on oblique ribs along the posterior flank. Their species differs from the Egyptian material by its more complex ornamentation pattern. The ribs are chevron-like on the central part of the flank and an additional set of steeply opisthocone to nearly vertical ribs are arranged in a narrow strip on the posterior part of the flank. Apart from the ribbing style, *Trigonucula (G.) aciloides* differs in having less-elongated valves, a smooth escutcheon, more or less central umbones, slightly rostrate valves, and in being less inflated. *Veteranella (Ledoides) langnongensis* Wen and Lan in Gu et al., 1976, as figured and described by Fang et al. (2009, p. 12, fig. 3.1–3.5), from the Upper Triassic of China differs in having a greater number of oblique to sub-vertical ribs along the posterior flank, a reticulate ornamentation on the central and anterior parts (except the umbonal area), a slightly convex ventral margin, sharp beaks, a narrower and longer rostrum, and in being much more elongated than the present species.

Costinuculana magharensis new species
Figures 4.1–4.9, 5.1–5.21

2014 Nuculoidea n. sp. Abdelhady, p. 172, fig. 5.4A, 5.4B.

2014 Nuculoidea n. sp.; Abdelhady and Fürsich, p. 181, fig. 6A, 6B.

Holotype.—Articulated specimen no. BSPG 2014V 1 (Fig. 5.13–5.17) from the middle Bathonian (Middle Jurassic) of Gebel Maghara, Egypt.

Paratypes.—Eight articulated specimens no BSPG 2014V I2, I3a, b, I4a, b, I5a, b from the middle Bathonian of Gebel Maghara, and one right valve no BSPG 2014V I5c.

Type locality.—Gebel Maghara, North Sinai, Egypt.

Diagnosis.—See genus.

Description.—Shells small (L = 10.5–17.3 mm; Table 1), elongated-rostrate in outline, strongly inequilateral, equivalved, moderately inflated (I/L = 29–38%), and posteriorly elongated with ribbed rostrum (Fig. 4). Antero-dorsal margin short, strongly convex, higher than postero-dorsal one, and meeting anterior margin in strongly rounded curve. Postero-dorsal margin long, slightly concave. Anterior margin strongly convex, meeting ventral margin in rounded angle. Posterior margin rostrate, its end broken off. Ventral margin broad, irregular, moderately convex toward anterior margin, slightly concave posteriorly, and forming rostrum with postero-dorsal margin. Umbones broad and strongly convex. Beaks small, strongly incurved posteriorly and situated, on average, 39% of total shell length from anterior end (Table 1). Escutcheon wide, moderately deep, ornamented with fine riblets, and delimited by blunt ridge; running from umbo to postero-dorsal margin (Figs. 4.5, 5.16, 5.17). Lunule narrow, lanceolate, deep, and demarcated (Fig. 5.12, 5.19). Hinge with numerous chevron-shaped teeth, points directed towards umbones (Figs. 5.21, 6). Anterior hinge carrying slightly more teeth (14) than posterior hinge (≥ 11). Ornamentation consisting of numerous well-developed commarginal ribs on anterior and central parts of valve, but irregular and opisthocline ribs along rostrum (9–12), separated by wide and deep interspaces (Fig. 4.1–4.9). Commarginal ribs well developed ventrally (Fig. 5.18), asymmetrical in cross-section with slightly convex, broad ventral sides and steeply inclined and slightly concave dorsal sides (Fig. 7.2). Oblique ribs variable in shape and size, straight to folded, bifurcated ventrally and occasionally postero-dorsally (Figs. 4.3, 4.4, 4.6–4.8, 5.7–5.9, 5.13, 5.14), covering an area ~45% of total valve length from posterior end. Close to ventral margin, these ribs are thicker, bifurcating, and are asymmetrical in cross-section with a steeply concave side anteriorly and slightly convex side in opposite direction (Fig. 7.2).

Etymology.—After the type locality Gebel Maghara, Sinai Peninsula, Egypt.

Remarks.—See genus.

Mode of life and functional morphology of *Costinuculana* n. gen.

Morphologically, *Costinuculana* n. gen. is narrowly elongated, rostrate, has a broadly convex anterior margin, and is moderately inflated with strong, oblique ribs along the rostrum. The long narrow valve (like in *Ryderia*) indicates a rapid burrower (Stanley, 1970). Recent nuculanids are shallow infaunal bivalves with inhalant and exhalant siphons, which usually burrow with their long axis vertical or steeply inclined (Cox, 1960). The posterior end is maintained above the sediment-water interface and the posterior siphons are never covered with sediment. They are deposit-feeders, feeding from the sediment surface by palp proboscides (Cox, 1960). These palp proboscides extend immediately ventral of the siphons and collect food from the surface of the substrate (Yonge, 1939, p. 86).

With respect to ribbing style, most ribs in bivalves are commarginal (“concentric”) or radial (longitudinal) (Checa and Jiménez-Jiménez, 2003). In a third, less-common ribbing pattern, the ribs are oblique (Seilacher, 1972) or discordant (Stanley, 1969), whereby ribs migrate along the margin with growth. According to Stanley (1969, 1970) and Seilacher (1972, 1973), one of the functions of oblique ribs in bivalves is to facilitate burrowing in soft sediments. For a burrowing-related function, ribs show a gentle slope in the burrowing direction and a steep, in some cases inverted, slope in the opposite direction (frictional asymmetry; Seilacher, 1972). For some other cases, Seilacher (1972) assumed that the oblique ribs were non-functional or had functions unrelated to burrowing. Later, Stanley (1981) and Savazzi (1982, 1983) showed experimentally that the radial ribs of several cardiids and of one arcid act to reduce the number of burrowing sequences required to complete burrowing.

Costinuculana magharensis n. gen. n. sp. has two kinds of ribs, commarginal and oblique ribs. The commarginal ribs are asymmetrical in cross-section, with a wide and slightly convex side in the burrowing direction, and a steeply inclined and slightly concave side in the opposite direction (Fig. 7.2). In contrast, the oblique ribs are thick and asymmetrical in cross-section close to the ventral margin, with a steeply concave side in the burrowing direction and a slightly convex side in the opposite direction (Fig. 7.2). At the beginning of burrowing, when the bivalve erected itself, the asymmetrical commarginal ribs facilitated the burrowing process (burrowing-related function). Once most of the bivalve had buried itself, the posterior oblique ribs provided stability for the organism in the soft substrate when the ribs were nearly perpendicular to the direction of burrowing (Fig. 7.2). In this case, the concave sides of the oblique ribs caught the sediment when the shell rotated forward during the burrowing process and kept the posterior end above

Figure 5. *Costinuculana magharensis* n. gen. n. sp. from the middle-upper Bathonian Kehailia Formation of Gebel Maghara, Egypt. All specimens are in shell preservation and articulated except Figure 5.21. In all specimens the tip of the rostrum is broken off: (1) right valve view; (2) dorsal view; BSPG2014V I4a; (3) left valve view showing thick irregular ribs with wide and deep interspaces; (4) right valve view with well-developed commarginal ribs; BSPG2014V I3b; (5) left valve view showing thick irregular ribs with sharp crests; (6) dorsal view; (7) right valve view with bifurcated ribs close to the ventral margin; BSPG2014V I4b; (8) right valve view; (9) close-up showing an inverted V-shaped rib close to the ventral margin; BSPG2014V I4c; (10) left valve view showing slightly folded ribs posteriorly and bifurcated ventrally; (11) right valve view; (12) dorsal view showing the lanceolate and demarcated lunule; BSPG2014V I3a; (13) left valve view, holotype; (14) close-up of Figure 5.13 showing the irregular and bifurcated ribs close to the ventral margin; (15) right valve view with serpulid; (16) dorsal view showing the moderately inflated valves; (17) close-up of Figure 5.16 showing wide and ornamented escutcheon, delimited by blunt ridges; BSPG2014V 1; (18) right valve view showing thick and well-developed commarginal ribs close to the ventral margin; (19) dorsal view; (20) left valve view; BSPG2014V I2; (21) right valve view showing numerous chevron-shaped teeth; BSPG2014V I5c. Scale bars = 2 mm.

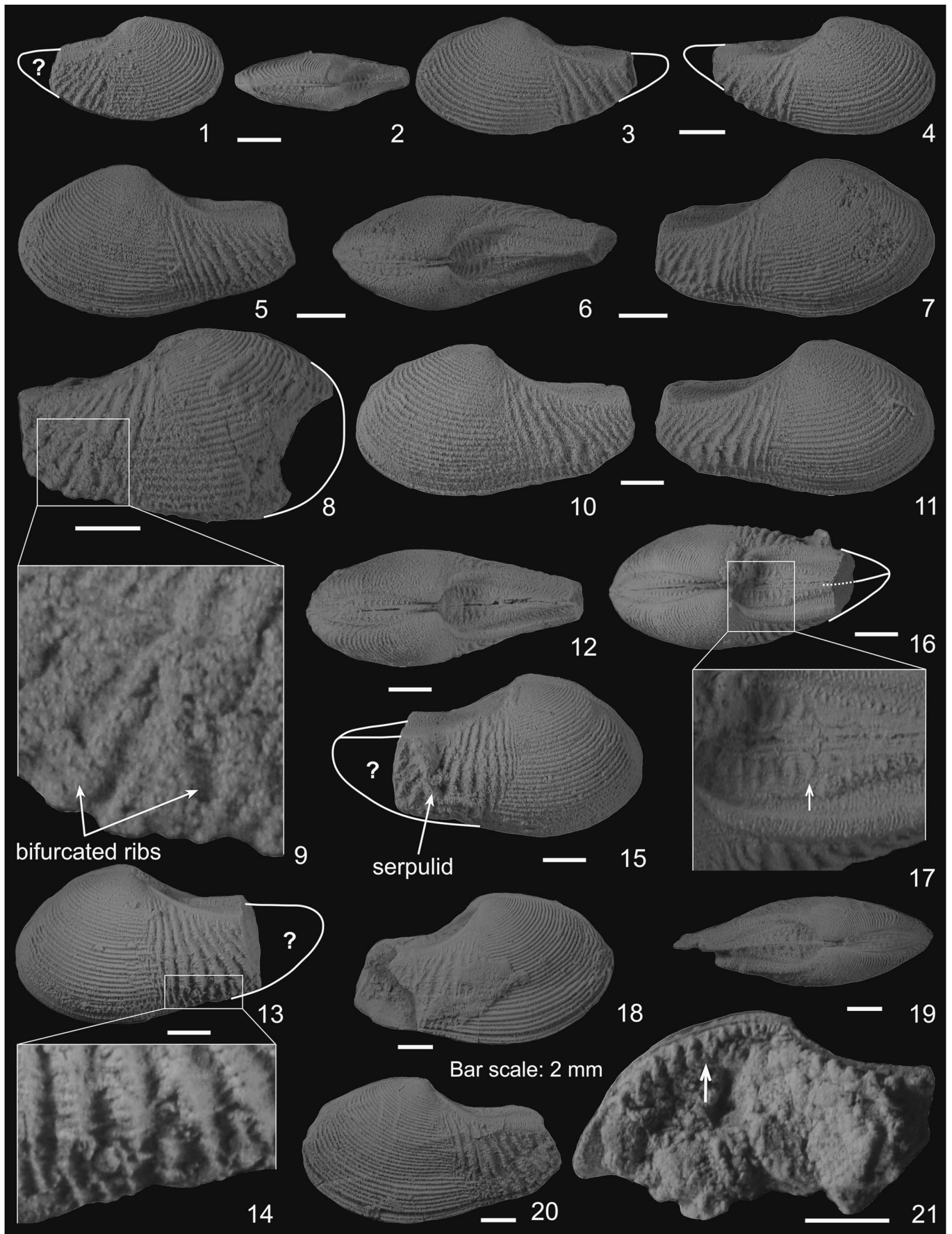


Table 1. Measurements (in mm) of *Costinuculana magharensis* n. gen. n. sp. from the Middle Bathonian of Gebel Maghara, Sinai. Abbreviations given in Figure 3.

Specimen	L	H	I	D	H/L	I/L	D/L	N. ribs
BSPG2014 V 1 (holotype)	16	7.8	6.1	6.4	0.49	0.38	0.4	12
BSPG2014 VI3a	17.3	7	5.2	6.5	0.40	0.30	0.38	13
BSPG2014 VI4a	10.5	5.2	3.1	4.3	0.49	0.29	0.41	8
BSPG2014 VI4c	15.5	6.5	4.7	6.2	0.42	0.30	0.40	15
BSPG2014 VI2	14.2	7	4.3	5.5	0.49	0.30	0.39	10
BSPG2014 VI3b	11.3	5.2	3.5	4.1	0.46	0.31	0.36	8
Range	10.5–17.3	5.2–7.8	3.1–6.1	4.1–6.5	0.40–0.49	0.29–0.38	0.36–0.41	8–15
Mean	14.13	6.45	4.48	5.5	0.46	0.31	0.39	11

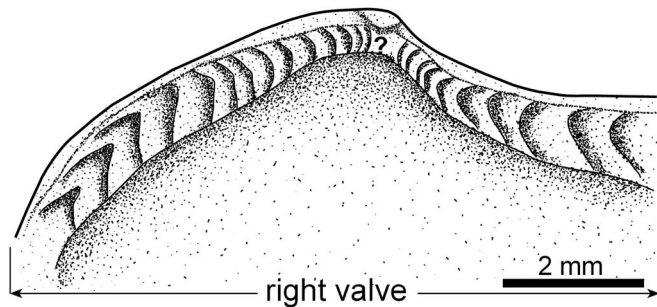


Figure 6. Hinge of the right valve of *Costinuculana magharensis* n. gen. n. sp. from the middle to upper Bathonian Kehailia Formation of Gebel Maghara; BSPG2014V I5c.

the sediment-water interface. Because the posterior end of the shell presumably remained above the sediment-water interface, the thick posterior-most oblique ribs probably had another function. Most likely, they strengthened the thin and elongated rostrum against durophagous predators such as ammonites. The inflated valves with their broadly convex anterior margin in addition helped the bivalve to maintain a stable position within the soft substrate and to keep the posterior end above the sediment-water interface.

Paleosynecological remarks

Based on the cluster analysis of Abdelhady and Fürsich (2014, p. 179, fig. 3), *Costinuculana magharensis* n. gen. n. sp. is a member of their *Nicaniella* (*N.*) *pisiformis* association. This association is found mostly in fine-grained sediments (mainly marly silt and marl) of the middle to upper Bathonian Kehailia Formation of Gebel Maghara. The dominant organisms of this association are bivalves (75.4%), whereas gastropods, brachiopods, corals, and echinoids are subordinate. According to Abdelhady and Fürsich (2014), the trophic nucleus consists of 12 species and is dominated by small, shallow-burrowing *Nicaniella* (*N.*) *pisiformis* J. de C. Sowerby (31.5%; Fig. 7.3), *Nuculoma variabilis* (J. de C. Sowerby) (10.9%), and *Ryderia decorata* (Douvillé) (8.3%). Shallow-infaunal organisms represent 67.8% of the total benthic fauna followed by epifaunal ones 28.2% (Fig. 7.1). With respect to the feeding habits, suspension-feeders dominate (54.2%), followed by deposit-feeders (28.1%), omnivores (12.7%), and microcarnivores (4.9%).

The fine-grained sediment and the abundance of shallow-infaunal organisms and deep-burrowing bivalves (altogether

67.8%) indicate that the *Nicaniella* (*N.*) *pisiformis* association occupied a soft substrate. Due to the activities of mobile taxa (40.7%; Abdelhady and Fürsich, 2014), the softness of substrate probably increased and thus became less attractive for epifaunal organisms. The *Nicaniella* (*N.*) *pisiformis* association reflects low-energy conditions, in which physical breakage was insignificant. All specimens of *Costinuculana* n. gen. except one are articulated, which implies a relatively low degree of reworking. According to the high percentage of suspension-feeders (54.2%), water energy must have been sufficient enough to keep nutrients in suspension. Moreover, the high diversity both in terms of evenness and species richness and the presence of stenohaline groups, such as ammonites and echinoids, indicate normal-marine, fully oxygenated low-stress conditions. For more details about the paleo-community see Abdelhady (2014, p. 170) and Abdelhady and Fürsich (2014, p. 179–184).

Conclusions

- (1) The bivalve *Costinuculana magharensis* n. gen. n. sp. (Nuculanida, Nuculanidae) is described from the middle to upper Bathonian Kehailia Formation of Gebel Maghara, North Sinai, Egypt.
- (2) The main morphological feature that distinguishes *Costinuculana* n. gen. from other nuculanid genera is the irregular opisthocline ribs on the rostrum, which cover an area ~45% of the total valve length from the posterior end. Other diagnostic features are the morphology of the escutcheon and lunule.
- (3) *Costinuculana magharensis* n. gen. n. sp. differs from related species by its small size and its well-developed irregular opisthocline ribs on the rostrum, moderately inflated valves, narrow, lanceolate, and sharply demarcated lunule, and wide and deep escutcheon with well-developed riblets.
- (4) The conspicuous oblique ribs in *C. magharensis* n. sp. probably helped the bivalve to maintain a stable position in the soft substrate. The oblique and bifurcated ribs increased the friction between the valves and sediment. In addition, these ribs probably reinforced the thin, elongated rostrum against durophagous predators (e.g., ammonites).
- (5) Paleosynecologically, the *Nicaniella* (*N.*) *pisiformis* association and the fine-grained substrate reflect low-energy conditions. The species diversity and evenness of the association indicate a stable environment suitable for the colonization by several guilds.

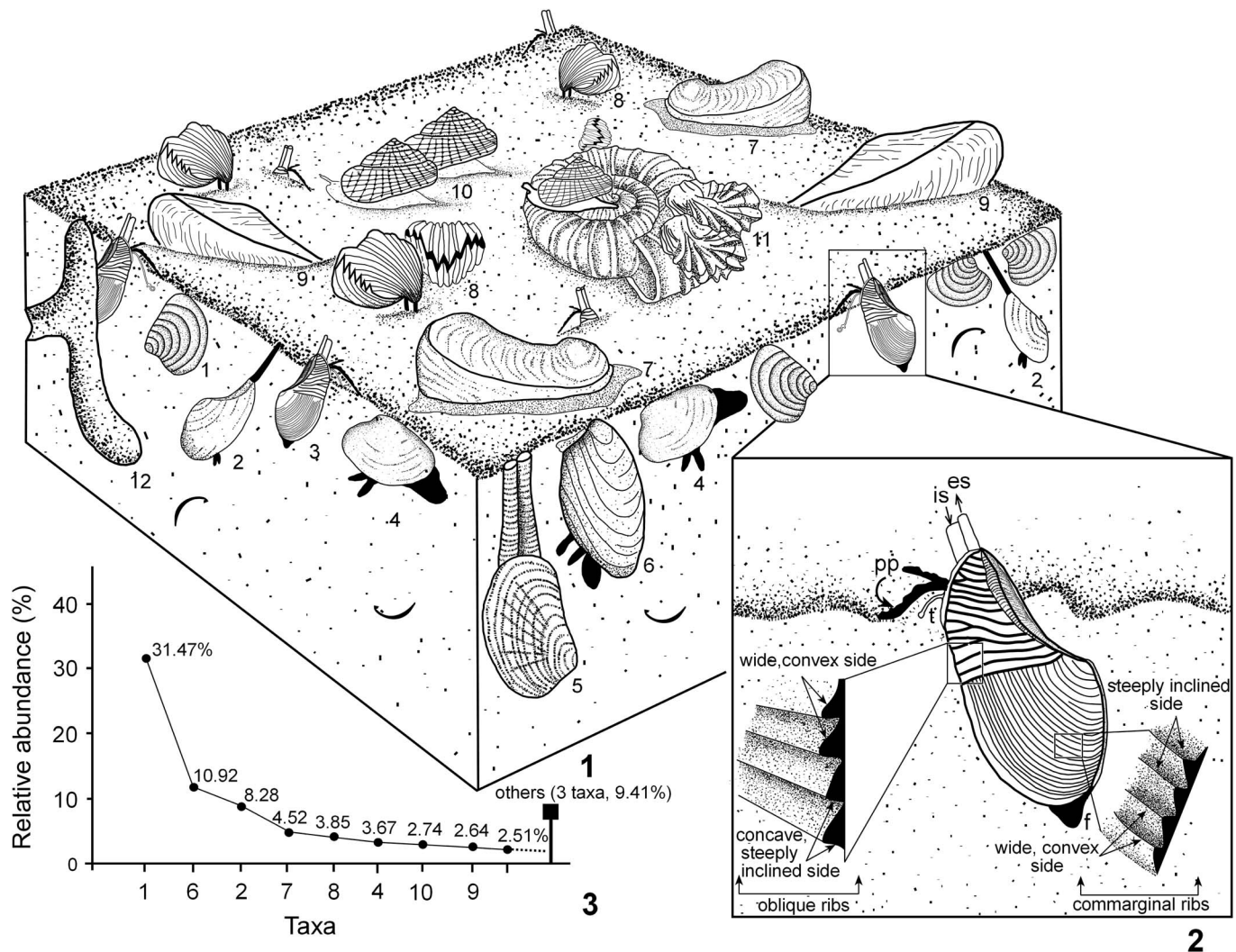


Figure 7. (1) Reconstruction of the *Nicaniella (N.) pisiformis* association of which *Costinuculana magharensis* n. gen. n. sp. is a member. 1 = *Nicaniella (N.) pisiformis* J. de C. Sowerby; 2 = *Ryderia decorata* (Douvillé); 3 = *Costinuculana magharensis* n. gen. n. sp. 4 = *Palaeonucula lateralis* (Terquem and Jourdy); 5 = *Pholadomya (Ph.) inornata* (J. de C. Sowerby); 6 = *Nuculoma variabilis* (J. de C. Sowerby); 7 = *Nanogyra nana* (J. Sowerby); 8 = *Daghanirhynchia angulocostata* Cooper; 9 = *Gervillella orientalis* (Douvillé); 10 = *Amphitrochus magharensis*, Douvillé; 11 = *Africogryphaea costellata* (J. de C. Sowerby); 12 = *Thalassinoides*; (2) mode of life of *Costinuculana magharensis*. is = inhalant siphon; es = exhalant siphon; pp. palp proboscides; t = tentacle. While the commarginal ribs aid the burrowing process, the oblique posterior ribs stabilize the shell within the substrate; (3) relative abundance (%) of some species of the trophic nucleus of the *Nicaniella (N.) pisiformis* association (number denotes taxa in Figure 7.1). Data taken from Abdelhady and Fürsich (2014).

Acknowledgments

The authors greatly appreciate the thoughtful reviews and valuable suggestions by Associate Editor M. Hautmann and two anonymous reviewers. A.A.A. wants to thank the German Academic Exchange Service (DAAD) and the Egyptian Mission (Ministry of High Education of Egypt) for their financial support through the German-Egyptian Research Long-term Scholarship (GERLS).

References

- Abdelhady, A.A., 2014, Palaeoenvironments and palaeoecology of the Middle and Upper Jurassic succession of Gebel Maghara (Sinai) [Doctoral Dissertation]: Erlangen, Friedrich-Alexander-Universität Erlangen-Nürnberg, 179 p. (http://epic.awi.de/36291/1/AbdelhadyAA_2014.pdf)
- Abdelhady, A.A., and Fürsich, F.T., 2014, Macroinvertebrate palaeo-communities from the Jurassic succession of Gebel Maghara (Sinai, Egypt): *Journal of African Earth Sciences*, v. 97, p. 173–193.
- Abdelhady, A.A., and Fürsich, F.T., 2015a, Quantitative biostratigraphy of the Middle to Upper Jurassic strata of Gebel Maghara (Sinai, Egypt): *Newsletters on Stratigraphy*, v. 48, p. 23–46.
- Abdelhady, A.A., and Fürsich, F.T., 2015b, Sequence architecture of a Jurassic ramp succession from Gebel Maghara (North Sinai, Egypt): implications for eustasy: *Journal of Palaeogeography*, v. 4, p. 305–330.
- Abdelhady, A.A., and Fürsich, F.T., 2015c, Palaeobiogeography of the Bajocian–Oxfordian macrofauna of Gebel Maghara (North Sinai, Egypt): implications for eustasy and basin topography: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 417, p. 261–273.
- Aberhan, M., 1994, Early Jurassic Bivalvia of northern Chile. Part 1. Subclasses Palaeotaxodonta, Pteriomorpha, and Isofilibranchia: *Beringeria*, v. 13, p. 3–115.
- Aberhan, M., 1998, Early Jurassic Bivalvia of western Canada. Part 1. Subclasses Palaeotaxodonta, Pteriomorpha, and Isofilibranchia: *Beringeria*, v. 21, p. 57–150.
- Aberhan, M., Scholz, A., and Schubert, S., 2011, Das Ober-Pliensbachium (Domerium) der Herforder Liasmulde - Teil 3 - Taxonomie und

- Paläoökologie der Bivalvia aus der Amaltheenton-Formation (Unterjura) der Herforder Liasmulde: Geologie und Paläontologie in Westfalen, v. 80, p. 61–109.
- Adams, H., and Adams, A., 1858, The Genera of Recent Mollusca, Arranged According to their Organization: London, Van Voorst, v. 2, p. 1–604.
- Al Far, D.M., 1966, Geology and coal deposits of Gebel El Maghara (N. Sinai): United Arab Republic Geologic Survey, Paper, v. 37, p. 1–59.
- Arkell, W.J., Bramkamp, R.A., and Steineke, M., 1952, Jurassic ammonites from Jebel Tuwaiq, central Arabia: Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences, v. 236, p. 241–313.
- Carter, J.G., Campbell, D.C., and Campbell, M.R., 2000, Cladistic perspectives on early bivalve evolution, in Harper, E.M., Taylor, J.D., and Crame, J.A., eds., The Evolutionary Biology of the Bivalvia: The Geological Society of London, Special Publication, v. 177, p. 47–79.
- Carter, J.G., Altaba, C.R., Anderson, L.C., Araujo, R., Biakov, A.S., Bogan, A.E., Campbell, D.C., Campbell, M., Chen, J.-H., Cope, J.C.W., Delvene, G., Dijkstra, H.H., Fang, Z.-J., Gardner, R.N., Gavrilova, V.A., Goncharova, I.A., Harries, P.J., Hartman, J.H., Hautmann, M., Hoeh, W.R., Hylleberg, J., Jyang, B.-Y., Johnston, P., Kirkendale, L., Kleemann, K., Koppka, J., Kříž, J., Machado, D., Malchus, N., Márquez-Aliaga, A., Masse, J.-P., McRoberts, C.A., Middelfart, P.U., Mitchell, S., Nevesskaja, L.A., Özer, S., Pojeta, J., Jr., Polubotko, I.V., Pons, J.M., Popov, S., Sánchez, T., Sartori, A.F., Scott, R.W., Sey, I.I., Signorelli, J.H., Silantiev, V.V., Skelton, P.W., Steuber, T., Waterhouse, J.B., Wingard, G.L., and Yancey, T., 2011, A synoptical classification of the Bivalvia (Mollusca): University of Kansas, Paleontological Contributions, no. 4, p. 1–47.
- Checa, A.G., and Jiménez-Jiménez, A.P., 2003, Evolutionary morphology of oblique ribs of bivalves: *Palaentology*, v. 46, p. 709–724.
- Chen, J.-H., and Yang, S.-Q., 1983, *Eleganuculana*, new genus, and some other bivalves from the Upper Triassic of Kangmar in Xizang: *Acta Palaentologica Sinica*, v. 22, p. 355–358. [in Chinese with English summary]
- Chen, J.-H., Liu, L., and Lan, X., 1983, Veteranellinae, a new subfamily of Nuculanidae (Bivalvia) with classificatory significance of ornamentations in Palaeotaxodonta: *Acta Palaentologica Sinica*, v. 22, p. 616–627. [in Chinese with English summary]
- Cox, L.R., 1960, The preservation of moulds of the intestine in fossil *Nuculana* (Lamellibranchia) from the Lias of England: *Palaentology*, v. 2, p. 262–269.
- Cox, L.R., 1969, General features of Bivalvia, in Moore, R.C., ed., *Treatise on Invertebrate Paleontology*, Part N, Mollusca 6, Bivalvia: Boulder, Co., Geological Society of America, p. N2–N129.
- Douvillé, H., 1916, Les terrains secondaires dans le Massif de Moghara a l'Est de l'Isthme de Suez: *Mémoire de l'Académie des Sciences*, Paris, v. 54, p. 1–184.
- Douvillé, H., 1925, Le Callovien dans le massif de Moghara: avec description des fossils par M. Cossmann: *Bulletin de la Société géologique de France*, série 4, v. 25, p. 305–328.
- Elias, M.K., 1956, Upper Mississippian and Lower Pennsylvanian formations of south-central Oklahoma: *American Association of Petroleum Geologists*, v. Special Volume 16, p. 56–134.
- Fang, Z.-J., Chen, J.-H., Chen, C.-Z., Sha, J.-G., Lan, X., and Wen, S.-X., 2009, Supraspecific taxa of the Bivalvia first named, described, and published in China (1927–2007): *The University of Kansas Paleontological Contributions, New Series*, v. 17, p. 1–157.
- Farag, I.A.M., 1957, On the occurrence of Lias in Egypt: *Egyptian Journal of Geology*, v. 1, p. 49–63.
- Farag, I.A.M., 1959, Contribution to the study of the Jurassic formations in the Maghara massif (northern Sinai, Egypt): *Journal of Geology of the United Arab Republic* (1961 for 1959), v. 3, p. 175–199.
- Farag, I.A.M., and Gatinaud, W., 1960a, Un nouveau genre de Terebratulides dans le Bathonien d'Egypte: *Journal of Geology of the United Arab Republic*, v. 4, p. 77–79.
- Farag, I.A.M., and Gatinaud, W., 1960b, Six espèces nouvelle du genre *Rhynchonella* dans le roches jurassiques d'Egypte: *Journal of Geology of the United Arab Republic*, v. 4, p. 81–87.
- Feldman, H.R., 1987, A new species of the Callovian (Jurassic) brachiopod *Septirhynchia* from northern Sinai: *Journal of Paleontology*, v. 61, p. 1156–1172.
- Feldman, H.R., Owen, E.F., and Hirsch, F., 1991, Brachiopods from the Jurassic of Gebel El-Maghara, northern Sinai: *American Museum Novitates*, no. 3006, p. 1–28.
- Feldman, H.R., Radulović, V.J., Hegab, A.A., and Radulović, B.V., 2012, Taxonomy and paleobiogeography of Late Bathonian brachiopods from Gebel Engabashi, Northern Sinai: *Journal of Paleontology*, v. 86, p. 238–252.
- Fletcher, H.O., 1945, A new genus *Glyptoleda* and a revision of the genus *Nuculana* from the Permian of Australia: *Records of the Australian Museum*, v. 21, p. 293–312.
- Fürsich, F.T., 1982, Upper Jurassic bivalves from Milne Land, East Greenland: *Bulletin Grønlands Geologiske Undersøgelse*, v. 144, p. 5–121.
- Gray, J.E., 1854, A revision of the arrangement of the families of bivalve shells (Conchifera): *The Annals and Magazine of Natural History* (series 2), v. 13, p. 408–418.
- Gu, Z.-W., Huang, B.-Y., Chen, C.-Z., Wen, S.-X., Ma, Q.-H., Lan, X., Xu, J.-T., Liu, L., Wang, S.-M., Wang, D.-Y., Qi, R.-Z., Huang, Z.-Q., Zhan, Z.-M., Chen, J.-H., and Wu, P.-L., 1976, *The Lamellibranch Fossils of China*: Beijing, Science Press, 580 p.
- Harris, G.D., and Palmer, K.V.W., 1946–1947, The Mollusca of the Jackson Eocene of the Mississippi Embayment (Sabine River to Alabama River): *Bulletins of American Paleontology*, v. 30, p. 1–564.
- Hautmann, M., Aghababou, B., and Krystyn, L., 2011, An unusual Late Triassic nuculid bivalve with divaricate shell ornamentation, and the evolutionary history of oblique ribs in Triassic bivalves: *Journal of Paleontology*, v. 85, p. 22–28.
- Hegab, A.A., 1989, New occurrence of Rhynchonellida (Brachiopoda) from the Middle Jurassic of Gebel El-Maghara, Northern Sinai: *Journal of African Earth Sciences*, v. 9, p. 445–453.
- Hegab, A.A., 1991, Biostratigraphic zonation of Bathonian–Callovian rocks from Gebel El-Maghara Northern Sinai, Egypt: *Journal of African Earth Sciences*, v. 13, p. 183–192.
- Hirsch, F., 1980, Jurassic bivalves and gastropods from northern Sinai and southern Israel: *Israel Journal of Earth Sciences*, v. 28, p. 128–163.
- Hodges, P., 2000, The Early Jurassic Bivalvia from the Hettangian and Lower Sinemurian of south-west Britain: *Monograph of the Palaeontographical Society*, London, v. 614, p. 1–64.
- Jaitly, A.K., Fürsich, F.T., and Heinze, M., 1995, Contributions of the Jurassic of Kachchh, western India. IV. The bivalve fauna. Part 1. Subclasses Palaeotaxodonta, Pteriomorpha, and Isofilibranchia: *Beringeria*, v. 16, p. 147–257.
- Kanjilal, S., and Singh, C.S.P., 1973, A new nuculanid genus from the Callovian of Kutch (Gujarat), India: *Proceedings of the Malacological Society*, London, v. 40, 469–471.
- Keeley, M.L., 1994, Phanerozoic evolution of the basins of Northern Egypt and adjacent areas. *Geologische Rundschau*, v. 83, p. 728–742.
- Korobkov, I.A., 1954, *Spravochnik i metodicheskoe Rukovodstvo po tretichnym molluskam Platinchatozhabernye* [Handbook on and Systematic Guide to the Tertiary Mollusca, Lamellibranchia]: Gosud. Nauchno-tech. Issledov. Nefti. Gorno-toplivnoi lit-ri, Leningradskoi Otdelenie. Leningrad Gosstoptekhizdat, 444 p. [in Russian]
- Link, H.F., 1807, Beschreibung der Naturalien-Sammlung der Universität zu Rostock. Abtheilung 3: Rostock, Adler, p. 101–165.
- Linnaeus, C., 1758, *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata*: Holmiae, Laurentius Salvius, v. 2, 824 p.
- Marwick, J., 1924, Palaeontological notes on some Pliocene Mollusca from Hawke's Bay: *Transactions and Proceedings of the New Zealand Institute*, v. 55, p. 191–201.
- Oppel, A., 1856, Die Juraformation Englands, Frankreichs und des südwestlichen Deutschlands: *Jahrbuch des Vereins für Vaterländische Naturkunde Württemberg*, v. 12, p. 121–556.
- Pandey, D.K., and Singh, C.S.P., 1981, A new species of *Indoculana* Kanjilal and Singh (Bivalvia) from the Lower Callovian (Jurassic) of Gora Doonger, in Pachchham Island, District Kachchh (Gujarat, India): *Journal of Paleontology*, v. 55, p. 1296–1297.
- Parnes, A., 1988, Middle Jurassic (Middle Bajocian–Middle Bathonian) ammonites from Gebel Maghara, Sinai, Egypt, in the collections of the Geological Survey of Israel: *Journal of African Earth Sciences*, v. 7, p. 707–733.
- Patte, E., 1926, Études paléontologiques relatives à la géologie de l'est du Tonkin (Paléozoïque et Trias): *Bulletin du Service Géologique de l'Indochine*, v. 15, p. 1–231.
- Pelseuer, P., 1889, Sur la classification phylogenetique de pelecypods: *Bulletin Scientifique de la France et de la Belgique*, v. 20 (sér. 3, no. 2), p. 27–52.
- Picard, L., and Hirsch, F., 1987, The Jurassic Stratigraphy in Israel and Adjacent Countries: Jerusalem, The Israel Academy of Sciences and Humanities, 106 p.
- Roth von Telegd, K., 1914, Felső-oligocén fauna Magyarországból: *Geologica Hungarica*, v. 1, p. 5–77.
- Savazzi, E., 1982, Shell sculpture and burrowing in the bivalves *Scapharca inaequivalvis* and *Acanthocardia tuberculata*: *Stuttgarter Beiträge zur Naturkunde, Serie A*, no. 353, p. 1–12.
- Savazzi, E., 1983, Constructional morphology of cardiid bivalves: an overview: *Bollettino della Società Paleontologica Italiana*, v. 22, p. 87–91.
- Seilacher, A., 1972, Divaricate patterns in pelecypod shells: *Lethaia*, v. 5, p. 325–343.

- Seilacher, A., 1973, Fabricational noise in adaptive morphology: *Systematic Zoology*, v. 22, p. 451–465.
- Sha, J.-G., Fürsich, F.T., Smith, P.L., and Wang, L., 1998, Palaeotaxodonta, Pteriomorpha, and Isofilibranchia (Bivalvia) from the Jurassic of the main ridge of the Tanggula Mountains, Qinghai-Xizang Plateau, China: *Beringeria*, v. 21, p. 3–55.
- Stanley, S.M., 1969, Bivalve mollusk burrowing aided by discordant shell ornamentation: *Science*, v. 166, p. 634–635.
- Stanley, S.M., 1970, Relation of shell form to life habits in the Bivalvia (Mollusca). *Memoir of the Geological Society of America*, v. 125, p. 1–296.
- Stanley, S.M., 1981, Infaunal survival: alternative functions of shell ornamentation in the Bivalvia (Mollusca): *Paleobiology*, v. 7, p. 384–393.
- Terquem, O., and Piette, E., 1865, *Le Lias inférieur de l'Est de la France comprenant la Meurthe, la Moselle, Le Grand-Duché de Luxembourg, la Belgique et la Meuse: Mémoires de la Société géologique de France*, v. 8, p. 1–175.
- Waterhouse, J.B., 1965, Palaeotaxodont bivalves from the Permian of New Zealand: *Palaeontology*, v. 7, p. 630–655.
- Wilton, C.P.N., 1830, *Memoir on the geology of the shore of the Severn, in the parish of Awre, Gloucestershire: Quarterly Journal of Science, Literature and the Arts*, v. Jan.–June, p. 64–73.
- Yonge, C.M., 1939, The protobranchiate Mollusca: a functional interpretation of their structure and evolution: *Philosophical Transactions of the Royal Society of London, Series B*, v. 230, p. 79–147.
- Zhang, R.-J., Wang, D.-Y., and Zhou, Z.-R., 1977, Bivalvia, in Hubei Institute of Geology, Bureau of Geology and Mineral Resources of Henan Province, Bureau of Geology and Mineral Resources of Hubei Province, Bureau of Geology and Mineral Resources of Hunan Province, Bureau of Geology and Mineral Resources of Guangdong Province, and Bureau of Geology and Mineral Resources of Guangxi Autonomous Region, eds., *Paleontological Atlas of Central Southern China: Beijing, Geological Publishing House*, v. 2, p. 470–533; v. 3, p. 4–65. [in Chinese]

Accepted 5 December 2016