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Revision of Jurassic Protobranch Bivalves from Gebel Maghara, northern Sinai, Egypt

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Abstract.—The Jurassic rocks of Gebel Maghara, northern Sinai, Egypt, contain a well-preserved and highly diverse macrobenthic fauna, dominated by bivalves. This fauna, particularly bivalves and gastropods, have received little attention in the last 100 years. In an attempt to provide a sound database on the marine bivalve diversity of Egypt during the Jurassic period, a first faunal group, the protobranch bivalves, is reviewed in detail. Sixteen taxa (three of them new), belonging to two orders, five families, and nine genera are systematically described and compared to closely related Jurassic taxa from various locations, particularly in Europe and India. New species are *Nuculoma douvillei* n. sp., *N. sinaiensis* n. sp., and *Palaeoneilo aegyptiaca* n. sp. In addition, *Palaeonucula cuneiformis* (J. de C. Sowerby), *P. muensteri* (Goldfuss), *Dacryomya diana* (d'Orbigny), *D. lacryma* (J. de. C. Sowerby), and *Praesaccella juriana* Cox are identified from Jurassic strata of Egypt for the first time. The younger records of the genus *Palaeoneilo* have not been accepted by some researchers**,** since almost all exhibit only limited features. The genus occurs with certainty in the Middle Jurassic (Bajocian−Bathonian) rocks of Egypt, based on well-preserved external and internal characters. Similarly, *Dacryomya* and *Ryderia* from Bathonian−Kimmeridgian rocks of Egypt are younger than previously recorded from other parts of the world. The identified genera have wide geographic ranges and have been reported from different faunal provinces, which suggests that latitudinal climate differences did not influence their distribution pattern to a great extent.

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Introduction

The Gebel Maghara displays a well-exposed marine Middle to Upper Jurassic succession, which contains, apart from some ammonites, a diverse and well-preserved benthic macrofauna, dominated by bivalves, gastropods, and brachiopods. The most comprehensive study of the Jurassic rocks of Gebel Maghara is that of Al Far (1966), who focused on sedimentologic and stratigraphic aspects. With respect to paleontology, some fossil groups, particularly bivalves and gastropods, have been neglected from a taxonomic point of view since the pioneer study of Douvillé in the early twentieth century (Douvillé, 1916). Although limited research has been carried out since then (e.g., brachiopods: Farag and Gatinaud, 1960; Hegab, 1989, 1991a, b; Feldman et al., 1991, 2012; Ali et al., 1997; bivalves and gastropods: Hirsch, 1980; Abdelhamid, 2002; Khalil, 2003; ammonites: Douvillé, 1916; Arkell, 1952; Parnes, 1988; echinoids: Fourtau, 1924), a comprehensive modern taxonomic study of some groups such as the bivalves and gastropods is still lacking. Abdelhady (2014) and Abdelhady and Fürsich (2014, 2015a, b, c) concentrated mainly on litho- and biostratigraphy, paleobiogeography, and paleoecology. The latter authors listed 232 benthic and nektonic macrofaunal taxa from Gebel Maghara, which were dominated by bivalves (60 species), followed by gastropods (52), ammonites (34), brachiopods (29), corals (28), echinoids and crinoids (16), sponges (7), serpulids (5), and a single crustacean species (Abdelhady, 2014, appendix B), but did not provide a taxonomic analysis. Therefore, their collections were given to the present authors for further processing and revising. Protobranch bivalves are common elements of fossil assemblages throughout the Phanerozoic, restricted to fully marine environments. Due to their detritivorous feeding habits, they only live in organic-rich bottoms as very active shallow burrowers (e.g., McAlester and Rhoads, 1967; Nicol, 1969, 1972; Damborenea, 1987; Damborenea and Pagani, 2019). The present protobranch bivalve specimens are well preserved, mostly articulated, and their internal characters, such as hinge teeth and muscle scars, can be recognized easily. The present study is the second taxonomic analysis of protobranch bivalves from the area, following the Ayoub-Hannaa et al. (2017) study of *Costinuculana magharensis* Ayoub-Hannaa, Abdelhady, and Fürsich, 2017.

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Locality and geological setting

Gebel Maghara is a dome-like structure covering an area of ∼400 km^2, situated in northern Sinai, 50 km south of the Mediterranean coast (Fig. 1.1). During the Triassic, the Tethys north of Gondwana started to rift and led to the formation of small intracratonic basins (horst-graben systems) with differential subsidence in northern Egypt (Keeley, 1994; Ayyad et al., 1998; Garfunkel, 1998; Moustafa et al., 1998). The opening of these basins started in Late Triassic–Early Jurassic time (Biju-Duval et al., 1979; Garfunkel and Derin, 1984; Mart, 1987). Gebel Maghara lies in one of these basins, consisting of an extensional half graben-like structure (Fig. 1.2), and comprises the thickest and most complete Jurassic outcrop in northern Sinai (1800 m; Al Far, 1966; Keeley, 1994). The stratigraphic scheme of Gebel Maghara is based mainly on Al Far (1966), who provided a complete classification and description of the Jurassic strata. Later, Hirsch (1980) and Picard and Hirsch (1987) modified Al Far's classification and compared the succession at Gebel Maghara with that of the adjacent Negev desert. According to Al Far (1966), the marine sediments are represented by the Rajabiah (Lower Jurassic), Bir Maghara, and Masajid formations, whereas the continental sediments include the Mashabba (Lower Jurassic), Shusha, and Safa formations. Abdelhady (2014) and Abdelhady and Fürsich (2015a, b, c) studied four sections in detail, from west to east Gebel Homayir (1190 m thick), Gebel Arousiah (1177 m thick), Gebel Engabshi (1025 m thick), and Gebel Mowerib (995 m thick) (Fig. 1.2). Three of them (Gebel Homayir, Gebel Arousiah, and Gebel Engabashi) belong to the western flank of the anticline with a dip of the strata varying from 15–30°, while the Gebel Moweribsection is exposed on the eastern flank dipping at an angle >60° in some parts.

The Jurassic succession of these sections has been subdivided into seven formations from older to younger, the Mahl, Bir Maghara, Safa, Kehailia, Arousiah, Tauriat, and Masajid formations (Fig. 1.3). All of these formations were originally introduced by Al Far (1966), Picard and Hirsch (1987), and recently revised by Abdelhady (2014). Figure 2 shows the lithologs, lateral facies changes, faunal content, and correlation of the sections studied. In addition, the age estimation of the studied section was resolved based on ammonites (Abdelhady and Fürsich, 2015a).

Materials and methods

Several thousand specimens of the benthic and nektonic macrofauna (∼9130) were collected by F.T. Fürsich in 1993 and by A.A. Abdelhady and F.T. Fürsich in 2012 from the Jurassic succession of Gebel Maghara. During that time, four sections, Gebel Homayir, Gebel Arousiah, Gebel Engabshi, and Gebel Mowerib, corresponding to an ∼20 km long W-E transect, were studied and measured using a Jacob Staff, hand lens, and 10% concentrated HCl. These studies included detailed

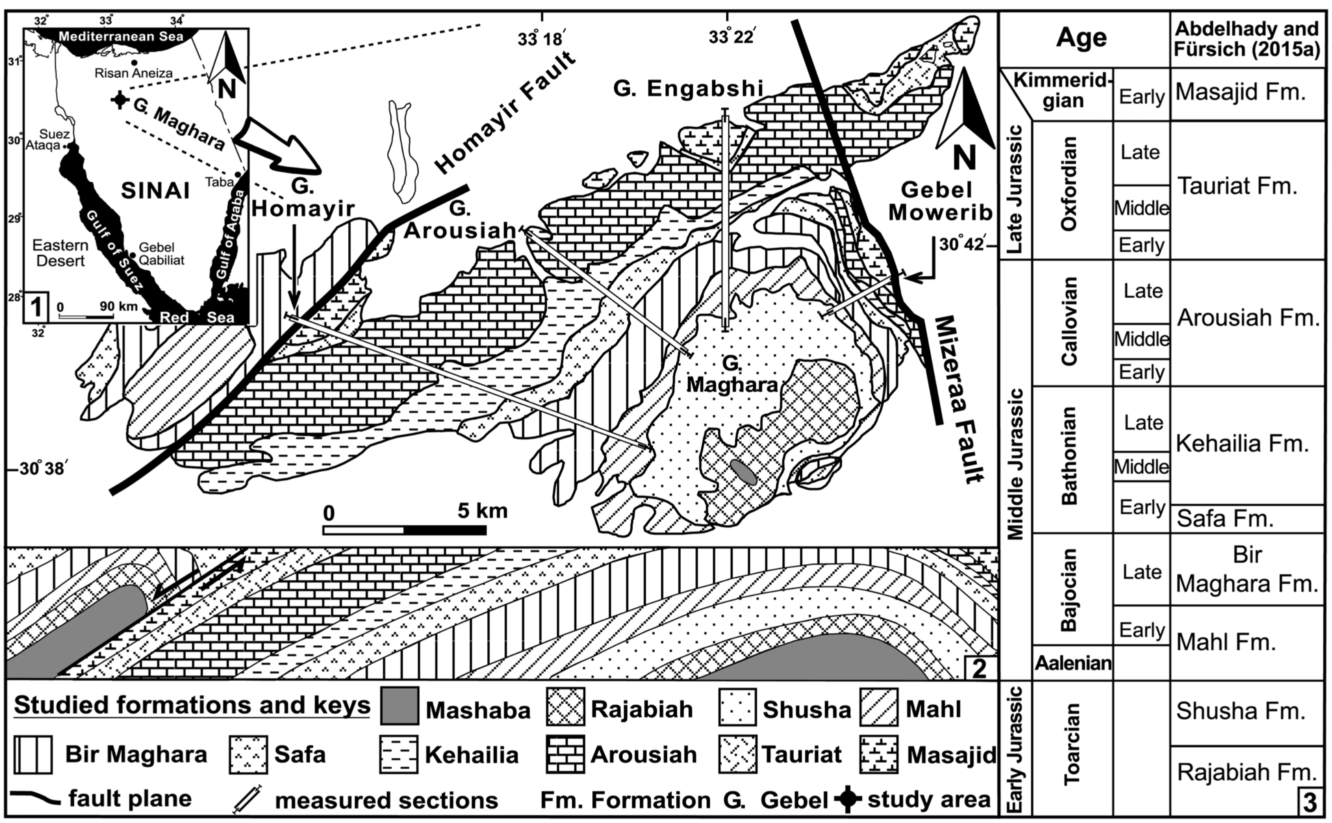

Figure 1. (**1**) Locality map of Gebel Maghara; (**2**) cross-section and geologic map (modified after Al Far, 1966; Hirsch, 1980) with position of the investigated sections of the Jurassic succession of Gebel Maghara; (**3**) the Jurassic subdivision and equivalent formations from older to younger (after Abdelhady and Fürsich, 2015a).

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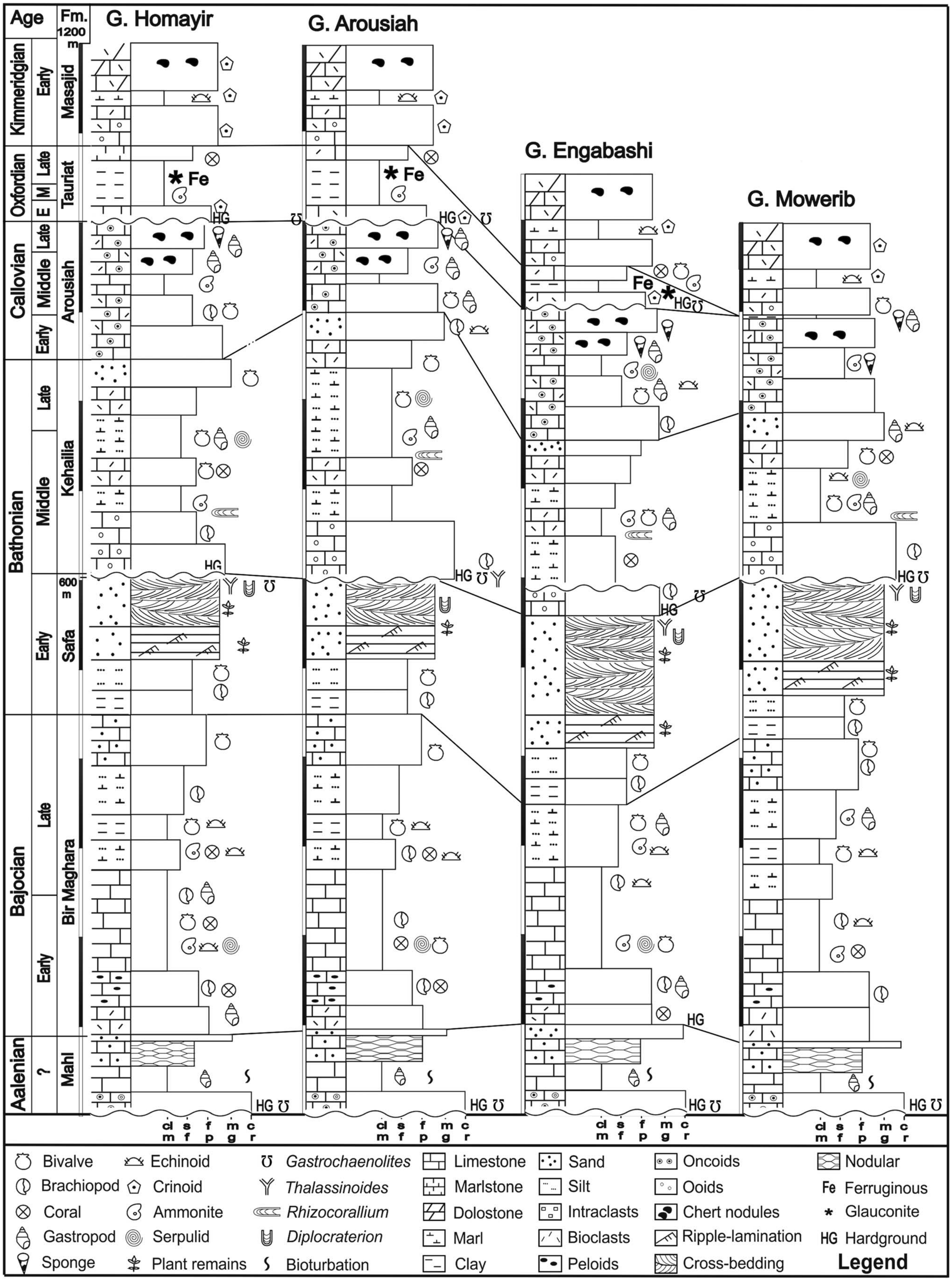

Figure 2. Logged sections and their correlations based on ammonites and lateral facies changes (after Abdelhady and Fürsich, 2014, 2015a, b). Vertical scales marked in 100-m increments.

documentation of the lithology, bed contacts, sedimentary structures, trace fossils, taphonomic observations, and bed by bed collecting of macrofossils. The collected macrofauna was identified during 2012–2014 as a part of a Ph.D. project by A.A. Abdelhady (2014). All specimens have been deposited in the collections of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich under the prefix BSPG 2014V.

The protobranch bivalve specimens are generally very well preserved, mostly articulated, and preserved with shell. A few specimens are composite molds and laterally deformed due to compaction. Most specimens have been prepared mechanically and cleaned by steel needles under a binocular microscope. Air abrasive was used to clean hinge and teeth. In order to obtain complete hinge structures, the rock matrix that covered the hinge plate was removed using diluted hydrogen peroxide (H_2O_2). The specimens were photographed after having been coated with ammonium chloride to enhance details of ornamental features and other internal features such as teeth and muscle scars. Identification was greatly supported by the Jurassic bivalve catalogue at the GeoZentrum Nordbayern of the Friedrich-Alexander-Universität, Erlangen. This catalogue contains photocopies of ∼95% of all figured Jurassic bivalves, which have been identified from different localities worldwide. In addition, each entry includes information on locality, stratigraphic level, authors, and publication date.

The systematic classification of the bivalves follows that of Carter et al. (2011). The synonymy lists contain only references, which have been carefully checked by the authors, beginning with the first reference of the particular taxon, and followed by literature records from the Jurassic of Egypt. More comprehensive synonymies can be found in the references cited. Abbreviations in synonymy lists and open nomenclature follow the indications given by Matthews (1973) and Bengtson (1988) to indicate the degree of confidence in allocation of each entry. In particular, the period in front of the year means the authors accept the responsibility for attaching this reference to the species under discussion.

Morphological terminology follows the glossary of Cox (1969) in the Treatise on Invertebrate Paleontology. The terminology of hinge teeth follows Babin (1966) and Carter et al. (2012; Fig. 3.4). Measured dimensions and terminology of teeth are given in Figure 3.1–3.3. Linear measurements (taken with a Vernier caliper, accurate to 0.1 mm) are in millimeters. Abbreviations for dimensions are: L = length, La = anterior length, Lp = posterior length, H = height, Iav = inflation of articulated valves, and Isv = inflation of a single valve. In the description of taxa, very small refers to a length of 1–5 mm

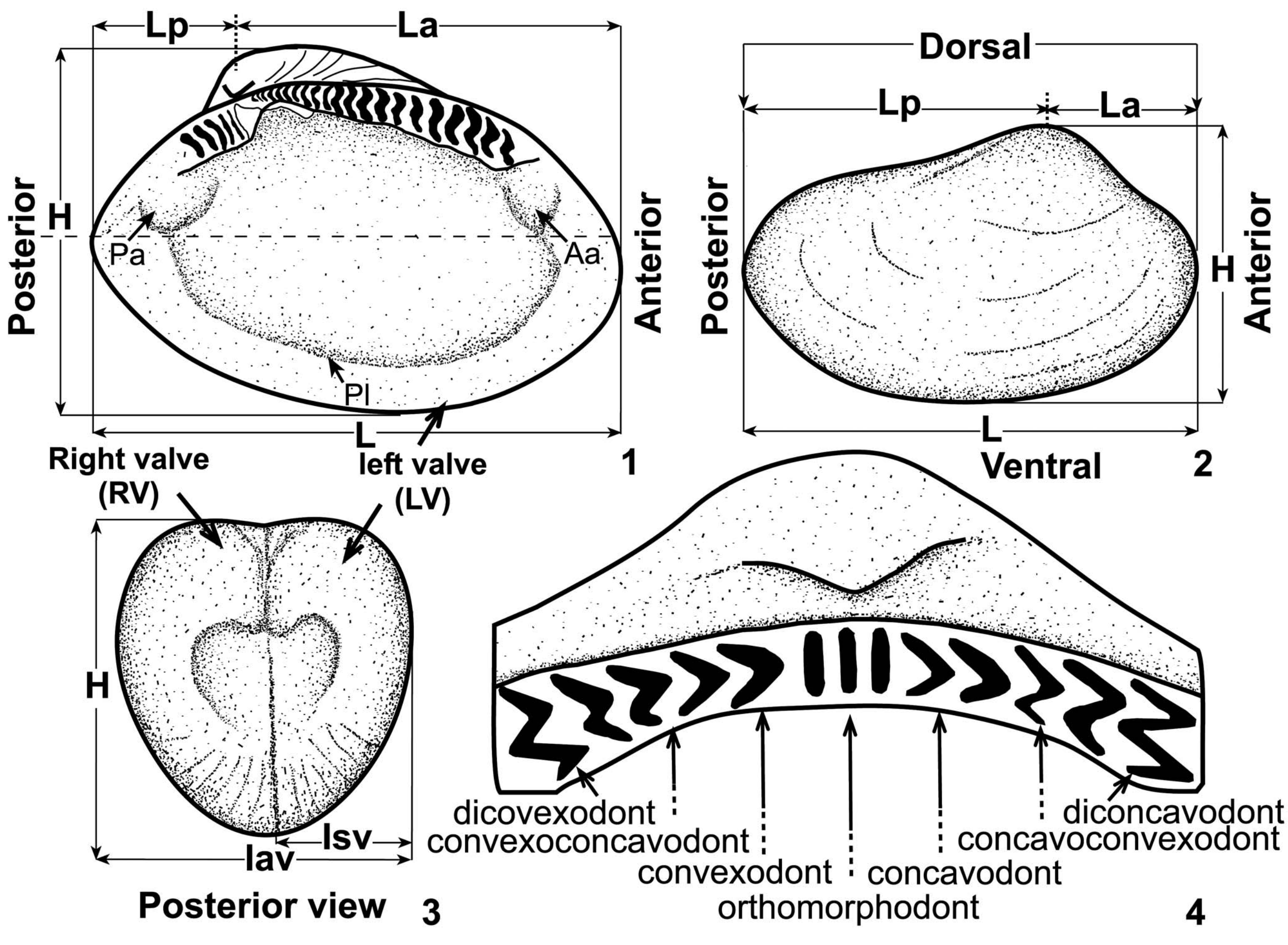

Figure 3. Measured dimensions and orientation of selective protobranch bivalves. (**1, 3**) *Nuculoma*, (**2**) *Palaeoneilo*, (**4**) terminology of dentition, based on Babin (1966, fig. 3) and Carter et al. (2012, fig. 207). See text for abbreviations.

and small to a length of 6–15 mm. A principal component analysis (PCA) using the PAST software, version 2.16 (Hammer et al., 2001), on a variance-covariance matrix of the log-transformed variables was carried out to clarify the morphological relationships of some of the taxa.

Repositories and institutional abbreviations.—All specimens examined in this study are deposited in the collections of the Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany, under the prefix BSPG 2014V and PIW 1991 III.

Systematic paleontology

Class Bivalvia Linnaeus, 1758
Clade Eubivalvia Carter et al., 2011
Subclass Protobranchia Pelseneer, 1889 (= Palaeotaxodonta Korobkov, 1954)
Superorder Nuculiformii Dall, 1889 (= Foliobranchia Ménégaux, 1889)
Order Nuculida Dall, 1889
Superfamily Nuculoidea Gray, 1824
Family Nuculidae Gray, 1824
Genus *Nuculoma* Cossmann, 1907 (= *Habonucula* Singh and Kanjilal, 1977)

Type species.—*Nucula castor* d'Orbigny, 1850, from the Callovian of France, monotypy; figured by Cottreau (1925, p. 153, pl. 39, figs. 23, 24).

Remarks.—Singh and Kanjilal (1977, p. 189) erected the new genus *Habonucula* from the lower Callovian rocks of the Kachchh Basin, India, based on the absence of escutcheon and smooth inner shell margins. Jaitly et al. (1995, p. 155) pointed out that these diagnostic features are not sufficient enough to erect a new genus, and therefore they regarded *Habonucula* as a junior synonym of *Nuculoma*. The latter view is followed here. *Nuculoma* can be distinguished from other Jurassic nuculid genera by its strongly opisthogyrate enrolled umbones, which usually overhang the posterior margin, and its surface, which carries numerous fine commarginal riblets (Jaitly et al., 1995). *Nuculoma* has a wide stratigraphic range, from the Lower Jurassic to Lower Cretaceous (e.g., Berriasian–lower Hauterivian) of northern Central Siberia (Sanin, 1976) and to Valanginian strata of eastern England (Kelly, 1984).

Nuculoma douvillei new species
Figures 4, 5.1–5.19, 6, 7

*1916 *Nucula variabilis*? Douvillé, p. 61, pl. 5, figs. 51–55 (non Sowerby, 1825).
v.2014 *Nuculoma variabilis*; Abdelhady, p. 72, fig. 5.4G, H.
v.2014 *Nuculoma variabilis*; Abdelhady and Fürsich, p. 181, fig. 6G, H.
v.2015a *Nuculoma variabilis*; Abdelhady and Fürsich, p. 41.

Holotype.—Articulated specimen BSPG 2014V 309/1 in shell preservation (Fig. 4.1–4.5), from the middle–upper Bathonian Kehailia Formation, Gebel Homayir, Sinai, Egypt.

Paratypes.—Three hundred and twelve specimens, in shell preservation, mostly articulated from Bathonian–Callovian rocks of the Maghara area (Fig. 6.1): 121 specimens from the middle–upper Bathonian Kehailia Formation (ammonite *Clydomphalites clydocromphalus* Zone), Gebel Homayir (BSPG 2014V 173/1–21; 174/1; 175/1–28; 308/1–53; 309/2–19); 19 specimens from the Kehailia Formation, Gebel Arousiah (BSPG 2014V 4/1–19); 17 from the same formation, Gebel Mowerib (BSPG 2014V 311/1–17); a single specimen from the Kehailia Formation, Gebel Engabashi (BSPG 2014V 167/1); 22 specimens from the upper third of the lower Bathonian Safa Formation, western Bir Maghara (BSPG 2014V 310/1–22); and 132 specimens from the Callovian Arousiah Formation (ammonite *Pachyceras lalandeanum*/*Erymnoceras philbyi* Zone), Gebel Mowerib (BSPG 2014V 178/1–132).

Diagnosis.—Small to very small, strongly oblique *Nuculoma*, variable in outline, ranging from elongated-ovate to subtrapezoidal, from sub-trigonal to rounded; higher than long or longer than high; strongly inflated; with smooth inner margins, no escutcheon, no lunule, sharply pointed and strongly enrolled beaks, a variable anterior margin (mostly truncated to slightly convex, occasionally narrow and strongly convex), a well-developed anterior umbonal ridge, highly variable anterior and posterior teeth in shape and size; upward-curved, shoehorn-shaped subhorizontal chondrophore in both valves; regular, widely spaced commarginal ribs at mid-flank, occasionally intercalated with faint commarginal growth lines, and smooth anterior and posterior flanks.

Occurrence.—Middle Bathonian to upper Callovian, Gebel Maghara, North Sinai (Fig. 6.2).

Description.—Shell small to very small, oblique; shape and outline variable, ranging from elongated-ovate (higher than long or longer than high; Table 1) to subtrapezoidal, from sub-trigonal to subrounded, equivalved, strongly inequilateral, and strongly inflated (Iav/L: 0.81–1.19). Maximum inflation slightly below umbo. Posterior end blunt, meeting ventral margin in rounded curve. Anterior margin variable in outline, ranging from truncated to sub-truncated, from slightly to strongly convex (Fig. 4.37–4.40), and meeting ventral margin in blunt angle. Internal margins smooth, umbonal cavity deep. No escutcheon and lunule. Umbones strongly inflated, triangular, elevated above hinge, and extremely enrolled posteriorly. Beak sharply pointed and opisthogyrate. Anterior umbonal ridge well developed dorsally, fading towards anteroventral corner, and separating a narrow, smooth anterior flank from rest of valve (Fig. 4.8, 4.28, 4.31). Anterior adductor muscle scar larger than posterior one, elongated-ovate to subrectangular, and located close to anterior margin (Fig. 5.2, 5.3). Posterior adductor muscle scar small, subrounded and located close to posterior margin below posterior teeth. Pallial line complete, without sinus. Hinge plate broad with strong, unequal teeth and sockets. Anterior part of hinge with 12–20 unequal orthomorphodont to slightly diconcavodont teeth, gradually increasing in size from anterior end to the middle of anterior hinge, where the teeth are

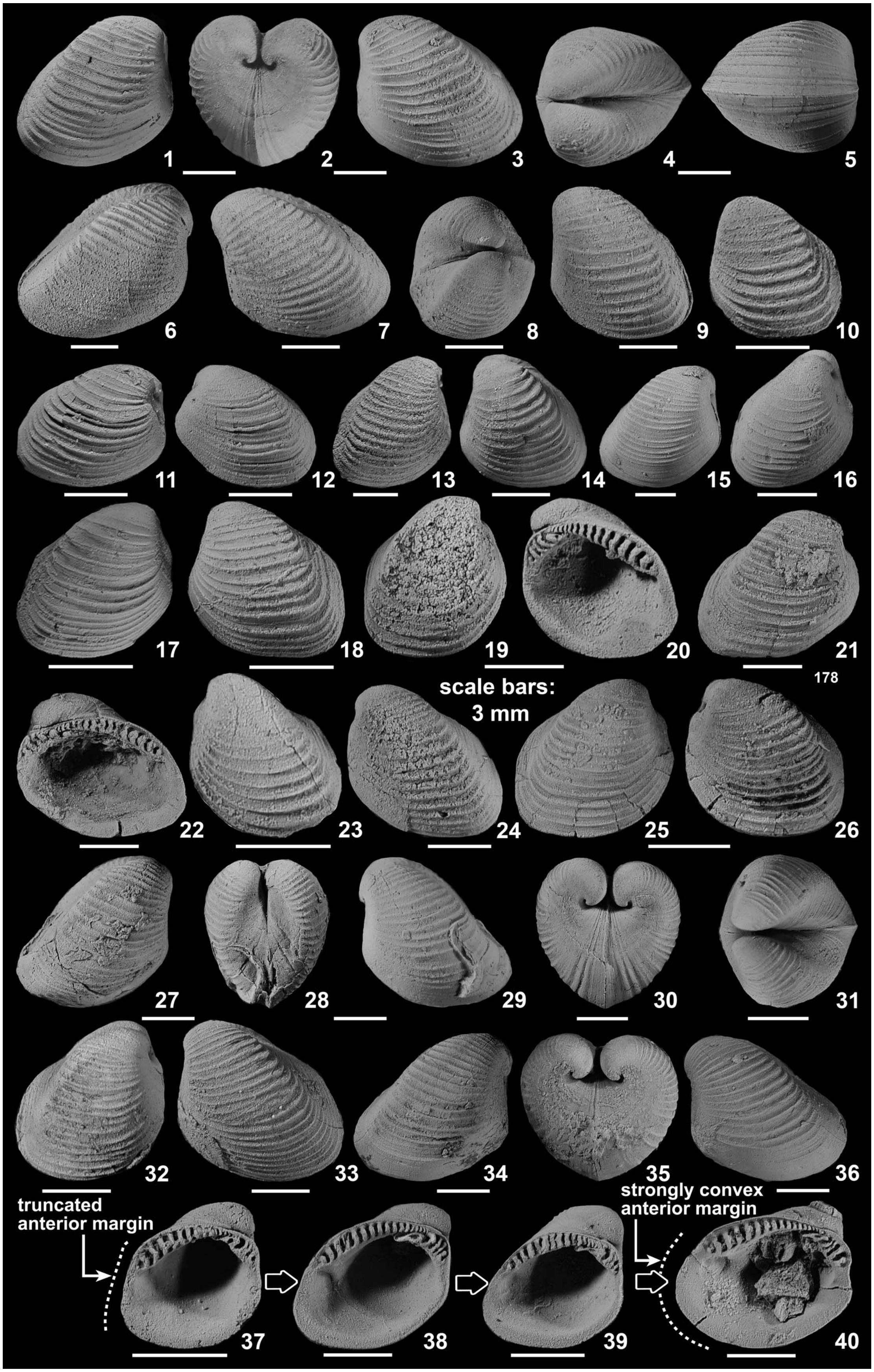

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Figure 4. (**1–40**) Variation in outline of *Nuculoma douvillei* n. sp. from the Bathonian–Callovian rocks of the Maghara area. (**1–5**) BSPG 2014V 309/1, holotype, Kehailia Formation, Gebel Homayir, (**1**) left valve exterior, (**2**) posterior view of articulated valves showing the absence of escutcheon, (**3**) right lateral view, (**4**) dorsal view, (**5**) ventral view. (**6–9**) Paratypes, Kehailia Formation, Gebel Homayir; (**6**) BSPG 2014V 173/1, left lateral view, (**7**) BSPG 2014V 173/1, right valve exterior, (**8**) BSPG 2014V 173/2, dorsal view showing a well-developed anterior umbonal ridge, (**9**) BSPG 2014V 173/3, right lateral view. (**10**) BSPG 2014V 167/1 paratype, Kehailia Formation, Gebel Engabashi, right lateral view showing widely spaced commarginal ribs intercalated between faint commarginal growth lines. (**11–16**) Paratypes, Kehailia Formation, Gebel Homayir; (**11**) BSPG 2014V 309/2, left valve, (**12**) BSPG2014V 309/3, right lateral view, (**13**) BSPG2014V 309/4, left lateral view, (**14**) BSPG2014V 309/5, right lateral view, (**15, 16**) BSPG 2014V 309/6 and BSPG 2014V 309/67, respectively, left lateral views. (**17–23**) Paratypes, Arousiah Formation, Gebel Mowerib; (**17**) BSPG 2014V 178/1, left lateral view, (**18**) BSPG 2014V 178/2, right lateral view, (**19, 20**) BSPG 2014V 178/3, left lateral view and left valve interior, respectively, (**21, 22**) BSPG 2014V 178/4, exterior and interior of left valve, respectively, (**23**) BSPG 2014V 178/5, exterior of right valve. (**24**) Paratype, BSPG 2014V 4/1, Kehailia Formation, Gebel Arousiah, right valve exterior. (**25–36**) Paratypes, Kehailia Formation, Gebel Homayir; (**25, 26**) BSPG 2014V 308/1, left lateral view, showing the subrounded outline of the species, and right lateral view, respectively, (**27–29**) BSPG 2014V 308/2, left lateral view, showing strongly oblique form of species, anterodorsal view, and right lateral view, respectively, (**30**) BSPG 2014V 308/3, posterior view, (**31**) BSPG 2014V 308/4, dorsal view, showing a well-developed anterior umbonal ridge, (**32**) BSPG 2014V 308/5, left valve, (**33**) BSPG 2014V 308/6, right valve, (**34–36**) BSPG 2014V 308/7, left lateral view, posterior view, showing the strongly inflated valves, and right lateral view, showing narrow rounded anterior margin; (**37**) BSPG 2014V 309/8, paratype, Kehailia Formation, Gebel Homayir, right lateral view showing a truncated anterior margin. (**38–40**) Paratypes, Safa Formation, western Bir Maghara; (**38**) BSPG 2014V 310/1, right valve interior, (**39**) BSPG 2014V 310/2, right lateral view, showing a slightly convex anterior margin, (**40**) BSPG 2014V 310/3, right lateral view. Specimens in (**37–40**) show increasingly convex anterior margins. Scale bars = 3 mm.

exceptionally large and thick, followed by an abrupt decrease in size till umbo (Fig. 5.3–5.5). Posterior hinge much shorter and broader than anterior one with 3–5 very large unequal teeth that are orthomorphodont and perpendicular to posterodorsal margin at posterior end, becoming strongly concavodont towards beak (occasionally convexodont in few specimens; Fig. 5.14, 5.19), gradually increasing in size towards umbo. Anterior and posterior valves with upward-curved, short, shoehorn-shaped subhorizontal chondrophore (Fig. 5.7, 5.9). Ornamentation consisting of regular, fine, widely spaced commarginal riblets on the middle flank of valve, decreasing in strength towards anterior and posterior margins (Fig. 4.3, 4.9, 4.34). Interspaces between riblets, occasionally carrying faint commarginal growth lines.

Etymology.—In honor of Prof. Dr. Joseph Henri Ferdinand Douvillé, French professor of paleontology at the École des Mines around the turn of the twentieth century, who documented the Jurassic fauna of Gebel Maghara for the first time.

Measurements.—See Table 1.

Remarks.—With respect to shell outline, *Nuculoma douvillei* n. sp. is a very variable species, ranging from subtrapezoidal to strongly oblique elongated-ovate with intermediate forms. Grouping, which was performed based on shell outline according to their specific H/L ratio, resulted in four groups (termed morphotypes / forms): form A (H/L = 0.80−0.90), form B (H/L = 0.91−1.02), form C (H/L = 1.03−1.10), and form D (H/L >1.10). PCA was applied to determine the clustering of the individuals and whether manual grouping has any statistical ground. Based on the variance-covariance matrix of the log-transformed variables (L, H, Iav, La, H/L, Iva/L), the first Principal Component (PC1) is strongly positively correlated with shell size (e.g., length [L], height [H], and length of anterior area [La]) and accounts for 84.5% of the variation in the data. However, there is no distinction among the four forms with respect to their range on PC2 (Fig. 7.1). In contrast, shell outline (H/L) is strongly positively correlated with Principal Component PC2 (= 8.427%; Fig. 7.3), where forms with higher H/L values have higher positive values on the PC2-axis (Fig. 7.1). The four forms (A–D) of *Nuculoma douvillei* n. sp. have significantly different PC2 (shell outline, H/L) values ($p < 0.001$; Fig. 7.2). PC1 versus PC3 shows high overlapping of the four forms. Moreover, the boxplot of the forms based on PC1 (shell size) shows that the four forms of *N. douvillei* n. sp. have a very similar size range except form B (Fig. 7.6). In summary, all forms are similar in size range but significantly differ in outline and inflation. The high overlapping of the four forms indicates that they belong to a single species (Fig. 7.1, 7.4).

Nuculoma douvillei n. sp. can be distinguished from other closely related Middle to Upper Jurassic *Nuculoma* species by having extremely opisthogyrate enrolled beaks, strongly inflated valves (Iav/L: 0.81–1.19), a well-developed anterior umbonal ridge, smooth inner margins, widely spaced commarginal ribs, a subtruncated to slightly convex anterior margin, and in lacking a lunule and escutcheon. The closest species is "*Habonucula*" *agrawali* Singh and Kanjilal, 1977, from the Lower Callovian of western India (Singh and Kanjilal, 1977, p. 190, pl. 1, figs. 1–12). The latter species resembles *N. douvillei* n. sp. in lacking escutcheon and lunule, but differs in having a more elongated-ovate and smooth valve (H/L = 0.67, holotype as opposed to 1.10 on average; Table 1), a less-incurved umbo, irregular fine commarginal ribs, in lacking an anterior umbonal ridge, and in being less inflated (Iav/L = 0.29 as opposed to 0.96 on average). *Nucula variabilis* J. de C. Sowerby, 1825 (p. 117, pl. 475, fig. 2) from the Middle Jurassic of England differs from the present species by having a more centrally placed umbo, a less-incurved beak, a well-defined escutcheon, and in being less inflated and smooth. Douvillé (1916) doubtfully identified *Nuculoma variabilis* from the Middle Jurassic rocks of Egypt (Gebel Arousiah, Sinai). Recently, Abdelhady (2014) and Abdelhady and Fürsich (2014, 2015a) followed Douvillé and assigned their specimens, which had been collected from the same area (Gebel Arousiah), to *N. variabilis*. In fact, the specimens figured by Douvillé (1916) and Abdelhady and Fürsich (2014, 2015a) are identical to *N. douvillei* n. sp., and therefore, have been included in the latter.

Although *N. castor* (d'Orbigny, 1850) of Cossmann in Thiéry and Cossmann (1907, p. 55, pl. 2, figs. 14, 15) from the Callovian of France also has an oblique valve, it differs from *N. douvillei* n. sp. by its much more oblique valve, strongly convex posterior and ventral margins, a less-incurved umbo, a smooth valve, and in being less inflated and more elongated than the present species. With respect to shell size and outline, *Nucula lacroixi* Flamand, 1911, from the Bathonian of Algeria

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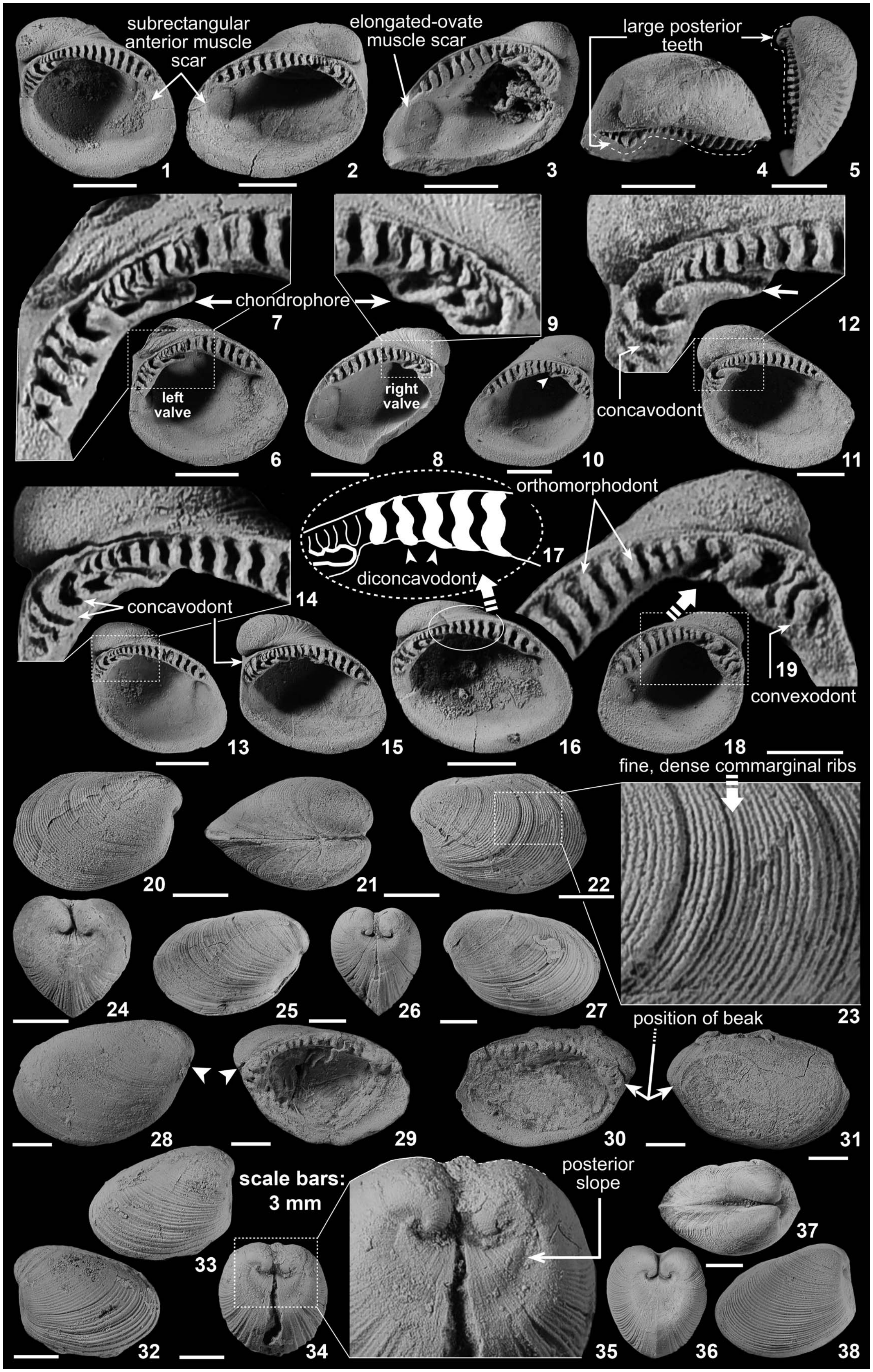
subrectangular anterior muscle scar
elongated-ovate muscle scar
large posterior teeth
1
2
3
4
5
chondrophore
7
9
12
left valve
right valve
concavodont
6
8
10
11
orthomorphodont
17
diconcavodont
14
concavodont
19
convexodont
13
15
16
18
fine, dense commarginal ribs
20
21
22
24
25
26
27
23
position of beak
28
29
30
31
scale bars: 3 mm
posterior slope
33
37
32
34
35
36
38

Figure 5. (**1–19**) Internal characters of *Nuculoma douvillei* n. sp. from the Bathonian–Callovian rocks of the Maghara area. (**1, 2**) Paratypes, Arousiah Formation, Gebel Moweri; (**1**) BSPG 2014V 178/6, left lateral view, (**2**) BSPG 2014V 178/7, right lateral view showing subrectangular anterior muscle scar and small rounded posterior muscle scar; (**3**) BSPG 2014V 310/4, paratype, Safa Formation, western Bir Maghara, incomplete right valve showing the elongated ovate anterior muscle scar; (**4**) BSPG 2014V 178/8, paratype, Arousiah Formation, Gebel Moweri, dorsal view of left valve showing abnormally large posterior teeth (arrowed). (**5–10**) Paratypes, Safa Formation, western Bir Maghara; (**5**) BSPG 2014V 310/5, posterodorsal view, showing large posterior teeth, (**6, 7**) BSPG 2014V 310/6, left lateral view and close-up showing shoehorn-shaped chondrophores (arrowed), respectively, (**8, 9**) BSPG 2014V 310/7, incomplete right valve and close-up showing a short subhorizontal chondrophore, respectively, (**10**) BSPG 2014V 310/8, right lateral view, with deep umbonal cavity; (**11, 12**) BSPG 2014V 309/9, paratype, Kehailia Formation, Gebel Homayir, left lateral view, interior and close-up showing concavodont teeth (arrowed) with short chondrophore; (**13, 14**) BSPG 2014V 178/9, paratype, Arousiah Formation, Gebel Moweri, interior left lateral view and close-up showing the large strongly concavodont teeth close to beak, respectively; (**15**) BSPG 2014V 309/10, paratype, Kehailia Formation, Gebel Homayir, left lateral view. (**16, 17**) BSPG 2014V 178/10, paratype, Arousiah Formation, Gebel Moweri, interior left lateral view and sketch of hinge showing slightly diconcavodont teeth, respectively; (**18, 19**) BSPG 2014V 310/9, paratype, Safa Formation, western Bir Maghara, right lateral view and close-up showing convexodont teeth of posterior hinge (arrowed), respectively. (**20–38**) *Nuculoma sinaiensis* n. sp. from the upper Lower Jurassic (Toarcian) to Middle–Upper Jurassic (Bajocian–Callovian and lower Kimmeridgian) of Gebel Maghara; (**20–24**) BSPG 2014V 303/1, holotype, Bir Maghara Formation, Gebel Arousiah; (**20**) left lateral view, (**21**) anterodorsal view showing the absence of a lunule, (**22**) right lateral view, (**23**) close-up showing fine, dense commarginal ribs, (**24**) posterior view of articulated valves showing the absence of escutcheon. (**25–27**) BSPG 2014V 313/1, paratype, Masajid Formation, western Bir Maghara; (**25**) left lateral view, (**26**) posterior view of articulated valves, (**27**) right lateral view; (**28–31**) paratypes, Masajid Formation, western Bir Maghara; (**28, 29**) left valve exterior and left valve interior showing terminal umbo (arrowed), (**30, 31**) BSPG 2014V 312/2, right valve interior and right valve exterior showing position of beak (arrowed); (**32–38**) paratypes, Masajid Formation, western Bir Maghara; (**32–35**) right valve exterior, left valve exterior, posterior, and close-up showing the posterior slope (= corselet), respectively, (**36–38**) BSPG 2014V 313/3, posterior, dorsal, and left lateral views, respectively. Scale bars = 3 mm.

(Flamand, 1911, p. 905, pl. 11, fig. 8a–d) resembles *N. douvillei* n. sp., but differs in having much more enrolled umbones, a shallow escutcheon, strongly convex posterior and ventral margins, and by details of the ornamentation pattern, especially at the umbonal area, which is smooth.

The other closely related species are *N. wynnei* Cox, 1940 (p. 23, pl. 1, figs. 29–31) and *N. blakei* Cox, 1940, (p. 24, pl. 1, figs. 24–28) from the Upper Bathonian of India. Cox (1940) differentiated *N. blakei* from *N. wynnei* by having a sinuous ventral margin and by its elongated form. Later, Kanjilal (1980, p. 333), Agrawal and Kachhara (1980, p. 474), Pandey and Agrawal (1984, p. 180), and Jaitly et al. (1995, p. 155, text-fig. 5) recorded numerous intermediate forms between *N. blakei* and *N. wynnei* and concluded that the two species of Cox are conspecific. Therefore, they regarded *N. blakei* as a junior synonym of *N. wynnei*, arguing that some transitional forms exist between the two species. Their view is followed here. The two species differ from *N. douvillei* n. sp. in having rounded ridges delineating the escutcheon, forming a sunken heart shape between the umbo and posteroventral margin (e.g., Cox, 1940, pl. 1, figs. 24c, 30b), fine and dense commarginal ribs, and in lacking anterior umbonal ridges. *Nuculoma kathrynae* Duff, 1978 (p. 21, pl. 1, figs. 2–5) from the Callovian of England resembles the present species in having strongly inflated valves and strongly opisthogyrate enrolled umbones, but it has a small cordate escutcheon, which reaches about halfway to the posteroventral angle, and its surface carries irregular commarginal growth lines. *Nucula pollux* d'Orbigny, 1850 (p. 339, no. 179) (Cottreau, 1925, p. 154, pl. 39, figs. 25–27) from the Callovian–Oxfordian of France differs in having a deep escutcheon, less-inflated valves, and more centrally placed umbones.

Nuculoma sinaiensis new species
Figures 5.20–5.38, 8.1–8.35, 9, 10

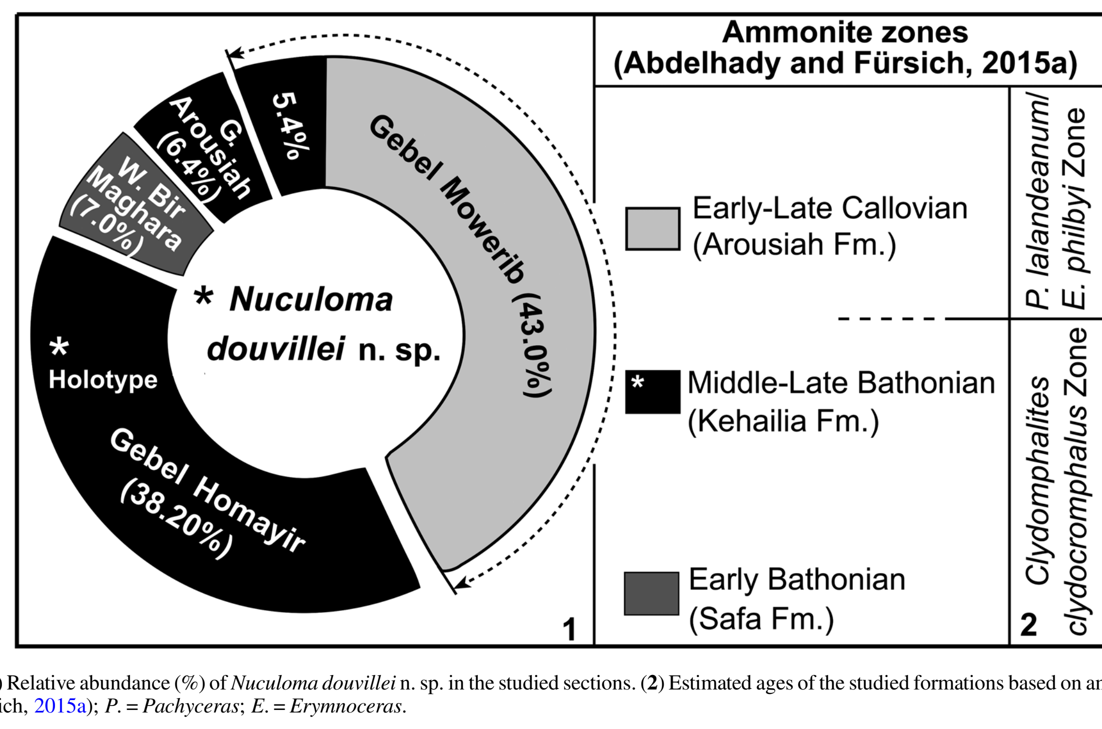

Figure 6. (**1**) Relative abundance (%) of *Nuculoma douvillei* n. sp. in the studied sections. (**2**) Estimated ages of the studied formations based on ammonites (Abdelhady and Fürsich, 2015a); *P.* = *Pachyceras*; *E.* = *Erymnoceras*.

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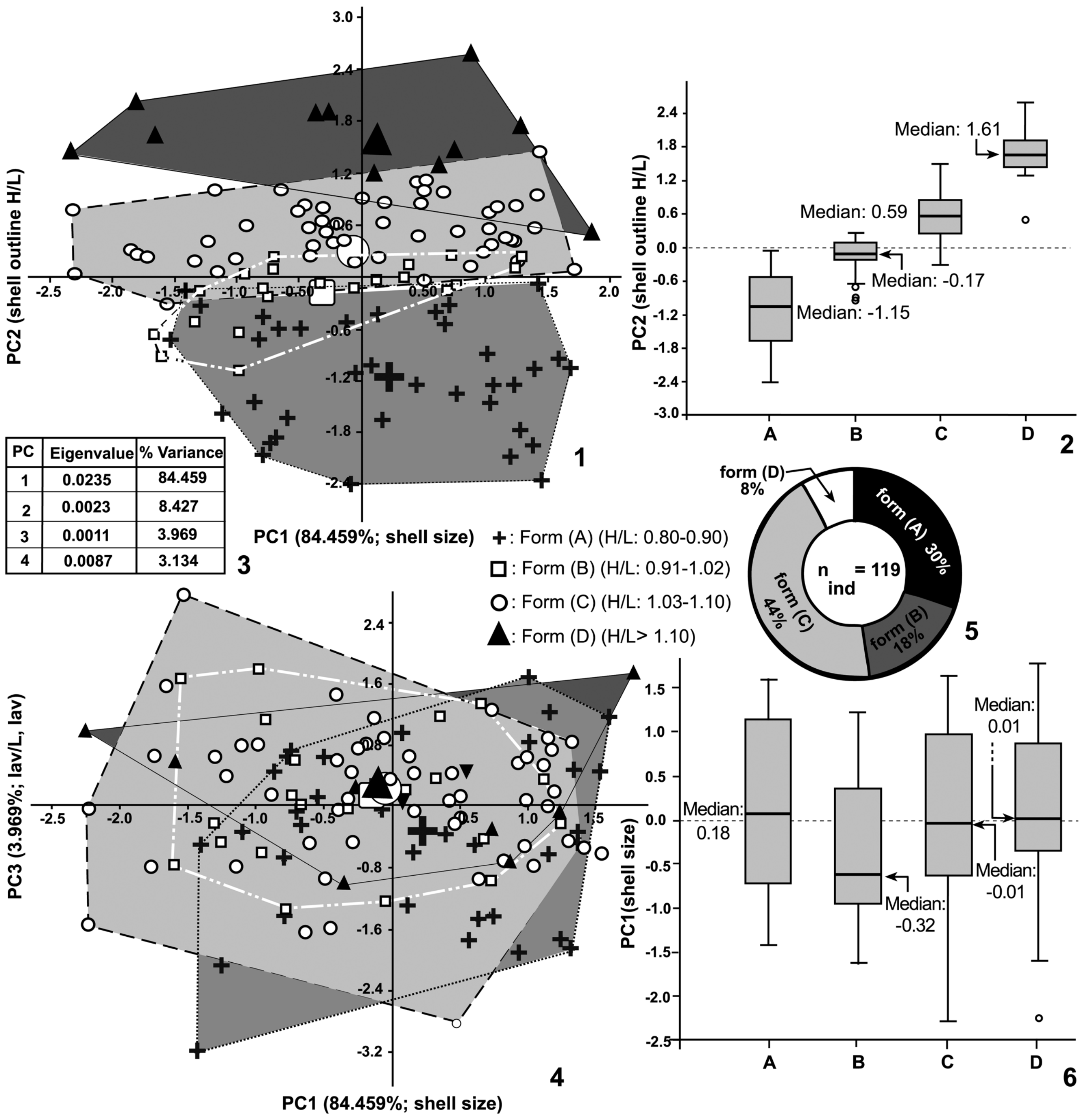

Figure 7. Principal component analysis (PCA) of *Nuculoma douvillei* n. sp. using the PAST software (Hammer et al., 2001). (**1**) Scatter plot of PC1 vs. PC2 showing overlap of different morphotypes. (**2**) Boxplot of the four forms (A–D) based on shell outline (PC2). (**3**) Percentage of variation explained by PCA of morphological variables. (**4**) Scatter plot of PC1 vs. PC3 also showing overlap of the different morphotypes based on shell size. (**5, 6**) Relative abundance of morphotypes collected from the studied sections and boxplot of the forms (A–D) based on shell size (PC1). The large symbols in the scatter plots represent the centroid value for the respective groups (A–D). For data see Appendix A.

Table 1. Measurements (in mm) of *Nuculoma douvillei* n. sp.

120 specimens	L	H	Iav	Al	H/L	Iav/L	Al/L
Range	3.3–9.5	3.5–10.0	2.8–9.10	3.0–8.2	0.85–1.31	0.81–1.19	0.74–0.95
Mean	6.94	7.62	6.68	6.10	1.10	0.96	0.88

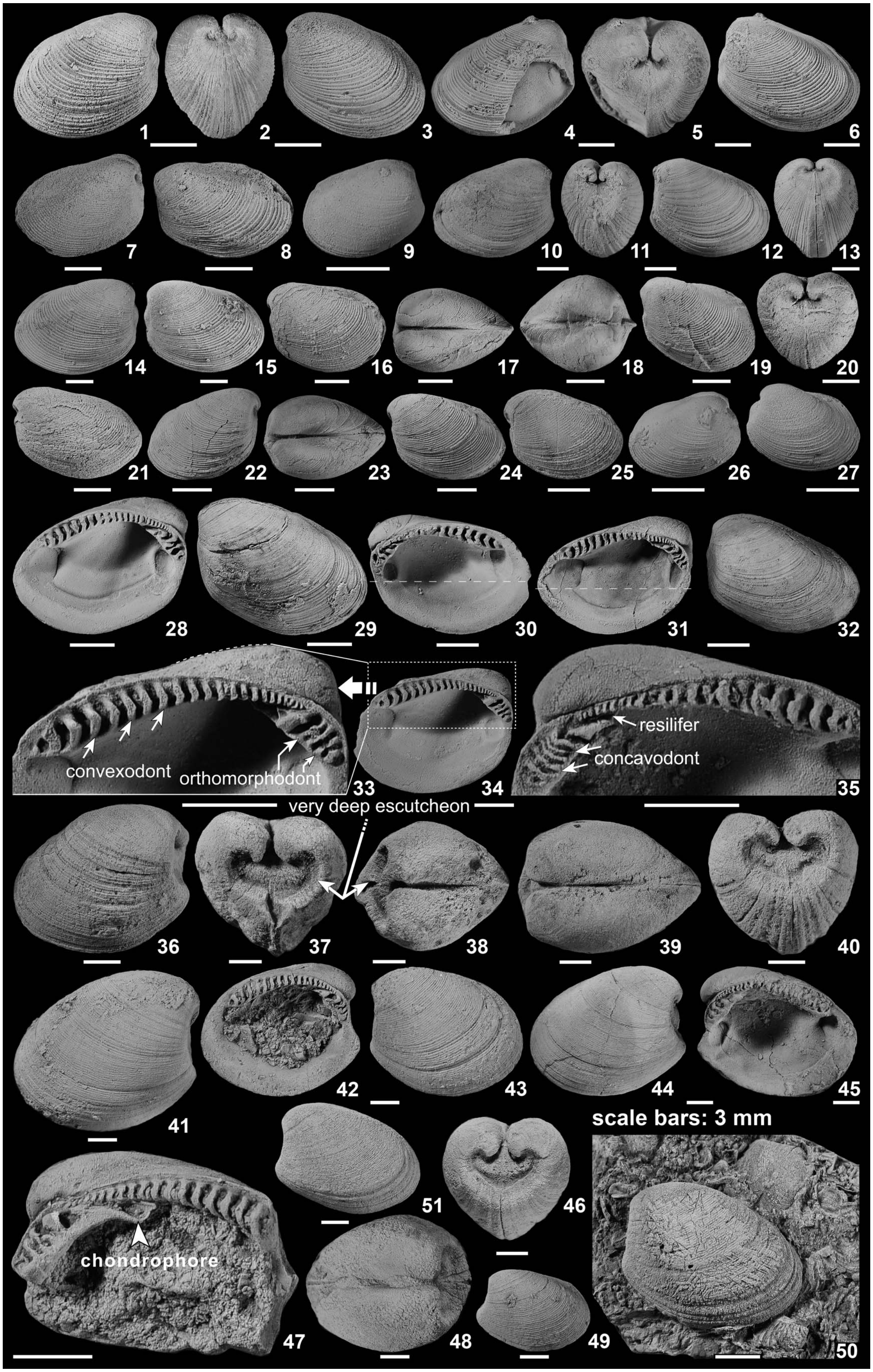

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Figure 8. (**1–35**) Paratypes of *Nuculoma sinaiensis* n. sp. from the Jurassic of Gebel Maghara, showing variation in outline and internal structures. (**1–15**) Masajid Formation, western Bir Maghara; (**1–3**) BSPG 2014V 316/1, left lateral view, posterior view showing the absence of escutcheon, and right lateral view, respectively; (**4–6**) BSPG 2014V 316/2, left lateral view, posterior view, and right lateral view, respectively; (**7**) BSPG 2014V 316/3, left lateral view; (**8**) BSPG 2014V 316/4, right lateral view, sub-trapezoidal form of species; (**9**) BSPG 2014V 316/5, left lateral view, (**10–12**) BSPG 2014V 313/4, left lateral view, posterior view of articulated valves showing absence of escutcheon, and right lateral view, respectively; (**13**) BSPG 2014V 313/5, posterior view, with a faint cordate escutcheon; (**14, 15**) BSPG 2014V 313/6, left lateral view of sub-rounded form of species and right lateral view, respectively. (**16–25**) Bir Maghara Formation, Gebel Arousiah; (**16, 17**) BSPG 2014V 303/2, right lateral view and anterodorsal view showing the absence of lunule, respectively (**18, 19**) BSPG 2014V 303/3, dorsal and right lateral views respectively, (**20, 21**) BSPG 2014V 303/4, posterior and right lateral view, respectively, (**22–24**) BSPG 2014V 303/5, left lateral view of sub-trapezoidal form, anterodorsal view showing lack of a lunule, and right lateral view showing the beak projecting beyond posterior margin, respectively, (**25**) BSPG 2014V 303/6, right lateral view; (**26, 27**) BSPG 2014V 315/1, Kehailia Formation, Gebel Engabashi; (**26**) left lateral and right lateral views, respectively, of elongated-ovate form of species; (**28–30**) Kehailia Formation, Gebel Homayir; (**28, 29**) BSPG 2014V 305/1, right valve interior view showing entire pallial line located some distance from ventral margin, and exterior view, (**30**) BSPG 2014V 305/2, left lateral view showing small rounded posterior adductor muscle scar. (**31, 32**) Kehailia Formation, Gebel Moweirb; (**31**) BSPG 2014V 306/1, right valve interior showing large rectangular anterior muscle scar and right valve exterior, respectively. (**33–35**) Kehailia Formation, Gebel Homayir; (**33**) BSPG 2014V 305/3, close-up showing anterior and posterior teeth, and right valve interior, respectively, (**35**) BSPG 2014V 305/4, close-up of hinge. (**36–51**) *Nuculoma wynnei* Cox (1940) from the Callovian of Kachchh, India. (**36–40**) Jumara Dome; (**36**) PIW 1991 III23/1, left lateral view, (**37, 38**) PIW 1991 III23/2, posterior view showing a very deep escutcheon, and dorsal view, respectively, (**39**) PIW 1991 III23/3, anterodorsal view, (**40**) PIW 1991 III23/4, posterior view showing a rounded ridge delineating the escutcheon. (**41–43**) Kaladongar, Pachchham Island; (**41**) PIW 1991 III32/1, left valve, (**42, 43**) PIW 1991 III32/2, right valve interior showing angulated posterior margin, and right valve, respectively. (**44–46**) Jhura Dome; (**44, 45**) PIW 1991 III29/1, left lateral view, and left valve view showing the internal features, respectively, (**46**) PIW 1991 III29/2, posterior view. (**47–49**) Jhura Dome; (**47**) PIW 1991 III46/1, left valve wshowing teeth and chondrophore, PIW 1991 III46/2, dorsal view, and PIW 1991 III46/1, right lateral view, respectively. (**50, 51**) Jumara Dome; (**50**) PIW 1991 III23/5, right valve and right lateral view, respectively, showing angulated posterior margin. Scale bars = 3 mm.

non .1840 *Nucula tenuistriata* J. de C. Sowerby (nomen dubium), pl. 22, fig. 3.
.1916 *Nucula tenuistriata*; Douvillé, p. 61, pl. 5, figs. 46–50 (non J. de C. Sowerby).
.1980 *Palaeonucula tenuistriata*; Hirsch, p. 130, pl. 1, fig. 7.
?1981 *Nuculoma* sp. cf. *Nucula tenuistriata*; Parnes, p. 26, pl. 3, fig. 17.
?1998 *Nuculoma* sp. Holzapfel, p. 94, pl. 3, fig. 1a–c.
?2002 *Palaeonucula tenuistriata*; Abdelhamid, p. 337, pl. 5, fig. 4.
v.2014 *Palaeonucula tenuistriata*; Abdelhady, p. 67.

Holotype.—Articulated specimen BSPG 2014V 303/1 with shell preservation from the upper Bajocian Bir Maghara Formation, Gebel Arousiah, Sinai (Fig. 5.20–5.24).

Paratypes.—One hundred twenty-eight specimens in shell preservation, mostly articulated, from the upper Lower Jurassic (Toarcian) to Middle–Upper Jurassic (Bajocian–Callovian and Lower Kimmeridgian) of Gebel Maghara: three specimens from the upper part of the lower Toarcian Rajabiah Formation (marl unit), Bir Maghara (BSPG 2014V 317/1–3), 14 specimens from the upper Toarcian Shusha Formation, Bir Maghara (BSPG 2014V 314/1–14); 16 specimens from the upper Bajocian Bir Maghara Formation, Gebel Arousiah (BSPG 2014V 303/2–17); six specimens from the upper third part of the lower Bathonian Safa Formation, Bir Maghara (BSPG 2014V 318/1–6); seven specimens from the middle–upper Bathonian Kehailia Formation, Gebel Engabashi (BSPG 2014V 304/1–2; 315/1–5); 13 specimens from the same formation at Gebel Homayir (BSPG 2014V 305/1–6) and Gebel Moweirb (BSPG 2014V 306/1–7); two specimens from the Callovian Arousiah Formation, Gebel Moweirb (BSPG 2014V 327/1–2); 49 specimens from the lower marl beds of the lower Kimmeridgian Masajid Formation, western Bir Maghara (BSPG 2014V 312/1–22; 316/1–27); and 18 specimens from the upper part of the Masajid Formation, western Bir Maghara (BSPG 2014V 313/1–18).

Diagnosis.—Small strongly inflated *Nuculoma* species, variable in outline, ranging from elongated-ovate to subtrapezoidal, from subrounded to subtrigonal; posterior margin truncated to slightly convex, anterior margin strongly convex; escutcheon lacking (occasionally delimited by a faint ridge, shallow cordate form), no lunule, anisomyarian with large subquadrate anterior adductor muscle scar and small elongated-ovate posterior muscle scar; pallial line entire (located some distance from ventral margin); umbones terminal to subterminal, projecting occasionally beyond posterior margin, causing posterior margin to be strongly oblique; growth lines irregularly spaced, fine.

Occurrence.—Toarcian to lower Kimmeridgian, Gebel Maghara, Sinai.

Description.—Shell small-sized, variable in outline, elongated-ovate to subtrapezoidal, subrounded to subtrigonal, longer than high (H/L = 0.82 on average; Table 2), equivalved, strongly inequilateral, and strongly inflated. Inflation greatest approximately one-third of total valve height from umbo. Anterior margin strongly rounded, meeting regularly convex ventral margin in rounded curve. Posterior margin truncated to slightly convex, strongly oblique, meeting ventral margin in a continuous rounded curve. Anterodorsal margin long, straight to slightly convex, and higher than posterodorsal one. Umbones strongly inflated, terminal to sub-terminal, strongly enrolled posteriorly, occasionally projecting beyond posterior margin at approximately mid-height of valve, forming a strongly oblique posterior margin (Fig. 5.28–5.31). Beaks sharply pointed and opisthogyrate. Escutcheon absent except in a few specimens where it is indistinct, cordate-shaped (Fig. 8.13). Posterior slope (= corselet) occasionally well developed, extending from umbo to about one-third of posterodorsal margin (Fig. 5.35). No lunule (Figs. 5.21, 8.23). Anterior adductor muscle scar shallowly impressed, large (~41% of total shell height), subrectangular to elongated-ovate, located close to anterior margin. Posterior adductor muscle scar smaller than anterior one, subrounded to elongated-ovate, its dorsal margin flat, located close to

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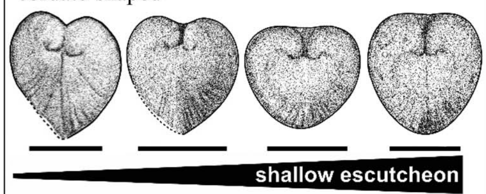
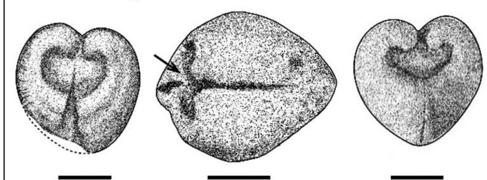
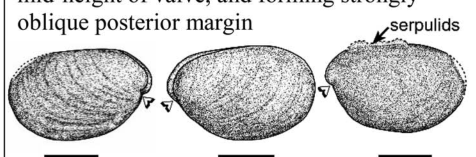
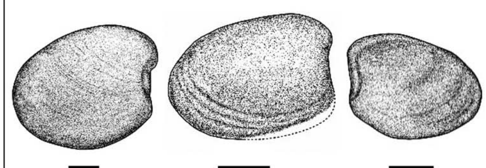
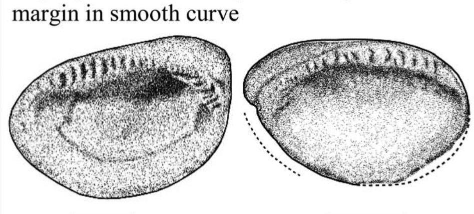
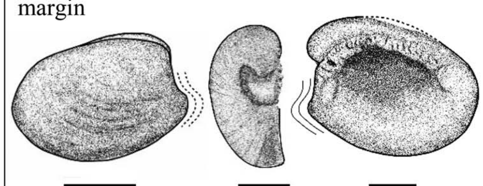
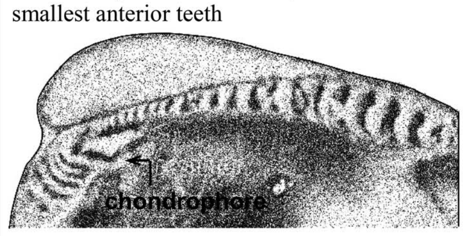
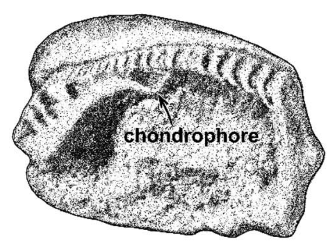
	***Nuculoma sinaiensis* n. sp.** (Toarcian–Lower Kimmeridgian, Sinai, Egypt)	***Nuculoma wynnei* Cox, 1940** (Callovian of Kachchh Basin, India)
Shell size	Very small to small (L: 5.3–13.7 mm; average 10.4 mm: 61 specimens)	Small to medium (L: 7.3–27.5 mm; average 15.20 mm: 69 specimens)
Shell outline	Elongated-ovate to subtrapezoidal, longer than high (H/L= 0.82 on average). See Figs 5.14–5.19; 8.1–8.17	Subtriangular to subrounded (see also Jaitly et al. (1995, p. 155, text-fig. 5); Fig. 8.20–8.32
Maximum inflation	Approximately one-third of total valve height from umbo	About the mid-height of valve
Escutcheon	Usually absent, occasionally very faint, cordate-shaped 	Large, well-defined, heart-shaped, bordered by rounded ridge 
Umbo	Terminal to subterminal, projecting occasionally beyond posterior margin at nearly mid-height of valve, and forming strongly oblique posterior margin 	Subterminal 
Posterior margin	Slightly convex to straight, meeting ventral margin in smooth curve 	Slightly concave to nearly straight, steeply oblique, forming obtuse angle with ventral margin 
Anterodorsal margin	Moderately convex	Strongly convex
Lunule	Very narrow, lanceolate, shallow	Absent
Chondrophore	Subtriangular, narrow, extending sub-horizontally towards anterior, below first five smallest anterior teeth 	Upward-curved spoon-shaped 
Posterior hinge	Reduced due to strongly enrolled umbones with orthomorphodont and slightly concavodont teeth	Wide, with strong orthomorphodont teeth
Muscle scar	Anterior muscle scar: large, rectangular to sub-square; Posterior muscle: much smaller, elongated-ovate	Anterior and posterior muscle scars elongated-ovate, slightly inequal
Pallial line	Thick, entire, located some distance from ventral margin	Entire, located close to ventral margin

Figure 9. Comparison between *Nuculoma sinaiensis* n. sp. from the Toarcian–lower Kimmeridgian of Gebel Maghara, Egypt, and *N. wynnei* Cox, 1940, from the Callovian of Kachchh Basin (western India) based on external and internal characters. All scale bars = 5 mm.

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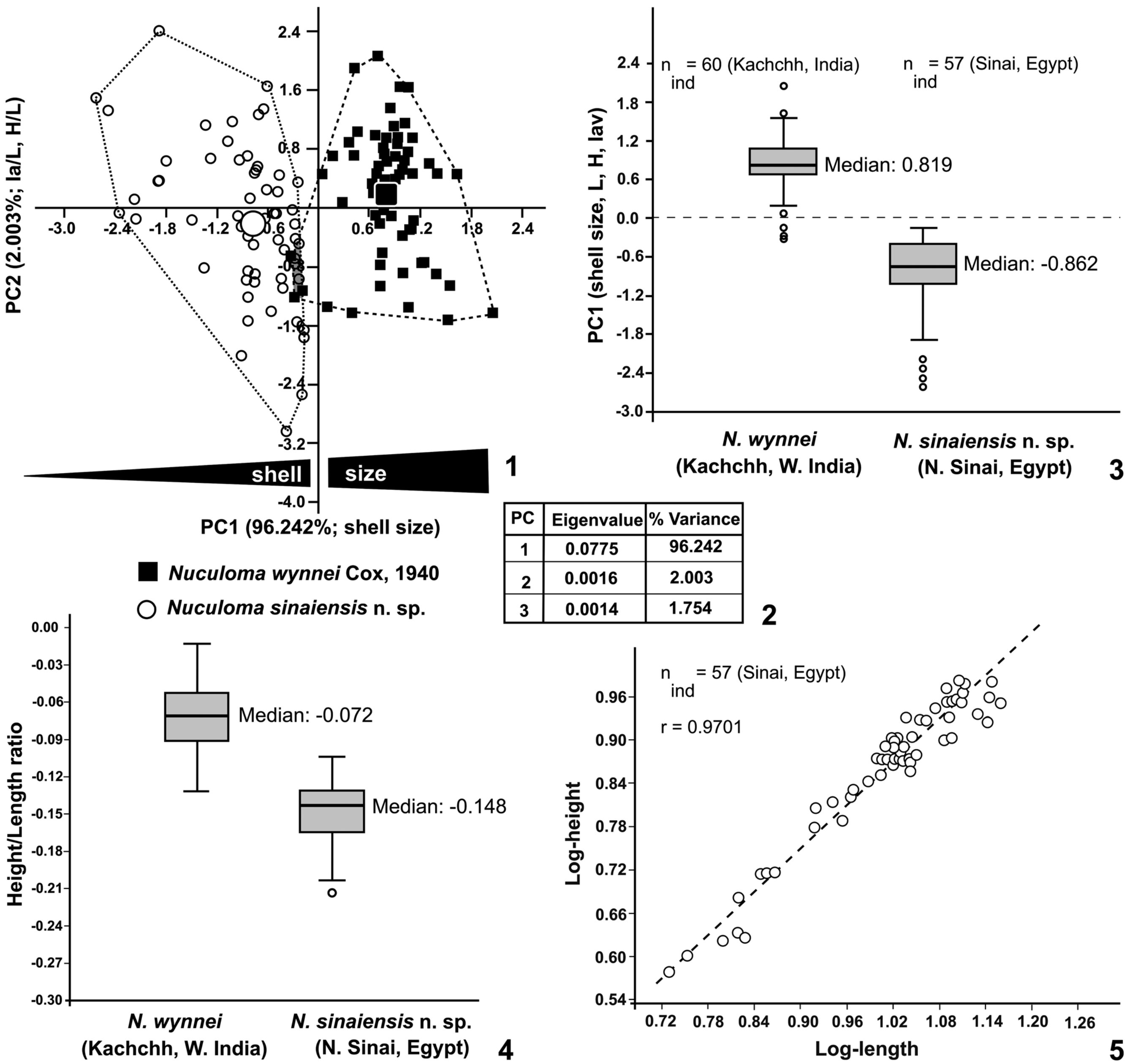

PC	Eigenvalue	% Variance
1	0.0775	96.242
2	0.0016	2.003
3	0.0014	1.754

Figure 10. Principal component analysis (PCA) of *Nuculoma sinaiensis* n. sp. from the Jurassic rocks (Toarcian–lower Kimmeridgian) of Gebel Maghara and *N. wynnei* Cox, 1940, from the Callovian of the Kachchh Basin (western India) using the PAST software (Hammer et al., 2001). (**1**) Scatter plot of PC1 vs. PC2 showing nearly complete separation between the species from Egypt and India. (**2**) Percentage of variation explained by PCA of morphological variables. (**3**) Boxplot of the two species based on shell size (PC1). (**4**) Boxplot of the two species based on shell outline (H/L). (**5**) Scatter plot of log-transformed height versus length of *N. sinaiensis* n. sp. The specimens from Kachchh are from the Fürsich collection in the Bayerische Staatssammlung für Paläontologie und Geologie, Munich. n_{ind} = number of individuals. See Appendix B for data.

posterodorsal margin below posterior teeth (Fig. 8.28, 8.30, 8.31). Pallial line thick, entire, located some distance from ventral margin (approximately one-third of total shell height from ventral margin; Fig. 8.28, 8.31). Hinge plate broad, slightly arched, with strong unequal teeth and sockets. Anterior hinge row with 16–25 (21 on average) convexodont teeth, gradually decreasing in size towards umbo (Fig. 8.33–8.35). Posterior part of hinge short, wide, with strong 3–5 orthomorphodont to slightly concavodont teeth, gradually increasing in size towards umbo (Fig. 8.33). The last one or two posterior teeth (below umbo) occasionally larger and thicker than others, with oblique triangular chondrophore, extending sub-horizontally below the first five smallest anterior teeth. Surface with fine, irregularly spaced, numerous commarginal growth lines of variable strength.

Etymology.—After Sinai Peninsula, northeastern Egypt.

Measurements.—See Table 2.

Remarks.—*Nuculoma sinaiensis* n. sp. can be distinguished from other Jurassic *Nuculoma* species by its small size (maximum length: 13.7 mm; maximum height: 11.2 mm; maximum inflation: 9.8 mm; Table 2); terminal to subterminal umbones

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Table 2. Measurements (in mm) of *Nuculoma sinaiensis* n. sp.

61 specimens	L	H	Iav	Al	H/L	Iav/L	Al/L
Range	5.3–13.7	5.0–11.20	4.30–9.8	5.0–13.5	0.69–0.97	0.60–0.80	0.78–0.99
Mean	10.40	8.53	7.13	9.34	0.82	0.69	0.90

projecting occasionally beyond posterior margin at nearly mid-height of valve, and strongly oblique posterior margin; a thick, entire pallial line, which extends some distance from ventral margin, and in lacking a lunule and escutcheon (occasionally present as very faint, cordate-shaped feature; Fig. 8.13). The specimen figured by Holzapfel (1998) as *Nuculoma* sp. from the upper Callovian–Oxfordian of southern Tunisia strongly resembles the present species in having strongly enrolled terminal umbones, strongly inflated valves, and in lacking an escutcheon, but its posterior margin is much more rounded than the *Nuculoma sinaiensis* n. sp. "*Habonucula*" *agrawali* Singh and Kanjilal, 1977, (p. 190, pl. 1, figs. 1–12) from the lower Callovian of western India also lacks an escutcheon, but differs in having a rounded posterior margin (sub-straight in the present species), a nearly smooth valve except for faint commarginal growth lines close to the ventral margin, and in being less inflated (holotype: Iav/L = 29.3%; paratypes: 38.5–58.3%; Singh and Kanjilal, 1977, p. 192) and more elongated (H/L: 0.67–0.73 as opposed to 0.69–0.97). In addition, the anterior teeth of "*H*." *agrawali* appear to be straight and stronger than those of the present species (variable in *N. sinaiensis* n. sp.). Another closely related taxon is *Nucula tenuistriata* J. de C. Sowerby, which was recorded from the Middle Jurassic (?Callovian) of India by J. de C. Sowerby (1840, pl. 22, fig. 3). Cox (1940, p. 23) included Douvillé's specimens of *N. tenuistriata* (1916, pl. 5, figs. 46–50) from the Middle Jurassic of Sinai (Egypt) in his new species *Nuculoma wynnei* Cox, 1940, (p. 23, pl. 1, figs. 29–31) from the Middle Jurassic of India—a view not accepted here, although Jaitly et al. (1995, p. 154) included not only the Egyptian material in the synonymy list of *N. wynnei* as suggested by Cox, but questionably also the Indian holotype of *Nucula tenuistriata* J. de C. Sowerby. The Egyptian material, however, is regarded herein as a separate species for the following reasons: (1) Douvillé (1916) did not illustrate either posterior or dorsal views to define the development of an escutcheon, which distinguishes it from other *Nuculoma* species; (2) the specimens figured by Douvillé have a sub-truncated posterior margin (angulated in *N. wynnei*; Fig. 8.42, 8.44, 8.51), terminal umbones, irregularly spaced fine commarginal growth lines; and (3) in *N. wynnei*, the rounded ridge, delineating the corselet sensu Duff (1978) and others (see Cox, 1940, pl. 1, figs. 29b, 30b; Jaitly et al., 1995, pl. 1, fig. 2c; Fig. 8.37, 8.38), forms a concave arch between the umbo and the posteroventral margin enclosing a well-defined, deep heart-shaped escutcheon (absent in the Egyptian material). Figure 9 shows a detailed comparison of *N. sinaiensis* n. sp. and *N. wynnei*. In addition, Principal Component Analysis (PCA) was carried out to show the shell size and morphological relationship between *N. wynnei* and *N. sinaiensis* n. sp. based on the variance-covariance (VCV) matrix of log-transformed variables such as length (L), height (H), inflation (Iav), height/length ratios (H/L), and inflation/length ratios (Iav/L) (Fig. 10.1, 10.2). The first Principal Component (PC1) accounts for 96.24% of the variation in the data, which positively correlates with shell size (H, L, Iav), whereas PC2 accounts for 2.0%, which positively correlates with shell outline (H/L) and inflation (Iav/L). The plots of PC1 versus PC2 indicate that *N. wynnei* and *N. sinaiensis* n. sp. differ in shell size as indicated by the near separation of the two convex hulls of the two species (Fig. 10.1). The boxplots of shell size of both species also show a distinct gap (median of *N. wynnei* 0.819, median of *N. sinaiensis* n. sp. −0.862; Fig. 10.3), whereby *N. wynnei* is distinctly larger than *N. sinaiensis* n. sp. Although the PC2 values of *N. wynnei* completely fall within the range of *N. sinaiensis* n. sp. (PC2), the boxplots based on height/length ratios indicate that some Egyptian specimens are more elongated than the Indian ones (Fig. 10.4). Douvillé (1916) doubtfully regarded *Nucula venusta* Terquem and Jourdy, 1871, from the Bathonian rocks of France as synonym of *P. tenuistriata*. However, the holotype of Terquem and Jourdy (1871, pl. 11, figs. 26–28) has a less-incurved, orthogyrate to slightly prosogyrate umbo.

Cox (1940, p. 24, pl. 1, figs. 24–28) erected *Nuculoma blakei* from the upper Bathonian–Callovian of Kachchh and differentiated it from *N. wynnei* by its elongated shape, an obtuse angle between posterior and ventral margins, and by its more sinuous ventral margin. Actually, *N. blakei* carries some similarities to *N. sinaiensis* n. sp., particularly the terminal umbones, which extend beyond the posterior margin (e.g., Cox, 1940, pl. 1, fig. 24a), but differs in having a well-defined, deep heart-shaped escutcheon, an angulated posterior margin (Cox, 1940, pl. 1, fig. 27a, c), in lacking a lunule, and in being larger and more elongated than *N. sinaiensis* n. sp. (L = 26.0 mm, H = 16.0 as opposed to L = 10.40, H = 8.53 mm on average; H/L = 0.61 as opposed to 0.82 on average; Table 2). Jaitly et al. (1995) regarded *N. blakei* and *N. wynnei* as conspecific, with *N. blakei* being a junior synonym, based on numerous intermediate morphotypes recorded by some authors (e.g., Agrawal, 1956, p. 54; Agrawal and Kachhara, 1980, p. 476–477; Kanjilal, 1980, p. 333; Pandey and Agrawal, 1984, p. 180). *Nucula* (*Nuculoma*) *castor* d'Orbigny, 1850, described and figured by Thiéry and Cossmann (1907, p. 55, pl. 2, figs. 14, 15) and Cossmann (1924, p. 42, pl. 6, figs. 32–35) from the Callovian of France differs in having a strongly oblique subtriangular valve, a subterminal umbo, a rounded anterior muscle scar, and in being less elongated and more strongly inflated than the present species.

Subfamily Palaeonuculinae Carter, 2001

Genus *Palaeonucula* Quenstedt, 1930

Type species.—*Nucula hammeri* Defrance, 1825, from the Upper Lias of France; original designation by Quenstedt (1930).

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Diagnosis.—An updated diagnosis has been provided by Hodges (2000, p. 13).

Remarks.—There is some confusion regarding the generic/subgeneric relationships among *Palaeonucula* Quenstedt, 1930, *Nuculopsis* Girty, 1911, and *Nuculoma* Cossmann, 1907. For instance, Quenstedt (1930) regarded *Palaeonucula* as a subgenus of the Paleozoic genus *Nuculopsis*. Cox (1940, p. 12) noted that the latter genus has a more primitive type of chondrophore than *Palaeonucula*, in which the chondrophore is wider and shorter, and not projecting into the shell cavity. Therefore, he placed *Palaeonucula* as a subgenus in *Nucula*, and accepted *Nuculoma* as a genus. The general shell morphology of *Palaeonucula* is similar to *Nucula* Lamarck, but the shell is non-nacreous and has smooth shell margins (Damborenea and Pagani, 2019, p. 929). In addition, species of *Nucula* should be restricted to forms with radial ribbing on the shell surface, which clearly distinguishes them from both *Palaeonucula* and *Nuculoma* (Duff, 1978, p. 23). Recently, Hodges (2000, p. 13) stated that the main differences between *Palaeonucula* and *Nuculoma* are that the latter has more strongly enrolled opisthogyrate umbones and fine, regular commarginal growth lines on the shell surface. For more details, see Duff (1978), Hodges (2000), and Damborenea and Pagani (2019, p. 929). The paleogeographic distribution of *Palaeonucula* during Middle–Late Triassic and Early Jurassic has been summarized by Ros et al. (2014, p. 10, fig. 1).

Palaeonucula cuneiformis (J. de C. Sowerby, 1840)
Figures 11.1–11.32, 12, 13

- *1840 *Nucula*? *cuneiformis* J. de C. Sowerby, pl. 22, fig. 4 and explanation.
- 1913 *Nucula spitiensis* Holdhaus, p. 428, pl. 95, figs. 11–13.
- 1913 *Nucula hyomorpha* Holdhaus, p. 430, pl. 95, figs. 14–17.
- .1916 *Nucula lateralis*; Douvillé, p. 60, pl. 5, fig. 45.
- non 1939 *Nucula cuneiformis*; Stefanini, p. 219, pl. 24 (25), fig. 3.
- .1940 *Nucula* (*Palaeonucula*) *cuneiformis*; Cox, p. 13, pl. 1, figs. 5–10.
- .1940 *Nucula* (*Palaeonucula*) *kaoraensis* Cox, p. 15, pl. 1, figs. 11–14.
- .1956 *Nucula* (*Palaeonucula*) *kaoraensis*; Agrawal, p. 51, pl. 7, fig. 3a.
- .1959 *Nucula cuneiformis*; Jaboli, p. 46, pl. 6, fig. 3.
- .1980 *Palaeonucula lateralis*; Hirsch, p. 130, pl. 1, figs. 5, 6.
- .1980 *Palaeonucula kaoraensis*; Kanjilal, p. 335, pl. 1, figs. 8–10.
- .1980 *Palaeonucula cuneiformis*; Kanjilal, p. 334, pl. 1, figs. 4–7.
- .1995 *Palaeonucula cuneiformis*; Jaitly et al., p. 155, pl. 1, figs. 8–17, pl. 2, figs. 1, 2, text-figs. 6–9.
- .1998 *Palaeonucula cuneiformis*; Kanjilal and Pathak, p. 30, pl. 1, fig. 1.
- .2002 *Palaeonucula lateralis*; Abdelhamid, p. 337, pl. 5, figs. 1, 2.
- .2003 *Palaeonucula lateralis*; Khalil, p. 308, pl. 1, figs. 9, 10.
- v.2014 *Palaeonucula lateralis*; Abdelhady, p. 72, fig. 5.4I, J.
- v.2014 *Palaeonucula lateralis*; Abdelhady and Fürsich, p. 181, fig. 6I, J.
- v.2019 *Palaeonucula cuneiformis*; Fürsich et al., p. 146, pl. 1, figs. 1–3.

Holotype.—*Nucula cuneiformis* J. de C. Sowerby, 1840, pl. 22, fig. 4, from the "Upper Secondary Formation" (Callovian) of Khera Hill (Keera Dome), Kachchh, western India.

Occurrence.—The species has a wide stratigraphic range, from Bajocian to Kimmeridgian strata of Kachchh, western India, upper Bathonian–Callovian strata of Madagascar, Middle–Upper Jurassic of Ethiopia, and from the Lower Jurassic (Toarcian) to early Kimmeridgian successions of Gebel Maghara, Sinai (present study, first record).

Description.—Shell small to medium-sized, highly variable in shape, ranging from elongated ovate to subtriangular, from sub-trapezoidal to strongly elongated (Fig. 12), inequilateral, equivalved, moderately inflated. Anterior area much longer than posterior area (Al/L: 0.67–0.80; Table 3). Anterodorsal margin slightly convex, meeting anterior margin in rounded curve. Posterodorsal margin short, weakly convex. Posterior margin narrow, angulated. Anterior end tapering, rounded, meeting ventral margin in rounded curve. Ventral margin irregularly and strongly convex (occasionally regularly convex). Umbo broad, slightly depressed, inflated, located approximately one-third of total valve length from posterior end (occasionally subterminal). Beaks pointed, slightly opisthogyrate. Anterior and posterior muscle scars oval, subequal, located close to anterior and posterior margins, respectively, and more strongly impressed towards dorsal margin (Fig. 11.12). Pallial line well-impressed, continuous, parallel to ventral margin. Anterior pedal retractor muscle scars (Apr) small, rounded, and located close to anterodorsal margin, below anterior hinge (Fig. 11.29–11.32). Escutcheon well developed, sub-ovate to cordiform, deep. Lunule generally absent, but occasionally faint, very shallow, lanceolate, narrow in few specimens. A well-developed rounded umbonal ridge running to posteroventral angle of shell with a slightly concave area located close to posterior margin (Figs. 11.6, 11.11, 13.1, 13.2). Hinge taxodont with numerous unequal teeth and sockets. Anterior part of hinge longer than posterior one with ∼22 small convexodont teeth, decreasing in size towards umbo (Fig. 11.28, 11.32). Posterior hinge with 8–10 convexodont teeth and sockets, gradually decreasing in size towards umbo. Chondrophore well developed, spoon-shaped, projecting sub-horizontally below the smallest teeth of anterior hinge close to beak (Fig. 11.32). Shell surface covered with irregularly spaced fine commarginal growth lines, variable in strength.

Materials.—One hundred and two specimens, mostly articulated, in shell preservation, from the Lower–Middle

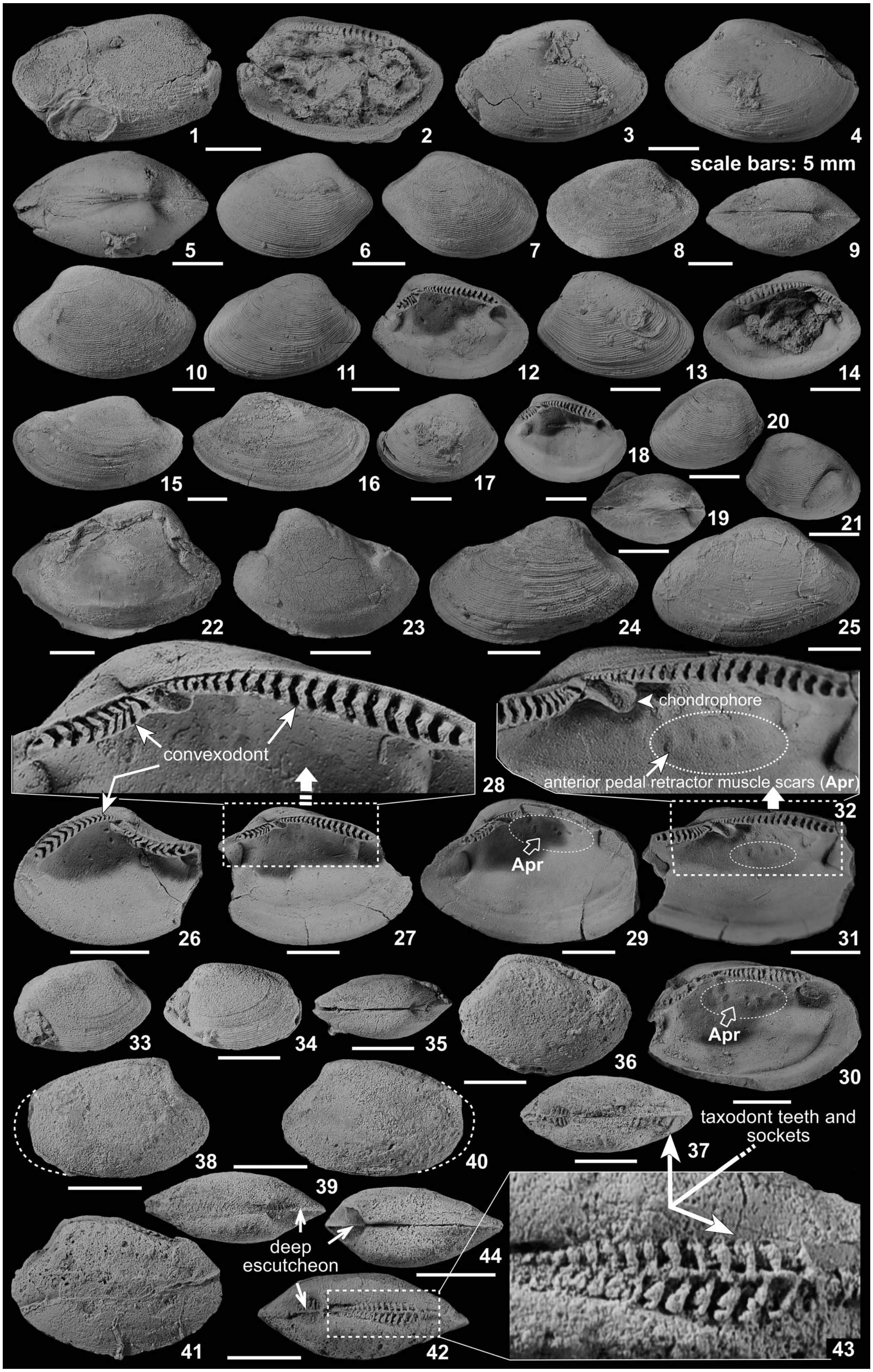

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Figure 11. (**1–32**) Variation and internal characters of *Palaeonucula cuneiformis* (J. de C. Sowerby, 1840) from the Lower–Middle Jurassic of Gebel Maghara. (**1, 2**) BSPG 2014V 328/1, Rajabiah Formation, western Bir Maghara; (**1**) left lateral view, elongated-ovate form, and left valve, interior, respectively. (**3–5**) BSPG 2014V 196/1, Kehailia Formation, Gebel Homayir; (**3**) left lateral, right lateral, and dorsal views of articulated valves; (**6, 7**) BSPG 2014V 188/1, Bir Maghara Formation, Gebel Arousiah; (**6**) left lateral view showing narrowly rounded posterior margin and shallow posterior sulcus,and right lateral view, respectively; (**8, 9**) BSPG 2014V 329/1, Masajid Formation, western Bir Maghara, left lateral and dorsal views, respectively; (**10**) BSPG 2014V 300/1, Kehailia Formation, Gebel Homayir, right lateral view; (**11–18**) Kehailia Formation, Gebel Homayir; (**11, 12**) BSPG 2014V 195/1, left lateral view and left valve, interior view, respectively, (**13, 14**) BSPG 2014V 195/2, exterior right lateral view and right valve interior view, respectively (**15, 16**) BSPG 2014V 195/3, left lateral and right lateral views, respectively, of elongated-ovate form, (**17, 18**) BSPG 2014V 195/4, subtriangular form of species, left lateral view of exterior and interior left valve view, respectively, showing hinge teeth and muscle scars; (**19–21**) BSPG 2014V 330/1, Masajid Formation, western Bir Maghara, (**19**) dorsal view, (**20**) left lateral view showing a shallow umbonal posterior sulcus, (**21**) right valve; (**22**) BSPG 2014V 199/1, Bir Maghara Formation, Gebel Arousiah, left lateral view, shell partly preserved; (**23**) BSPG 2014V 198/1, Kehailia Formation, Gebel Homayir, right lateral view, composite mold, subtriangular form; (**24**) BSPG 2014V 185/1, Kehailia Formation, Gebel, Engabashi, left valve, elongated form; (**25**) BSPG 2014V 194/1, Kehailia Formation, Gebel, Arousiah, left valve. (**26–30**) Internal characters of *P. cuneiformis* from the Kehailia Formation, Gebel Engabashi; (**26**) BSPG 2014V 186/1, right lateral view, interior, (**27, 28**) BSPG 2014V 186/2, left lateral and close-up views, respectively, showing anterior and posterior convexodont teeth, (**29**) BSPG 2014V 186/3, left lateral view showing well-developed anterior pedal retractor muscle scars (Apr), (**30**) BSPG 2014V 186/4, left lateral view showing entire pallial line, Apr (arrowed), and muscle scars; (**31, 32**) BSPG 2014V 200/1, Kehailia Formation, Gebel Engabashi, left valve and close-up, respectively, showing sub-horizontally projecting spoon-shaped chondrophore, Apr (arrowed), and teeth. (**33–44**) *Palaeonucula fraasi* (Noetling, 1887) from the Middle–Upper Jurassic of Gebel Maghara. (**33–35**) BSPG 2014V 179/1, Kehailia Formation, Gebel Mowerib, left lateral, right valve, and dorsal views, respectively. (**36–40**) Masajid Formation, western Bir Maghara: (**36, 37**) BSPG 2014V 334/1, right lateral and dorsal views, respectively, (**38–40**) BSPG 2014V 334/2, left lateral view, dorsal view with deep escutcheon (arrowed), and right lateral view, respectively; (**41–44**) Bir Maghara Formation, Gebel Arousiah; (**41–43**) BSPG 2014V 301/1, right valve, dorsal view, and close-up, respectively, showing taxodont teeth and sockets, (**44**) BSPG 2014V 301/2, dorsal view showing deep escutcheon (arrowed). Scale bars = 5 mm.

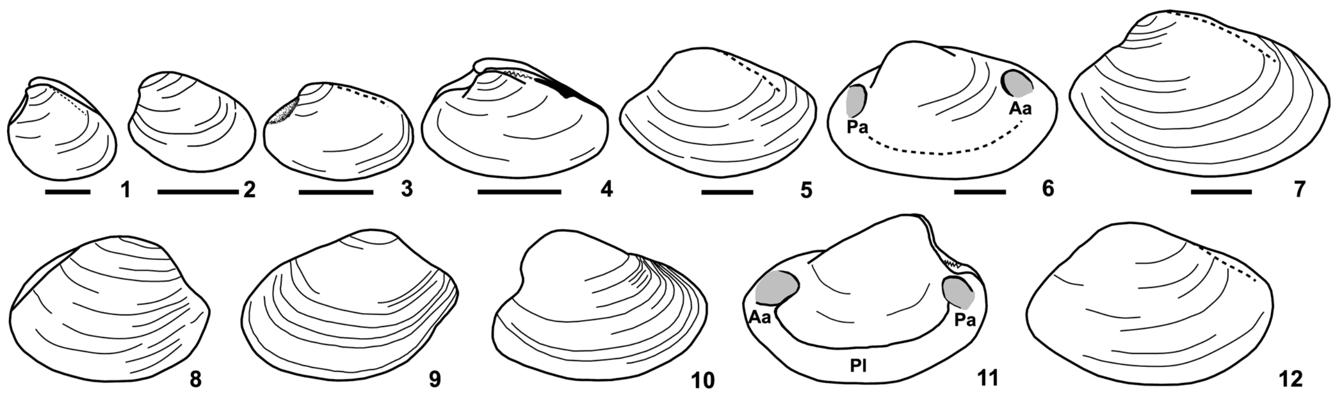

Figure 12. (**1–12**) Variation in outline of *Palaeonucula cuneiformis* (J. de C. Sowerby, 1840) from the Lower–Middle Jurassic of the Maghara area. Specimens from several populations. Aa, anterior adductor muscle scar, Pa, posterior adductor muscle scar, Pl, pallial line. Scale bars = 5 mm.

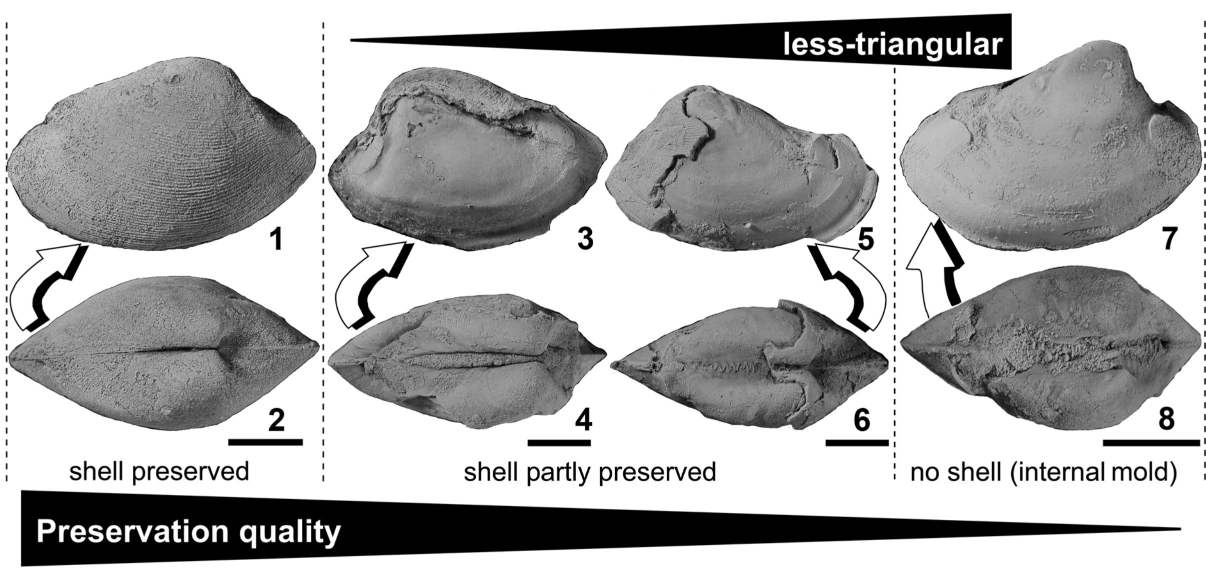

Figure 13. Effect of preservation quality on the shell outline of *Palaeonucula cuneiformis* (J. de C. Sowerby, 1840) from the Lower–Middle Jurassic of the Maghara area, Sinai. (**1, 2**) BSPG 2014V 300/1, Kehailia Formation, Gebel Homayir, Maghara area. (**3–6**) Bir Maghara Formation, Gebel Arousiah; (**3, 4**) BSPG2014V 199/1, (**5, 6**) BSPG 2014V 199/2; (**7, 8**) BSPG 2014V 198/1, Kehailia Formation, Gebel Homayir, Maghara area. Scale bars = 5 mm.

Jurassic of the Maghara area, Sinai: a single specimen from the Toarcian Rajabiah Formation, western Bir Maghara (BSPG 2014V 328/1); two specimens from the upper Bajocian Bir Maghara Formation, Gebel Engabashi (BSPG 2014V 183/1–2); 14 specimens from the same formation, Gebel Arousiah (BSPG 2014V 188/1–10; 189/1; 190/1–3); two specimens from the Lower Bathonian Safa Formation, Gebel Arousiah (BSPG 2014V 191/1–2); 20 specimens from the middle–upper Bathonian Kehailia Formation, Gebel Engabashi (BSPG 2014V 185/1; 186/1–11; 199/1–3; 200/1–4; 302/1); 13 specimens from the same formation, Gebel Homayir (BSPG 2014V 193/1–5; 195/1–5; 198/1; 300/1–2); 17 specimens from the Kehailia Formation, Gebel Arousiah (BSPG 2014V 194/1; 196/1–3; 197/1–13); 20 specimens from the same formation, Gebel Mowerib (BSPG 2014V 181/1; 202/1–19); a single specimen from the Callovian Arousiah Formation, Gebel Mowerib (BSPG 2014V 182/1); a single specimen from the same formation at Gebel Engabashi (BSPG 2014V 5/1); and 11 specimens from the basal part of the lower Kimmeridgian Masajid Formation, western Bir Maghara (BSPG 2014V 323/1–3; 329/1; 330/1; 383/1; 386/1–4; 388/1).

Measurements.—See Table 3.

Remarks.—It is interesting to note that *Palaeonucula cuneiformis* (J. de C. Sowerby, 1840) preserved with shell is elongated-ovate (Fig. 13.1, 13.2), whereas specimens preserved as internal molds have completely different shapes (e.g., sub-triangular or sub-trapezoidal; Fig. 13.3–13.8), which led many authors to erect new genera and species, which are regarded as nomina dubia. With respect to general outline and length/height ratios, *P. cuneiformis* is, therefore, a highly variable species (Fig. 12). The present specimens fall well within the range of variation of the species as documented by Cox (1940, figs. 5–14) and Jaitly et al. (1995, text-fig. 9) from the upper Bajocian–Tithonian of Kachchh, western India, and by Fürsich et al. (2019, figs. 1–3) from the Callovian–Oxfordian of Madagascar. *Palaeonucula cuneiformis* can be distinguished from other Jurassic *Palaeonucula* species by having a deep, ovate escutcheon, an asymmetrical or regularly convex ventral margin, a posteriorly directed umbo, and in lacking a lunule (occasionally poorly developed, e.g., Jaitly et al., 1995. pl. 1, fig. 14b). Although the preservation of *Nucula spitiensis* and *N. hyomorpha*, which were erected by Holdhaus (1913) from the Middle Jurassic of India, is poor, they fall within the range of variation of *P. cuneiformis* and are considered herein as synonyms of the latter. *Nucula lateralis* Terquem and Jourdy, 1871, has been recorded from the Middle–Upper Jurassic of Gebel Maghara (Sinai) by some authors, including Douvillé (1916), Abdelhamid (2002), Khalil (2003), Abdelhady (2014), and Abdelhady and Fürsich (2014). Fürsich and Werner (1987, p. 108) regarded *Nucula lateralis* as a synonym of *Palaeonucula menkii* (Roemer, 1836), which has been recorded from the lower–middle Kimmeridgian of the Lusitanian Basin (Portugal). According to Fürsich and Werner (1987), the length/height ratio and the degree of regularity of the convexity of ventral margin of the latter species are highly variable, and it is, therefore, difficult to separate the various Middle and Upper Jurassic species such as *Nucula lateralis* Terquem and Jourdy, 1871 (p. 107, pl. 11, figs. 19, 20), *N. amata* d'Orbigny, 1850 (p. 310, no. 255) (Thevenin, 1913, p. 150, pl. 27, figs. 26, 27), *N. waltoni* Morris and Lycett, 1853 (p. 52, pl. 5, fig. 14), and *N. pseudo-menkii* de Loriol, 1901 (p. 89, pl. 5, figs. 22, 23) from *P. menkii*. Consequently, Fürsich and Werner (1987) regarded the latter species as junior synonyms of *P. menkii*, arguing that numerous transitional forms exist between two or more of these species. Actually, *P. menkii* (Roemer, 1836) carries some similarities to *P. cuneiformis*, but differs in having a sharply demarcated, narrow, and deep lunule (see the holotype of Roemer, 1836, p. 98, pl. 6, fig. 10b), and its surface is covered with widely spaced and thick commarginal ribs. Agrawal and Kachhara (1977), Pandey and Agrawal (1984), and Jaitly et al. (1995) regarded *Nucula* (*Palaeonucula*) *kaoraensis* Cox, 1940, and *N.* (*P.*) *blanfordi* Cox, 1940, from the Middle–Upper Jurassic of India as junior synonyms of *P. cuneiformis*, arguing that numerous transitional forms exist between the latter species (but see Fürsich et al., 2022).

Another very close species appears to be *P. hausmanni* (Roemer, 1836) (p. 98, pl. 6, fig. 12a–d) from the Jurassic of North Germany. The latter species has an irregular convex ventral margin, a more prominent beak, a distinct shallow lunule, a nearly straight anterodorsal margin, and widely spaced strong commarginal ribs. According to Damborenea and Pagani (2019, p. 930–931), the type species of the genus, *P. hammeri* (Defrance, 1825) (Quenstedt, 1851, p. 527, pl. 44, figs. 4–5; 1856, p. 313, pl. 43, figs. 7–12; Schenck, 1934, p. 35, pl. 2, fig. 20, pl. 4, fig. 1), from the Toarcian–Bajocian of Europe, has a more posteriorly placed umbo and a subrectangular inflated shell. The same applies to its possible synonym

Table 3. Measurements (in mm) of *Palaeonucula cuneiformis* (J. de C. Sowerby, 1840). Sv = inflation of the single valve.

Specimens	L	H	Iav	Isv	Al	H/L	Iav/L	Al/L
BSPG 2014V 5/1	20.1	13.4	10.5	—	16.1	0.67	0.52	0.80
BSPG 2014V 186/1	20.7	16.5	—	5.4	14.8	0.80	0.26 (Sv)	0.71
BSPG 2014V 186/2	18.2	11.7	—	5.0	12.7	0.64	0.27 (Sv)	0.70
BSPG 2014V 186/3	13.5	10.2	7.0	—	10.0	0.75	0.52	0.74
BSPG 2014V 186/4	11.7	7.8	—	2.5	8.1	0.67	0.21 (Sv)	0.69
BSPG 2014V 199/1	24.8	16.4	11.2	—	20.2	0.66	0.45	0.81
BSPG 2014V 199/2	22.5	15.1	10.3	—	18.2	0.67	0.46	0.81
BSPG 2014V 200/1	15.3	10.5	—	4.5	10.7	0.68	0.29 (Sv)	0.70
BSPG 2014V 200/2	13.5	10.5	—	4.0	9.8	0.77	0.29 (Sv)	0.72
BSPG 2014V 202/1	21.2	14.7	12.2	—	14.3	0.69	0.57	0.67
BSPG 2014V 202/2	5.8	4.0	3.1	—	4.4	0.69	0.53	0.76
BSPG 2014V 202/3	6.3	4.3	3.5	—	4.4	0.68	0.56	0.70

(Schenck, 1934, p. 37; Aberhan, 1998, p. 64), *P. hausmanni* (Roemer, 1836, p. 98, pl. 6, fig. 12a–d; Kuhn, 1935, p. 120, pl. 8, figs. 33a, b, 41a–d). In addition, *P. hammeri* has a more inflated valve, sharply pointed beaks, an asymmetrically convex ventral margin, and a distinct lunule (e.g., Quenstedt, 1856, p. 313, pl. 43, figs. 7–12). *Nucula calliope* d'Orbigny, 1850, figured by Cossmann (1924, p. 41, pl. 6, figs. 38–40) and Cottreau (1925, p. 153, pl. 18, figs. 21, 22) from the Callovian of France, by Makowski (1952, p. 5, pl. 5, fig. 2) from the Callovian of Poland, and by Duff (1978, p. 25, pl. 1, figs. 14–16, 18–21) from the Callovian of England, has a more prominent beak, well-demarcated, wide, and deep lunule and escutcheon, and is less elongated and more inflated than *P. cuneiformis*.

Palaeonucula fraasi (Noetling, 1887)
Figures 11.33–11.44, 14.1–14.5

.1877 *Nucula variabilis*; Fraas, fig. 24 (non Sowerby).
*1887 *Nucula Fraasi* Noetling, p. 34, pl. 5, figs. 12, 12a, b.
.1980 *Palaeonucula fraasi*; Hirsch, p. 132, pl. 1, figs. 1–4.
.1999 *Palaeonucula fraasi*; Abdel-Gawad and Gameil, p. 777, pl. 2, fig. 1.
.2002 *Palaeonucula fraasi*; Abdelhamid, pl. 1, fig. 1.
.2003 *Palaeonucula fraasi*; Khalil, p. 307, pl. 1, figs. 11–16.

Holotype.—*Nucula fraasi* Noetling, 1887, pl. 5, fig. 12 from the Jurassic of Hermon, Syria.

Occurrence.—Lower Jurassic of Syria and Middle–Upper Jurassic (upper Bajocian–lower Oxfordian) of El Minshera area (Abdel-Gawad and Gameil, 1999) and Gebel Maghara, Sinai (Hirsch, 1980; Khalil, 2003; present study).

Description.—Shell small, outline elongated-ovate, inequilateral, equivalved, longer than high (H/L: 0.62–0.71), moderately inflated (Iav/L: 0.39–0.49; Table 4). Inflation greatest close to umbonal area. Anterior area larger than posterior one (Al/L: 0.68–0.77). Anterodorsal margin straight to slightly convex dorsally, meeting anterior margin in rounded angle. Posterodorsal margin short, slightly convex dorsally. Anterior and posterior margins convex, meeting ventral margin in rounded curves. Ventral margin regularly convex. Umbo wide, inflated, located one-third of total valve length from posterior end. Beaks small, sharply pointed, opisthogyrate. Escutcheon ovate to cordate, deep (Figs. 11.39, 11.44, 14.2). No lunule. Hinge taxodont with numerous teeth and sockets, decreasing in size towards umbo (Figs. 11.43, 14.4). Anterior part of hinge longer than posterior one with 15–20 chevron-shaped teeth and sockets. Posterior part of hinge with ~5–7 teeth and sockets. Ornamentation consisting of numerous fine commarginal ribs (Fig. 11.33, 11.34).

Materials.—Twenty-three specimens, mostly preserved as composite molds, occasionally in shell preservation, from the Middle–Upper Jurassic of Gebel Maghara: four specimens from the Upper Bajocian Bir Maghara Formation, Gebel Arousiah (BSPG 2014V 301/1–4); a single specimen from the middle–upper Bathonian Kehailia Formation, Gebel Engabashi (BSPG 2014V 333/1); 16 specimens from the same formation at Gebel Homayir (BSPG 2014V 331/1–5; 332/1), Gebel Mowerib (BSPG 2014V 179/1–5), and Gebel Arousiah (BSPG 2014V 307/1–5); and two specimens from the lower Kimmeridgian Masajid Formation, western Bir Maghara (BSPG 2014V 334/1–2).

Measurements.—See Table 4.

Remarks.—The present specimens correspond well to the material figured and described by Noetling (1887, fig. 5, fig. 12, 12a, b) from the Lower Jurassic of Syria as *Nucula fraasi*. The latter species can be distinguished from other *Palaeonucula* species identified herein by having a deep cordate escutcheon, a regularly rounded ventral margin, numerous fine commarginal ribs, sharply pointed and slightly opisthogyrate beaks, in lacking a lunule, and in being less inflated. Noetling (1887) included *Nucula variabilis* J. de C. Sowerby of Fraas (1877) from Lower Jurassic strata of Syria in the synonymy list of his new species. This view is accepted here, because *N. variabilis* has a rounded-subtrigonal valve, a shallow lunule, and its umbo is located slightly posterior of mid-length of valve. Similarly, *Palaeonucula cuevitana* Aberhan, 1994 (p. 9, pl. 1, figs. 1–4, text-fig. 2) from the Lower Jurassic (upper Hettangian) of northern Chile and *P. triangularis* Duff, 1978 (p. 23, pl. 1, figs. 6–13, 17, 23, text-fig. 6) from the Middle Jurassic (Callovian) of England have rounded-triangular valves. In addition, *P. cuevitana* has no escutcheon and its valve is smaller than the present species (L = 7.6–9 mm, H = 5.9–7.0 mm). With respect to shell outline, another close species appears to be *P. cuneiformis* (J. de C. Sowerby, 1840) from the Middle Jurassic of India (J. de C. Sowerby, 1840, pl. 22, fig. 4), but the latter differs in being more inflated and larger in size, and in having posteriorly directed umbones, which are terminal to sub-terminal in some varieties (see Jaitly et al., 1995, pl. 1, figs. 8–17, pl. 2, figs. 1, 2; present study, Fig. 12).

Palaeonucula variabilis (J. de C. Sowerby, 1825)
Figure 14.6–14.19

*1825 *Nucula variabilis* J. de C. Sowerby, p. 117, pl. 475, fig. 2.
.1829 *Nucula variabilis*; Phillips, p. 151, pl. 9, fig. 11, pl. 11, fig. 19.
.1833 *Nucula variabilis*; Zieten, p. 77, pl. 57, fig. 9a–c.
.1853 *Nucula variabilis*; Morris and Lycett, p. 51, pl. 5, figs. 13, 13a, pl. 9, fig. 5.
.1856 *Nucula variabilis*; Quenstedt, p. 188, pl. 23, fig. 28.
.1857 *Nucula variabilis*; Quenstedt, p. 765, pl. 93, fig. 15.
?1899 *Nucula variabilis*; Greppin, p. 98, pl. 9, figs. 2, 2a, b.
non .1916 *Nucula variabilis*?; Douvillé, p. 61, pl. 5, figs. 51–55 (= *Nuculoma douvillei* n. sp.).
1938 *Nucula variabilis*; Kuhn, p. 132, pl. 2, figs. 16a, b.
?1973 *Nucula variabilis*; Romanov, p. 29, pl. 1., figs. 28, 28a.
.1986 *Palaeonucula variabilis*; Pugaczewska, p. 50, pl. 15.4–15.7.
non .2014 *Nuculoma variabilis*; Abdelhady and Fürsich, p. 181, fig. 6G, H (= *Nuculoma douvillei* n. sp.).

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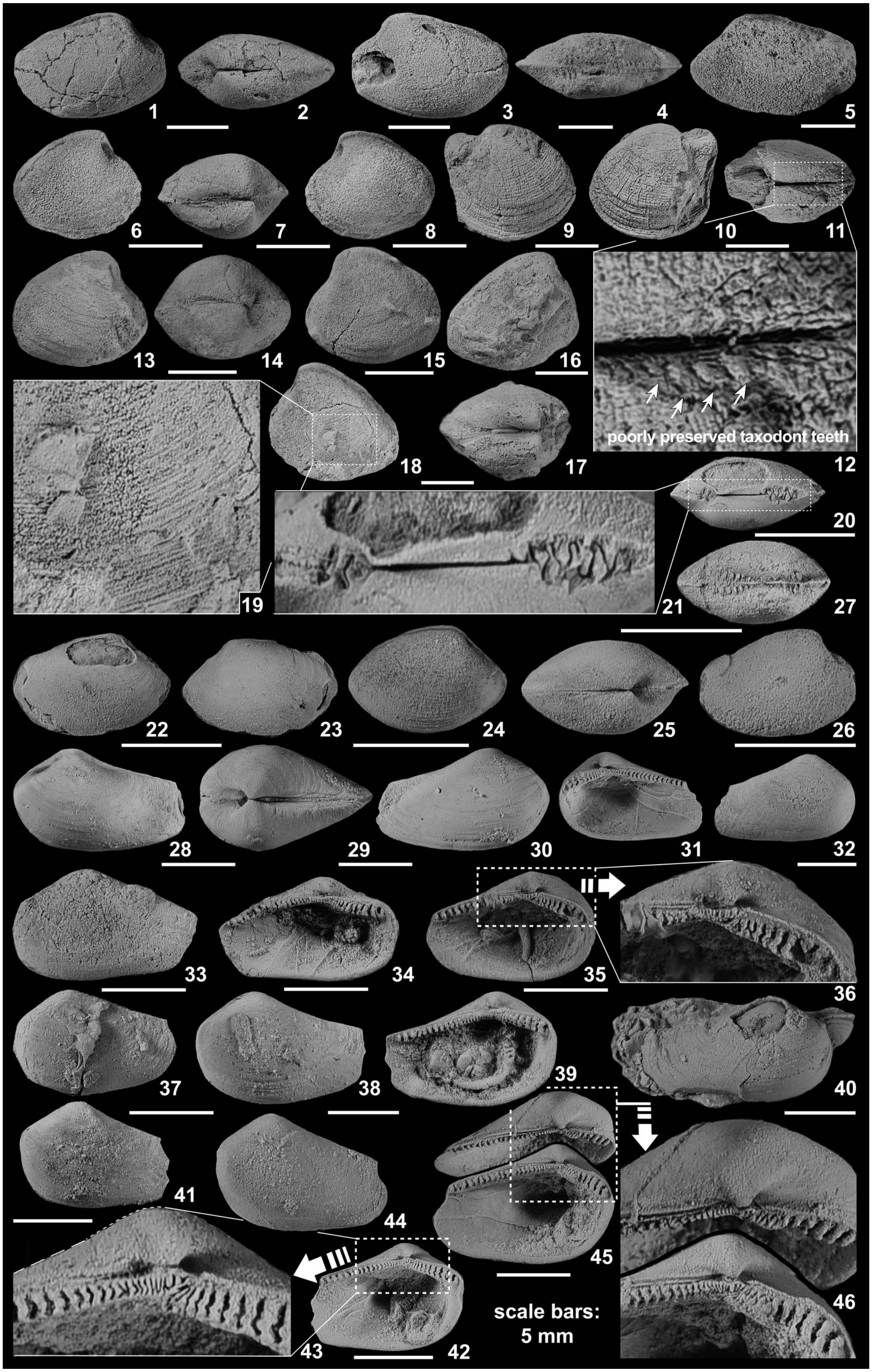

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Figure 14. (**1–5**) *Palaeonucula fraasi* (Noetling, 1887) from the middle–upper Bathonian Kehailia Formation, Gebel Homayir. (**1–3**) BSPG 2014V 331/1, left lateral view of composite mold, dorsal view, and right valve, respectively; (**4, 5**) BSPG 2014V 331/2, dorsal view showing traces of taxodont hinge, and internal mold of right valve, respectively. (**6–19**) *Palaeonucula variabilis* (J. de C. Sowerby, 1825) from the Middle–Upper Jurassic of Gebel Maghara; (**6–8**) BSPG 2014V 335/1, Masajid Formation, western Bir Maghara, left lateral view of composite mold, dorsal view, and right lateral view, respectively. (**9–15**) Kehailia Formation, Gebel Moweirib; (**9–12**) BSPG 2014V 319/1, right valve, left valve, dorsal view, and close-up, respectively, showing poorly preserved taxodont hinge, (**13–15**) BSPG 2014V 319/2, left lateral view showing slightly oblique sub-trigonal valve, dorsal view, and right lateral view, respectively; (**16–19**) BSPG 2014V 335/2, Masajid Formation, western Bir Maghara, left valve, dorsal view, right lateral view, and close-up showing fine, commarginal growth lines, respectively. (**20–27**) *Palaeonucula* sp. A. from the Middle–Upper Jurassic of Gebel Maghara; (**20–23**) BSPG 2014V 336/1, Kehailia Formation, Gebel Homayir, (**20**) dorsal view of articulated valves, (**21**) close-up showing traces of taxodont hinge (arrowed), (**22**) left lateral view, (**23**) right lateral view; (**24–27**) Masajid Formation, western Bir Maghara; (**24, 25**) BSPG 2014V 337/1, left lateral view and dorsal view showing deep escutcheon, respectively, (**26, 27**) BSPG 2014V 337/2, left lateral and dorsal views showing taxodont hinge. (**28–46**) *Palaeoneilo aegyptiaca* n. sp. from the Middle Jurassic (Bathonian−Callovian) of Gebel Maghara. (**28–30**) BSPG 2014V 249/1, holotype, Kehailia Formation, Gebel Homayir, left lateral view, dorsal view showing pointed and slightly prosogyrate beaks, and right valve, respectively; (**31–46**) paratypes, Bir Maghara Formation, Gebel Arousiah: (**31, 32**) interior view of left valve and exterior view of right valve, respectively, (**33, 34**) BSPG 2014V 144/2, left lateral view and interior view of left valve, respectively, (**35–37**) BSPG 2014V 144/3, interior view of left valve, close-up showing slightly convexodont to concavo-convexodont teeth, and left valve exterior, respectively, (**38, 39**) BSPG 2014V 144/4 left valve and left valve interior, respectively, (**40**) BSPG 2014V 144/5, right valve of elongated-ovate form of species, (**41–43**) BSPG 2014V 144/6, left valve, internal view of left valve, and close-up, respectively, showing slight overlap of posterior teeth above anterior row of teeth below umbo and no resilifer, (**44–46**) BSPG 2014V 144/7, left valve, interior and dorsal views of left valve, and close-up, respectively, showing the absence of resilifer and slight overlap of posterior teeth above anterior row of teeth. Scale bars = 5 mm.

Table 4. Measurements (in mm) of *Palaeonucula fraasi* (Noetling, 1887).

Specimens	L	H	Iav	Al	H/L	Iav/L	Al/L
BSPG 2014V 179/1	11.0	7.3	5.4	8.5	0.66	0.49	0.77
BSPG 2014V 301/1	16.5	10.2	?7.5	11.5	0.62	?0.45	0.70
BSPG 2014V 301/2	14.2	9.2	5.7	9.6	0.64	0.40	0.68
BSPG 2014V 301/3	10.0	6.2	4.4	7.7	0.62	0.44	0.77
BSPG 2014V 331/1	17.2	11.0	7.4	11.5	0.64	0.43	0.68
BSPG 2014V 333/1	14.0	9.0	?5.8	10.2	0.64	?0.41	0.73
BSPG 2014V 334/1	13.7	9.8	6.3	10.2	0.71	0.46	0.74
BSPG 2014V 334/2	12.3	7.7	4.8	9.5	0.63	0.39	0.77

Holotype.—*Nucula variabilis* J. de C. Sowerby, 1825, pl. 475, fig. 2, from the "Great Oolite" (Bathonian) of Ancliff, southern England.

Occurrence.—Upper Bajocian–lower Bathonian of Poland, Bajocian of Switzerland, Aalenian–Bathonian of southeastern England, Middle Jurassic (Bajocian) of Germany, upper Bajocian of central Asia (Moldavia and Turkmenia), and middle Bathonian–lower Kimmeridgian of the Maghara area, Sinai (present study).

Description.—Shell small, outline sub-trigonal, slightly oblique, inequilateral, equivalve, slightly longer than high (H/L: 0.83–0.95; Table 5), strongly inflated, and anterior length greater than posterior one. Maximum inflation at umbonal area. Anterodorsal margin slightly convex, meeting anterior margin in a nearly right angle. Posterodorsal margin short, slightly concave, meeting posterior margin in rounded angle. Anterior and posterior margins convex and meeting ventral margin in rounded curves. Ventral margin slightly convex. Umbo wide, inflated, not enrolled, located posteriorly (approximately one-third of total valve length from posterior end). Beaks sharply pointed, slightly opisthogyrate. Escutcheon well excavated, moderately wide, cordate-shaped, moderately deep. No lunule. Specimens are articulated, but the anterodorsal margin shows a taxodont hinge (Fig. 14.12). Shell thin, covered with distinct, fine, commarginal growth lines (Fig. 14.19).

Table 5. Measurements (in mm) of *Palaeonucula variabilis* (J. de C. Sowerby, 1825).

Specimens	L	H	Iav	Al	H/L	Iav/L	Al/L
BSPG2014V 319/1	9.5	9.0	6.5	7.2	0.95	0.68	0.75
BSPG2014V 319/2	10.3	8.8	7.3	7.2	0.85	0.71	0.69
BSPG2014V 335/1	8.4	7.0	5.7	6.2	0.83	0.68	0.74
BSPG2014V 335/2	13.0	12.4	9.2	9.5	0.95	0.71	0.73

Materials.—Six specimens, in shell preservation, from the middle Bathonian–lower Kimmeridgian of Gebel Maghara: four specimens from the middle–upper Bathonian Kehailia Formation, Gebel, Moweirib (BSPG 2014V 319/1–4) and two specimens from the higher part of the Masajid Formation (lower Kimmeridgian), western Bir Maghara (BSPG 2014V 335/1–2).

Measurements.—See Table 5.

Remarks.—*Palaeonucula variabilis* (J. de C. Sowerby, 1825) can be distinguished from other Jurassic *Palaeonucula* species such as *P. triangularis* Duff (1978, p. 23, pl. 1, figs. 6–13, 17, 23, text-fig. 6) from the Callovian of England and *P. cuevitana* Aberhan (1994, p. 9, pl. 1, figs. 1–4, text-fig. 2) from the Hettangian of northern Chile by having a slightly oblique sub-trigonal valve, a slightly convex ventral margin, a strongly inflated umbo, and in lacking a lunule. Moreover, its beak is located about one-third of the total valve length from the posterior end (sub-submesial in other taxa). The present specimens are closest in size, outline, and ornamentation to *Nucula* (*Palaeonucula*) *stoliczkai* Cox, 1940) (p. 20, pl. 1, figs. 21–23) from the Bathonian–Callovian rocks of India, but the latter has a well-rounded ventral margin, a sharply demarcated escutcheon (Cox, 1940, pl. 1, fig. 21b), and is much more trigonal than the present species. *Nucula variabilis* J. de C. Sowerby, as figured by Greppin (1899) and Romanov (1973) from the Bajocian of Switzerland and Russia, respectively, differ in being much more elongated than the holotype of J. de C. Sowerby (H/L = 0.83, J. de C. Sowerby, 1825, pl. 475, as opposed to 0.65, Romanov, 1973, pl. 1.28) and in having sub-terminal umbones. With respect to shell size and outline, the specimens from Switzerland and Russia are, in fact, much closer to *P. cuneiformis* (J. de C. Sowerby, 1840) (pl. 22, fig. 4) than to *N. variabilis*, and therefore, they are questionably regarded as junior synonyms of the latter. *Palaeonucula navis* (Piette, 1856) of Hodges (2000, p. 14, pl. 1, figs. 1–29, text-figs. 7–14) from the Lower Jurassic of

Table 6. Measurements (in mm) of *Palaeonucula* sp. A.

Specimens	L	H	Iav	Al	H/L	Iav/L	Al/L
BSPG 2014V 336/1	7.2	4.7	3.7	5.5	0.65	0.51	0.76
BSPG 2014V 337/1	6.1	4.2	3.5	5.0	0.69	0.57	0.81
BSPG 2014V 337/2	5.5	3.9	3.0	4.2	0.71	0.55	0.76
BSPG 2014V 337/3	5.1	3.5	2.6	4.1	0.68	0.51	0.80

England resembles *Palaeonucula variabilis* in having a subtrigonal shell, but differs in having a convex ventral margin, distinct escutcheon and corselet (Hodges, 2000, text-fig. 12b), and in being more inflated than the present species. In addition, the British species is stratigraphically older than *P. variabilis* (Lower Jurassic; Hodges, 2000, p. 21, text-fig. 14). The strongly inflated valves (maximum inflation close to ventral margin), sub-mesial umbo, and strongly convex ventral margin distinguish *Palaeonucula monnandi* (Chavan, 1952) figured by Delvene (2001, p. 50, pl. 1, fig. 5) from the upper Oxfordian–lower Kimmeridgian of Spain from *P. variabilis*.

Palaeonucula sp. A
Figure 14.20–14.27

Description.—Very small, nuculiform elongated-ovate, longer than high (H/L: 0.65–0.71), inequilateral, equivalved, moderately inflated. Anterior area greater than posterior one (Al/L: 0.76–0.81; Table 6). Anterodorsal margin slightly convex, meeting anterior one at nearly right angle. Posterodorsal margin short, sub-straight. Posterior margin narrow, blunt. Anterior margin strongly convex, narrow, meeting the regularly convex ventral margin in rounded curve. Umbo broad, inflated, located approximately one-third of total valve length from posterior end. Beaks sharply pointed, slightly opisthogyrate. Escutcheon narrow, deep, ovate (Fig. 14.25). Lunule very shallow, lanceolate, narrow. Hinge taxodont with numerous unequal teeth and sockets (Fig. 14.21, 14.27). Shell surface with fine commarginal threads.

Materials.—Five specimens in shell preservation from the Middle–Upper Jurassic of Gebel Maghara: a single specimen from the middle–upper Bathonian Kehailia Formation, Gebel Homayir (BSPG 2014V 336/1) and four specimens from the basal part of the Lower Kimmeridgian Masajid Formation, western Bir Maghara (BSPG 2014V 337/1–3; BSPG 2014V 420/1).

Measurements.—See Table 6.

Remarks.—With regard to overall shape and shell margins, the present specimens correspond well to *Palaeonucula menkii* (Roemer, 1836) as figured, for example, by Roemer (1836, p. 98, pl. 6, fig. 10) from the Middle Jurassic of North Germany, by Fürsich and Werner (1987, p. 108, pl. 1, figs. 1–3) from the Upper Jurassic of Portugal, and by Jaitly et al. (1995, p. 158, pl. 2, figs. 3–6) from the Middle–Upper Jurassic of western India. According to Delvene (2001, p. 50), *P. menkii* is a medium-sized nuculid with an average length of 14.0 mm. Because the holotype of Roemer (1836, p. 98, pl. 6, fig. 10) is much larger than the present specimens (L = 19.5 mm as opposed to L = 6.0 mm on average, Table 6), it is better to keep them in open nomenclature. The present specimens resemble *P. fraasi* (Noetling, 1887) from the Lower Jurassic of Syria (Noetling, 1887, fig. 24) in general outline, but the latter differs in having a less-inflated valve and in being larger than the present material.

Superorder Nuculaniformii Carter, Campbell, and Campbell, 2000
Order Nuculanida Carter, Campbell, and Campbell, 2000
Superfamily Malletioidea Adams and Adams, 1858
Family Cucullellidae Fischer, 1886
Subfamily Palaeoneilinae Babin, 1966
Genus *Palaeoneilo* Hall and Whitfield, 1869

Type species.—*Nuculites constricta* Conrad, 1842, from the Middle Devonian of New York State; subsequent designation by Hall (1885).

Remarks.—Some earlier workers (e.g., Hallam, 1976, 1977; Duff, 1978) did not accept *Palaeoneilo* as a Jurassic genus, because originally it has been recorded from Paleozoic rocks (e.g., Devonian of North America; Hall and Whitfield, 1869). The genus is also known from the Triassic of Europe, Mexico, Chile, New Zealand, China, and Japan and from the Jurassic of Switzerland, England, Sweden, Russia, India, and Japan (Damborenea, 1987, p. 54). Duff (1978) included some Jurassic species of *Palaeoneilo* in *Mesosaccella* Chavan, 1946, due to the lack of a resilifer and presence of a shallow radial sulcus close to the posterodorsal side. *Mesosaccella* originally had been erected on specimens from Campanian–Maastrichtian rocks (Upper Cretaceous) of Germany and had been placed in the family Nuculanidae by Müller (1847, p. 17, pl. 2, fig. 1).

Recently, Hryniewicz et al. (2014, p. 16) followed Duff's (1978) view and assigned some Jurassic *Palaeoneilo* species, such as *P. elliptica* (Goldfuss, 1837) from the Rhaetian–Pliensbachian of Europe (Palmer, 1973; Hodges, 2000) and *P. morrisi* (Deshayes, 1853) from the Callovian of England and France (Duff, 1978), to *Mesosaccella*, but on the basis of shell outline and ornamentation. Therefore, there is some confusion in the literature about the assignment of Mesozoic species to *Palaeoneilo* or *Mesosaccella*. Cox (1937) and Cox et al. (1969) stated that *Palaeoneilo* ranged from the Ordovician to the end of the Mesozoic and that there is no reason to separate the Paleozoic and Mesozoic species in different genera—a view that is not followed here. In fact, the distinction between the two genera is very difficult, especially because the type species of *Palaeoneilo* (*Nuculites constricta* Conrad, 1842, p. 249) from Middle Devonian strata of New York State is poorly known. According to Cox et al. (1969, p. N237) and Sha and Fürsich (1994, p. 40), the presence of a faint depression between anterior and posterior teeth below umbo, foreshadowing a resilifer, is typical of *Mesosaccella*. However, Carter (1990) observed a very small resilifer in the right valve of *Palaeoneilo elliptica* (Goldfuss, 1837) from the Lower Jurassic of Germany. In addition, some Devonian *Palaeoneilo* species also have a break in the alignment of the anterior and posterior hinge teeth (Hodges, 2000, p. 28). According to Aberhan (1998, p. 66), a feature common to both species-groups of *Palaeoneilo* (see Cox, 1937) is the tendency of the posterior teeth to pass above the anterior row of teeth in the area below the umbo. In the present study, the arrangement of hinge teeth is also variable; some specimens have continuous series of anterior and posterior teeth without resilifer, whereas the smallest posterior teeth of other specimens slightly extend above the anterior teeth below the umbo (Fig. 14.36, 14.43, 14.46). It is obvious that the absence or presence of a small depression between the posterior and anterior teeth is not a distinct enough feature to differentiate between the two genera.

Nuculites constricta Conrad, 1842, the type species of *Palaeoneilo* from the Middle Devonian of New York State, has a sulcus extending from the umbo to posteroventral corner. Referring to the extensive literature on this aspect, the majority of the Triassic and Jurassic *Palaeoneilo* species (as well as the present material) lacks a posteroventral sulcus. The latter is confirmed by Wasmer and Hautmann in Wasmer et al. (2012, p. 1048), who stated that the posterior flank of Triassic *Palaeoneilo* species lacks a shallow radial posteroventral sulcus. Cox (1937, p. 192–193), therefore, identified two groups within the genus *Palaeoneilo* ranging through the Paleozoic and Mesozoic. The first group can be distinguished by having a shallow posteroventral sulcus, as in the type species of *Palaeoneilo*, whereas the second group lacks this feature. Although the type species of *Mesosaccella* (*Nucula foersteri* Müller, 1847) from the Upper Cretaceous of Germany lacks the posteroventral sulcus, it exhibits a few other diagnostic features that are not present in the type of *Palaeoneilo*, including (1) a deeply excavated, comparatively narrow, well-demarcated lunule (absent or shallow in *Palaeoneilo*); (2) a long, narrow, and deep escutcheon (lacking in the type species of *Palaeoneilo*); (3) sharply pointed orthogyrate beaks; (4) angulated anterior and posterior ends (variable in *Palaeoneilo*); and (5) a relatively well-ornamented shell surface (smooth in *Palaeoneilo*).

Fürsich and Werner (1987, p. 111) and Sha and Fürsich (1994, p. 40) tried to amend the generic characteristics of *Mesosaccella* to include some additional diagnostic characters such as: (1) an elongated to slightly rostrate shell (less elongated than *Palaeoneilo*), (2) an entire pallial line or a shallow pallial sinus, (3) lack of a posterior sulcus, (4) straight or slightly concave anterior and posterior rows of teeth, and (5) an external amphidetic ligament. It is interesting to note that these features fit well some Cretaceous nuculanid taxa such as *Nuculana speetoniensis* Woods, 1899 (p. 3, pl. 1, figs. 6, 7) and *N. lineata* (J. de C. Sowerby, 1835) of Woods (1899, p. 7, pl. 1, figs. 28–32) from the Aptian–Albian of England; *Nuculana*? *mutuata* Stephenson, 1953 (p. 57, pl. 10, figs. 10–12) from the Cenomanian of Texas, *Mesosaccella donganensis* Sha and Fürsich, 1994) (p. 40, pl. 1, figs. 8–10, text-figs. 28, 29), and *M.*? *wunsuliensis* Sha and Fürsich, 1994 (p. 41, pl. 1, figs. 3–7, text-figs. 30, 31) from the Lower Cretaceous (Berriasian–Valanginian) of northeastern China.

For the reasons stated above, it is better to assign these Cretaceous species to *Mesosaccella* (as a Cretaceous genus). In agreement with Hodges (2000), *Palaeoneilo* is thought to be a conservative genus morphologically that changed very little in general shape from the Ordovician to Early Jurassic time interval. Ros et al. (2014, p. 16) pointed out that the last occurrence of

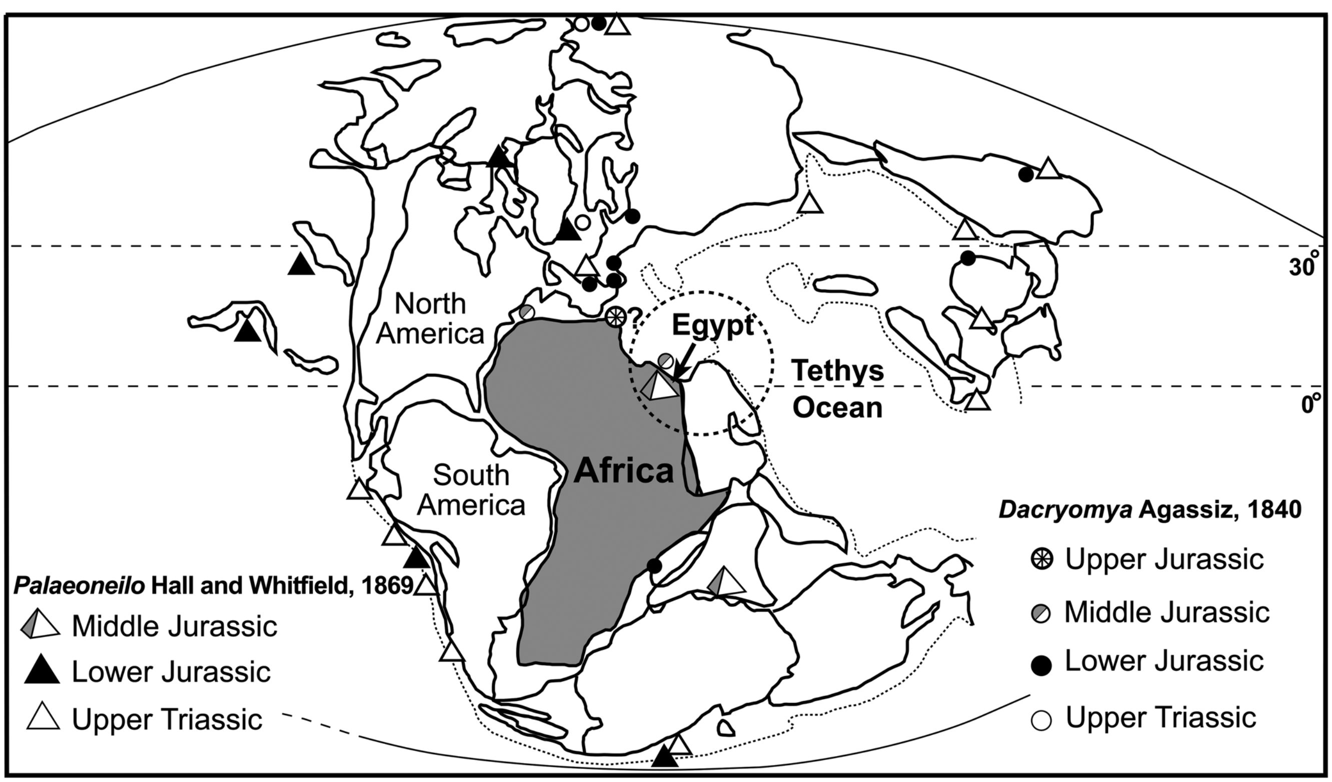


Figure 15. Paleogeographic distribution of *Palaeoneilo* Hall and Whitfield, 1869, and *Dacryomya* Agassiz, 1840, during Upper Triassic and Jurassic time (after Scotese, 2001). Data taken from Hayami (1961), Cox (1965), Choubert and Faure-Muret (1967), Kanjilal and Singh (1973), Kanjilal (1985), Aberhan (1994, 1998), Holzapfel (1998), Delvene (2001), Aberhan et al. (2011), Ros et al. (2014), and Jaitly (2017).

Palaeoneilo is in the upper Lower Jurassic (Toarcian) and did not accept any younger records, "since almost all have descriptive problems." As is demonstrated here, the genus certainly also occurs in the Middle Jurassic (Bajocian−Bathonian) of Gebel Maghara. This is its first record from Middle Jurassic rocks, not only in Egypt but also in North Africa (see Ros et al., 2014, fig. 3; Fig. 15).

Palaeoneilo aegyptiaca new species
Figures 14.28–14.46, 16.1–16.16, 17

Holotype.—Articulated specimen in shell preservation from the middle–upper Bathonian Kehailia Formation, Gebel Homayir (BSPG 2014V 249/1) (Fig. 14.28–14.30).

Paratypes.—Twenty-nine specimens, mostly disarticulated, in shell preservation: 23 specimens from the lower–upper Bajocian Bir Maghara Formation, Gebel Arousiah, Sinai (BSPG 2014V 143/1; 144/1–22), two specimens from the lower–upper Callovian Arousiah Formation, Gebel Mowerib (BSPG 2014V 136/1–2), and four specimens from the middle–upper Bathonian Kehailia Formation, Gebel Homayir (BSPG 2014V 241/1; 249/2–4).

Diagnosis.—Small Palaeoneilinae, variable in shape and outline, ranging from subtrapezoidal to subpentagonal, from elongated-ovate to subtriangular, strongly inequilateral, moderately to strongly inflated dorsally, compressed posteriorly, with an angulated anterior margin, a subtruncated posterior margin, a straight to slightly convex ventral margin, no posterior umbonal ridge or escutcheon, a shallow elongated-ovate lunule, sharply pointed and slightly prosogyrate beaks, a wide hinge with continuous series of gradidentate anterior and posterior teeth without resilifer, forming an obtuse angle of ∼130–145°; the smallest posterior teeth occasionally overlapping the anterior row of teeth below umbo; shell surface smooth.

Occurrence.—Lower Bajocian to upper Bathonian, Gebel Maghara.

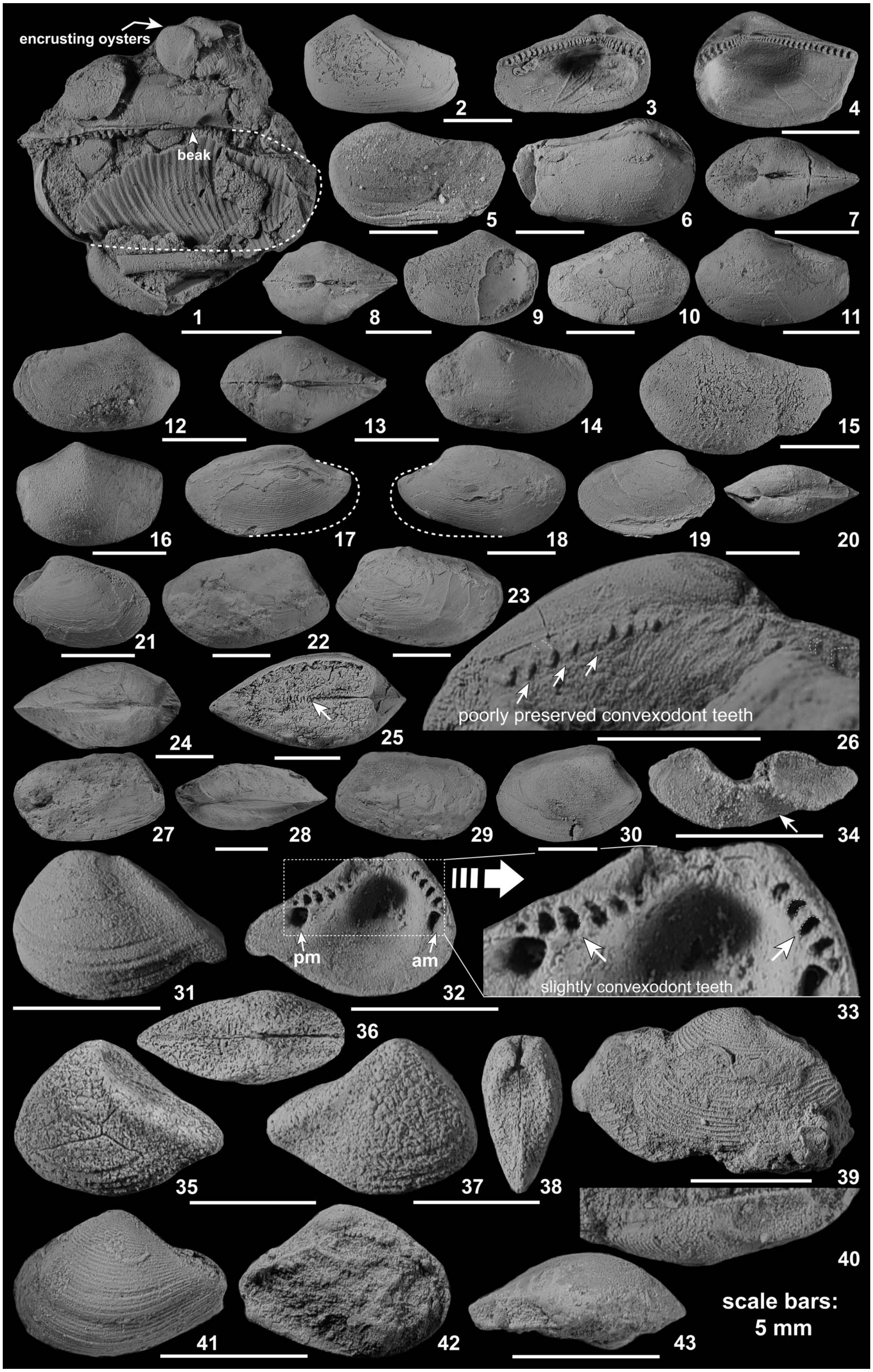
Description.—Shell small, variable in outline ranging from subtrapezoidal to subpentagonal (distinctly longer than high), from elongated-ovate to subtriangular (Fig. 17), longer than high (H/L ratio ∼0.60, on average; Table 7), inequilateral, equivalved, moderately to strongly inflated. Inflation greatest approximately one-third of total shell height from umbo, curvature flattening to slightly concave close to posterior margin, but no radial sulcus. Posterodorsal margin straight with narrow groove extending up to 3 mm from umbo towards posterior margin and referring to position of external amphidetic ligament (Fig. 14.46). Anterodorsal margin straight to slightly convex, forming a nearly right angle with anterior margin. Anterior margin narrowly angulated (Figs. 14.41, 16.2, 16.14, 17.1), meeting ventral margin in rounded curve. Posterior margin narrow, slightly convex to subtruncated and occasionally pointed. Ventral margin slightly convex to straight, occasionally sinuate close to posteroventral margin (Fig. 14.34). Umbones broad, little inflated, situated from one-third to one-fourth of total valve length from anterior end. Beaks sharply pointed, small, orthogyrate to slightly prosogyrate. No escutcheon or posterior umbonal ridge. Lunule shallow, narrow, elongated-ovate, deeply sunken towards beaks (Fig. 16.7, 16.8, 16.13). Posterior adductor muscle scar small, rounded. Hinge taxodont, gradidentate, arranged in two rows meeting below beak without resilifer (Fig. 14.46). Posterior hinge with 21–30 straight to slightly convexodont teeth, decreasing in size gradually towards umbo. Anterior hinge broad with 6–10 slightly convexodont to concavo-convexodont teeth, forming an obtuse angle of ∼130–145° with posterior hinge. Rows of teeth uninterrupted below umbo (Fig. 16.3, 16.4). Smallest posterior teeth occasionally extending above anterior row of teeth below umbo (Fig. 14.36, 14.43, 14.46). Shell surface smooth except for faint commarginal growth lines close to ventral margin.

Etymology.—After the type area of the species (Egypt).

Measurements.—See Table 7.

Remarks.—*Palaeoneilo aegyptiaca* n. sp. is a very variable species with respect to shape and shell outline (Fig. 17). It can be distinguished from other Jurassic *Palaeoneilo* species by having a smooth surface, a subtruncated posterior margin, an angulated anterior margin, a sharply pointed and slightly prosogyrate beak, a narrow elongated-ovate lunule (more sunken towards beaks), and by lacking an escutcheon and posterior umbonal ridge. The closest species appears to be *Palaeoneilo galatea* (d'Orbigny, 1850), which has been recorded from Lower Jurassic strata of central and western Europe. *Palaeoneilo galatea* differs, however, in having broad and depressed umbones, a rounded anterior margin, and a posterior umbonal ridge forming a flattened to weakly concave area between it and the posterodorsal margin (e.g., Aberhan et al., 2011, pl. 1, figs. 3, 4; Karapunar et al., 2020, pl. 2, figs. 4, 6). Moreover, it is less elongated and less inflated (H/L = 0.58, Iav/L = 0.33, respectively; Dumortier, 1869). In addition, the posterior and anterior teeth of *P. galatea* are straight to slightly concave, and meet in a more obtuse angle than *P. aegyptiaca* n. sp. (e.g., 156°, Damborenea, 1987, as opposed to 130–145°). *Palaeoneilo aegyptiaca* n. sp. also shares some similarities with *Leda trapezoidalis* Monke, 1888 (p. 216, pl. 2.3, figs. 8–8a) from the Lower Jurassic of Germany, which has been regarded as a synonym of *P. galatea* by Hodges (2000, p. 28) and Aberhan et al. (2011, p. 69). *Leda alpina* d'Orbigny, 1850 (p. 336, no. 136) from the Callovian of France figured by Cottreau (1925, p. 143, pl. 17 [38], fig. 3) differs in having a narrow and strongly convex posterior margin, a regularly rounded ventral margin, a concave posterodorsal margin, a straight anterodorsal margin, compressed umbones, and is more elongated than the present species (H/L = 0.46 as opposed to 0.60 on average; Table 7), and is much more inflated dorsally.

Mesosaccella morrisi (Deshayes, 1853) of Duff (1978, p. 28, pl. 1, figs. 22, 23–33, text-fig. 7) and Fürsich and Pan (2014, p. 6, pl. 1, figs. 1–3) from the Callovian–Oxfordian of England and Iran, respectively, resemble *P. aegyptiaca* n. sp. in having an angulated anterior margin and an elongated and inflated valve, but differ in having submesial umbones, well-


encrusting oysters
beak
1
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3
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18
19
20
21
22
23
24
25
poorly preserved convexodont teeth
26
27
28
29
30
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31
pm
am
32
slightly convexodont teeth
33
36
35
37
38
39
40
41
42
43
scale bars:
5 mm

←

Figure 16. (**1–16**) Variation in outline of *Palaeoneilo aegyptiaca* n. sp. paratypes from the Middle Jurassic of Gebel Maghara. (**1**) BSPG 2014V 136/1, Arousiah Formation, Gebel Mowerib, left valve, elongated-ovate form with oyster encrustations; (**2, 3**) BSPG 2014V 144/8, Bir Maghara Formation, Gebel Arousiah, left lateral view showing angulated anterior margin and left valve interior, respectively; (**4**) BSPG 2014V 249/2, Kehailia Formation, Gebel Homayir, right valve interior showing a continuous series of gradidentate anterior and posterior teeth without resilifer; (**5–16**) Bir Maghara Formation, Gebel Arousiah; (**5, 6**) BSPG 2014V 144/9, left lateral view of elongated-ovate form with straight ventral margin and right lateral view, respectively, (**7**) BSPG 2014V 144/10, dorsal view, (**8**) BSPG 2014V 144/11, dorsal view, (**9–11**) BSPG 2014V 144/12, right lateral view, right valve, and left valve, respectively, of less elongated-ovate form of species, (**12–14**) BSPG 2014V 144/13, right valve, dorsal view with narrow lunule, and left lateral view of sub-pentagonal form of species, (**15**) BSPG 2014V 144/14, left lateral view, (**16**) BSPG 2014V 144/15, left lateral view of sub-triangular form of species. (**17–30**) Variation in outline of *Palaeoneilo muensteri* (Goldfuss, 1841) from the Lower Jurassic (Toarcian) Rajabiah Formation, western Bir Maghara. (**17, 18**) BSPG 2014V 338/1, right lateral view and left valve respectively, (**19–21**) BSPG 2014V 338/2, right valve, (**20**) dorsal view showing the deep lunule, and left valve, respectively, (**22–24**) BSPG 2014V 338/3, right lateral view, left valve, and dorsal view, respectively, (**25**) BSPG 2014V 338/4, dorsal view showing traces of taxodont hinge (arrowed), (**26**) BSPG 2014V 338/5, close-up showing the poorly preserved convexodont teeth (arrowed), (**27–29**) right valve, dorsal view, and left valve, respectively, (**30**) BSPG 2014V 338/7, right valve. (**31–38**) *Dacryomya diana* (d'Orbigny, 1850) from the middle−late Bathonian Kehailia Formation, Gebel Mowerib. (**31–34**) BSPG 2014V240/1; (**31**) left lateral view showing narrow posterior end with deep sulcus, (**32**) interior view of left valve, (**33**) close-up showing few slightly convexodont teeth and small, sub-rounded anterior and posterior adductor muscle scars, (**34**) dorsal view showing a well-developed posterior umbonal ridge with deep sulcus (arrowed), (**35–38**) BSPG 2014V240/2, left valve, dorsal view, right valve, and posterodorsal view, respectively. (**39–43**) *Dacryomya lacryma* (J. de C. Sowerby, 1824) from the Lower−Middle Jurassic of Gebel Maghara. (**39, 40**) BSPG 2014V 339/1, Bir Maghara Formation, Gebel Arousiah, left lateral and dorsal views, respectively, (**41–43**) BSPG 2014V BSPG 2014V 340/1, Kehailia Formation, Gebel Mowerib, (**41**) left valve, (**42**) left valve interior with traces of taxodont hinge, (**43**) dorsal view. Scale bars = 5 mm.

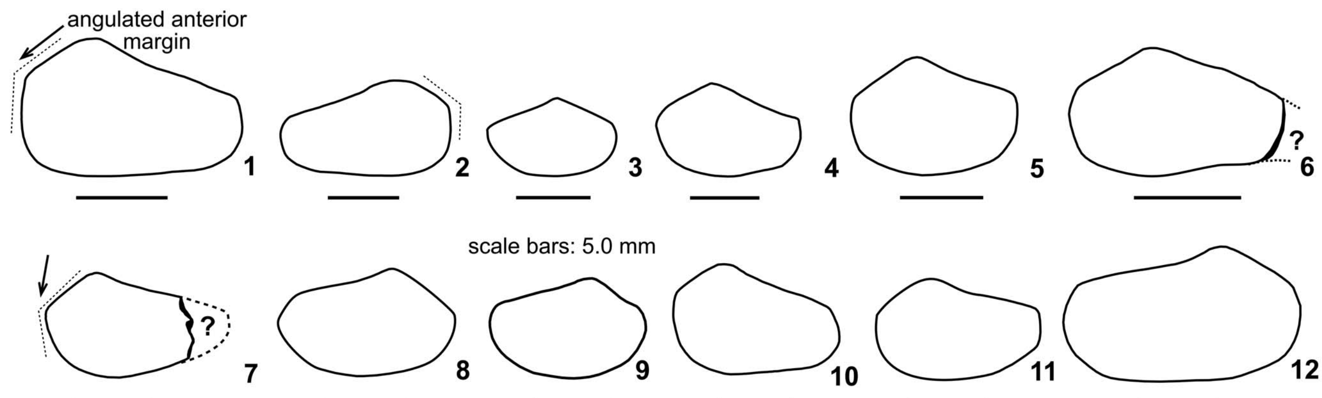

Figure 17. (**1–12**) Variation in outline of *Palaeoneilo aegyptiaca* n. sp. from the Middle Jurassic of Gebel Maghara. Specimens from several populations collected from the studied sections. Scale bars = 5 mm.

developed commarginal ribs, small resilifers, regularly rounded ventral margins, and less-prominent beaks. *Palaeoneilo*? *patagonidica* (Leanza, 1942) figured and described by Damborenea and Pagani (2019, p. 939, figs. 6.10–16, 7.6) from the Lower Jurassic of Argentina has strongly rounded shell margins, less-prominent beaks, less-inflated valves, and a higher number of anterior teeth (up to 13 as opposed to 6–10 in *P. aegyptiaca* n. sp.). *Leda palmae* (J. de C. Sowerby, 1825) figured by Dumortier (1869, p. 120, pl. 19, figs. 3, 4) from the Lower Jurassic of France differs from the present species by subcentral umbones and rounded margins. Cox (1965, p. 25, pl. 1, fig. 1) erected *P. asaharbitensis* from Bathonian–?Callovian beds of Kenya based on a single internal mold. The latter species probably falls within the range of

Table 7. Measurements (in mm) of *Palaeoneilo aegyptiaca* n. sp.

Specimens	L	H	Iav	Isv	Al	H/L	Iav/L	Al/L
BSPG 2014V 144/1	11.6	7.0	—	3.5	4.0	0.60	0.30	0.34
BSPG 2014V 144/2	9.8	6.8	6.0	—	4.3	0.69	0.61	0.44
BSPG 2014V 144/3	13.2	7.7	6.8	—	5.2	0.58	0.51	0.39
BSPG 2014V 144/4	11.2	6.7	6.0	—	4.7	0.60	0.53	0.42
BSPG 2014V 144/5	12.0	7.3	—	3.5	3.9	0.61	0.29	0.33
BSPG 2014V 144/6	?10.8	6.3	—	3.0	4.1	0.58	0.27	0.38
BSPG 2014V 249/1	11.7	6.6	6.2	—	4.5	0.56	0.53	0.38

variation of known Jurassic *Palaeoneilo* species. However, *P. asaharbitensis* differs from *P. aegyptiaca* n. sp. in having a strongly rounded anterior margin, and its posterodorsal margin is straight, oblique, and forms an acute angle with the posterior margin. *Palaeoneilo bornholmiensis* (von Seebach, 1865) figured by Troedsson (1951, p. 150, pl. 16, fig. 3, text-fig. 39) from the Lower Jurassic of Sweden resembles *P. aegyptiaca* n. sp. in having an elongated valve, anteriorly placed umbones, smooth shell surface, but differs in having a convex ventral margin, a rounded anterior margin, slightly concave antero- and posterodorsal margins, and in being smaller (L = 7.5, H = 4.0 mm) and more elongated than the present species. The latter diagnostic features clearly fall into the range of variation of *Palaeoneilo elliptica* (Goldfuss, 1837) and, therefore, has been regarded as a junior synonym of the latter by Hodges (2000, p. 28). de Loriol (1899) described and figured *Nucula longiuscula* Mérian from the Oxfordian of Switzerland (de Loriol, 1899, p. 159, pl. 10, figs. 23–25) (Mérian only used the species name on a museum label; de Loriol subsequently established the species with Mérian as author). Based on the hinge structure, his specimens likely belong to *Palaeoneilo*, but differ from *P. aegyptiaca* n. sp. in having a strongly concave anterodorsal margin, well-developed lunule and escutcheon, less prominent beaks, and in being more inflated.

Palaeoneilo muensteri (Goldfuss, 1841)
Figure 16.17–16.30

.1837 *Nucula elliptica* Goldfuss, p. 153, pl. 124, fig. 16a–e [non *Nucula elliptica* Phillips, 1829].
*1841 *Nucula Münsteri* Goldfuss, p. 304. [nom. nov. for *Nucula elliptica* Goldfuss, 1837].
.1852 *Nucula tunicata* Quenstedt, p. 529, pl. 44, fig. 9.
.1888 *Leda trapezoidalis* Monke, p. 216, pl. 2.3, figs. 8, 8a.
p.1936 *Leda galathea*; Kuhn, p. 259, pl. 9, fig. 9a, b; non fig. 5a–c [= *Palaeoneilo galatea* (d'Orbigny, 1850)].
p.1937 *Palaeoneilo galatea*; Cox, p. 191, pl. 5, figs 5–7, non fig. 4.
.1951 *Palaeoneilo oviformis* Troedsson, p. 151, pl. 16, figs. 7, 8, 12, 17.
.1951 *Palaeoneilo galatea*; Troedsson, p. 149, pl. 16, figs. 1, 2, 6, (9–11?).
.1951 *Palaeoneilo bornholmiensis*; Troedsson, p. 150, pl. 16, fig. 3.
.1990 *Palaeoneilo elliptica*; Carter, p. 159, fig. 12A–E.
.2000 *Palaeoneilo elliptica*; Hodges, p. 28, pl. 2, figs. 1–30, text-figs. 25–33 (with extensive synonymy).
non .2008 *Palaeoneilo elliptica*; Scholz et al., p. 274, fig. 4A, B.
.2011 *Palaeoneilo elliptica*; Aberhan et al., p. 68, pl. 1, figs. 1, 2.
.2020 *Palaeoneilo muensteri*; Karapunar et al. p. 11, pl. 2, figs. 1–3, pl. 10, fig. 9, text-figs. 4–6.

Holotype.—*Nucula elliptica* Goldfuss, 1837, pl. 124, fig. 16a–e from the Lower Jurassic (Pliensbachian) of Germany.

Occurrence.—Lower Jurassic of Germany (Pliensbachian), southwestern England (Sinemurian), France, Upper Triassic of Italy, New Zealand, South America, and from Lower Jurassic (Toarcian) of Sinai (present study, first record).

Description.—Shell small, outline subelliptical, inequilateral, longer than high (H/L = 0.63 on average; Table 8), equivalved, and moderately inflated. Maximum inflation at about anterior third of total valve length. Posterior area approximately twice as long as anterior one. Posterodorsal margin straight, slightly convex, meeting posterior margin in rounded angle. Anterodorsal margin short, slightly concave, forming a blunt angle with anterior margin. Posterior margin rounded, narrow, occasionally sharply rounded, meeting ventral margin in continuous rounded curve. Ventral margin gently convex. Umbo low, moderately inflated, located about one-third of total valve length from anterior end. Beak hardly prominent and slightly prosogyrate. Hinge teeth not well preserved, but clearly taxodont (Fig. 16.25, 16.26). Posterior teeth partially well preserved, convexodont, and gradually decreasing in size towards beak (Fig. 16.26). No escutcheon. Lunule well defined, cordate, moderately deep. Shell surface smooth except for fine commarginal ribs close to ventral margin (Fig. 16.17, 16.18).

Table 8. Measurements (in mm) of *Palaeoneilo muensteri* (Goldfuss, 1841).

Specimens	L	H	Iav	Al	H/L	Iav/L	Al/L
BSPG 2014V 338/1	15.6	10.0	?6.5	4.5	0.64	?0.41	0.29
BSPG 2014V 338/2	9.2	5.7	3.6	3.3	0.61	0.39	0.36
BSPG 2014V 338/3	12.4	7.8	5.1	3.8	0.63	0.41	0.31
BSPG 2014V 338/4	16.2	8.5	5.6	6.3	0.52	0.34	0.38

Materials.—Ten composite molds, occasionally in shell preservation (BSPG 2014V 338/1–10), from the Lower Jurassic (Toarcian) Rajabiah Formation, western Bir Maghara (BSPG 2014V 317/1–10), Gebel Maghara.

Measurements.—See Table 8.

Remarks.—Hodges (2000) carefully examined *Palaeoneilo muensteri* [as *Palaeoneilo elliptica* (Goldfuss, 1837)] and analyzed a large number of specimens from the Lower Jurassic (Lower Lias) of England. He noted that the species is highly variable with respect to height/length ratio, shell inflation, and length of anterior area (see biometric analyses of Hodges, 2000, p. 29–31, text-figs. 25–30, and shell forms, pl. 2, figs. 1–30). The present material clearly falls into the range of variation given by Hodges (2000). Karapunar et al. (2020) discussed the problematic aspects of the species name, which was erected by Goldfuss (1837) as *Nucula elliptica* from the Lias of northern Germany. After a detailed discussion, they corrected the name of the species to *Palaeoneilo muensteri*—a correction that is accepted here (see Karapunar et al., 2020, p. 12–13 for details). *Palaeoneilo muensteri* can be distinguished from other Lower Jurassic *Palaeoneilo* species by having an elliptical to subelliptical valve, a narrowly rounded posterior margin (occasionally angulated), a faintly convex ventral margin, a slightly prominent, slightly prosogyrate beak, a deep lunule, and by lacking an umbonal posterior ridge. In addition, Hodges (2000) noted that the flank of *P. elliptica* carries fine commarginal striae obliquely crossed by straight striae. He considered the latter ornament as a diagnostic feature of *P. elliptica*. Recently, Karapunar et al. (2020) observed the same ornamentation in other Lower Jurassic *Palaeoneilo* species, such as *P. galatea*. It generally seems to be visible in well-preserved preserved specimens of the genus *Palaeoneilo*. The most closely related species is *P. galatea* (d'Orbigny, 1850), which has been recorded from the Lower Jurassic at different localities in Europe, South America, and China. According to Hodges (2000), *P. galatea* can be distinguished from *P. elliptica* by having an angulate posterior margin. In addition, *P. galatea* has a well-developed posterior umbonal ridge and a flattened to feebly concave area between the umbonal ridge and posterodorsal margin (see Kuhn, 1935, pl. 18, fig. 30a–c; Aberhan et al., 2011, pl. 1, figs. 3, 4; Karapunar et al., 2020, pl. 2, figs. 4–6).

The high variability of *P. muensteri* prompted some authors to erect new species such as *Nucula tunicata* Quenstedt, 1852, and *Leda trapezoidalis* Monke, 1888, from Germany, and *Palaeoneilo oviformis* Troedsson, 1951, from Sweden. Hodges (2000) revised these latter species and noted that most of them lie well within the range of variation of *P. muensteri* (as *P. elliptica*)—a view that is followed here.

"*Nucula*" *patagonidica* from the Lower Jurassic of Argentina was erected by A. Leanza (1942, p. 151, pl. 1, figs. 1, 2, 4, non fig. 3). The latter species strongly resembles *P. muensteri* in having an elongated shell, little prominent beaks, and low umbones, but differs in having strongly rounded shell margins. In addition, the hinge plate of "*N.*" *patagonidica* is gently convex throughout without posterodorsal angle and its external surface is less inflated with faint commarginal growth lines that become stronger ventrally (Damborenea, 1987, p. 54–55; Damborenea and Pagani, 2019, p. 939, fig. 6.10–6.16). Hodges (2000, p. 28) and Scholz et al. (2008, p. 274) regarded *P. patagonidica* (Leanza, 1942) as a junior synonym of *P. elliptica* (Goldfuss), arguing that some transitional forms exist between the two species. Damborenea and Pagani (2019) did not accept the latter view and kept it as a separate species. *Palaeoneilo aegyptiaca* n. sp. from the early–late Bajocian Bir Maghara Formation (described above) has an elongated subtrapezoidal valve, a smooth surface, an angulated anterior margin, a sharply pointed orthogyrate to slightly prosogyrate beak, and no lunule. With respect to general outline, height/length ratio, and ornamentation, *Leda alpina* d'Orbigny (1850, p. 336, no. 136) from the Callovian of France figured by Cottreau (1925, p. 143, pl. 17 [38], fig. 3) resembles the present species, but differs in having a straight anterodorsal margin (forming an obtuse angle with the posterodorsal margin), a strongly rounded posterior margin, a strongly concave posterodorsal margin, and more-inflated umbones. For more details concerning *P. muensteri* and other closely related taxa, see Hodges (2000, p. 34), Aberhan et al. (2011, p. 68–69), and Karapunar et al. (2020, p. 12–13).

Superfamily Nuculanoidea Adams and Adams, 1858
Family Polidevciidae Kumpera, Prantl, and Růžička, 1960
Genus *Dacryomya* Agassiz, 1840

Type species.—*Nucula lacryma* J. de C. Sowerby, 1824, from the "Great Oolite" (Bathonian) of Ancliff, southern England; subsequent designation by Herrmannsen (1846, p. 368).

Remarks.—According to Ros et al. (2014, p. 20), there is no consensus about the family affiliation of the genus *Dacryomya*. It was assigned to Nuculanidae (e.g., Cox et al., 1969; Hayami, 1975), Nuculidae (e.g., Hodges, 2000; Karapunar et al., 2020) or to Polidevciidae (Carter, 1990; Jaitly et al., 1995; Delvene, 2001). The Ordovician–Upper Jurassic subfamily Polidevciinae was erected by Kumpera et al. (1960, p. 33–34) during their revision of the Nuculanidae from the Ostrava-Karviná District based on a strong posterior umbonal ridge, a short rostrum, and an internal ligament. Later, Carter (1990) raised the subfamily Polidevciinae to family rank (Polidevciidae Kumpera et al., 1960) based on ligament structure and shell microstructure. Recently, Carter et al. (2015, p. 3) added other diagnostic features for this family, such as (1) nacreous, not porcelaneous shells; (2) a shallow to deep submarginal resilium; (3) an external weakly mineralized ligament; and (4) paleotaxodont hinge teeth.

In agreement with Ros et al. (2014, p. 20), *Dacryomya* is provisionally assigned herein to the family Polidevciidae until a larger data base is available to investigate carefully the ligamental structure. For more details concerning the diagnostic features of Polidevciidae and comparison with closely related families, see Ros et al. (2014) and Carter et al. (2015, p. 3, 6). Apart from ligament structure, the genera that belong to Polidevciidae can be distinguished from other nuculanid genera such as *Nuculana* and *Ryderia* by having a relatively short rostrum, strong posterior umbonal ridge (folded in cross-section), deep umbonal posterior sulcus, well-developed shallow escutcheon (without distinct ridge), a smaller number of anterior and posterior teeth, and a greater inflation. According to Ros et al. (2014, p. 20, fig. 4), *Dacryomya* has a long stratigraphic range (from Norian to Kimmeridgian) and probably also occurs in the Lower Triassic. It has been recorded from Upper Triassic–Lower Jurassic rocks of England and Lower Jurassic rocks of Portugal, Germany, Switzerland, France, China, Japan, Siberia, and the Arctic region. The youngest record of the genus is from the Upper Oxfordian Sot de Chera Formation of Spain (Delvene, 2001). Mongin (1967, p. 41, pl. 1, figs. 15, 16) recorded *Nuculana* (*Dacryomya*) cf. *D. lacryma* (Sowerby) from the Bathonian of Morocco, and Holzapfel (1998, p. 95, pl. 3, fig. 5a, b) recorded *Dacryomya acuta* Mérian (of de Loriol, 1899, p. 164, pl. 10, figs. 29–32) from the Callovian–Oxfordian of southern Tunisia. Because Holzapfel's specimens are internal molds, her placement of the specimen in *Dacryomya* is somewhat doubtful. Based on Figure 13, Holzapfel's specimen is much closer to *Palaeonucula* than *Dacryomya*. In the present study, *Dacryomya* is recorded from the Lower–Middle Jurassic of Egypt for the first time (Fig. 15).

Dacryomya diana (d'Orbigny, 1850)
Figure 16.31–16.38

.1837 *Nucula mucronata*; Goldfuss, p. 155, pl. 125, fig. 9a–d (non Sowerby, 1825).
*1850 *Leda Diana* d'Orbigny, p. 253.
p.1856 *Nucula claviformis*; Quenstedt, p. 313, pl. 43, fig. 4, non figs. 5, 6.
.1856 *Leda Diana*; Oppel, p. 398.
.1874 *Leda diana*; Dumortier, p. 298, pl. 6, figs. 14, 15.
p.1884 *Nucula claviformis*; Quenstedt, p. 804, pl. 63, fig. 22, non fig. 23.
.1904 *Leda diana*; Borissjak, p. 42, pl. 3, fig. 1-b.
.1929 *Leda* cf. *diana*; Frebold, p. 265, pl. 3 (35), fig. 7.
.1966 *Nuculana diana*; Klöcker, p. 222, fig. 2.
.1990 *Nuculana diana*; Etter, pl. 3, fig. 8 (right valve).

Holotype.—*Nucula mucronata* Goldfuss, 1837, pl. 125, fig. 9, from "E stratis Lias dictis Franconiae et Württembergiae" (Lower Jurassic of southern Germany).

Occurrence.—Lower–Middle Jurassic strata of southwestern Spitsbergen, France, Germany, Russia, and from the Middle Jurassic of Sinai (present study, first record).

Table 9. Measurements (in mm) of *Dacryomya diana* (d'Orbigny, 1850).

Specimens	L	H	Iav	Isv	H/L	Iav/L	Isv/L
BSPG 2014V 240/1	7.5	5.5	3.5	—	0.73	0.47	—
BSPG 2014V 240/2	7.0	5.2	—	1.9	0.74	—	0.27

Description.—Small nuculaniform shell, subtriangular in outline, inequilateral, equivalved, longer than high (H/L = 0.73; Table 9), with short posterior rostrum, and moderate inflation. Anterior margin strongly convex, meeting ventral margin in rounded curve. Posterodorsal margin slightly concave. Anterodorsal margin slightly convex. Posterior end of rostrum narrow, short, and angular. Umbo inflated, triangular, and located slightly anterior of the mid-length of valve. Beak sharply pointed and slightly opisthogyrate. Posterior umbonal ridge blunt, extending from umbo to posteroventral corner, and separating strongly concave posterodorsal flank from the rest of valve (Fig. 16.34). Deep sulcus anterior of the posterior umbonal ridge (max. width: 2.2 mm) widening posteroventrally (Fig. 16.31, 16.35). Escutcheon shallow, elongated, lanceolate, and ornamented with faint riblets. Lunule narrow and shallowly depressed. Anterior and posterior adductor muscle scars subrounded, isomyarian, strongly impressed, and located close to anterior and posterodorsal margin, respectively (Fig. 16.32). Pallial line distinct, entire. Inner shell margin smooth. Hinge plate wide, with rows of slightly convexodont teeth (Fig. 16.33). Shell surface smooth except for well-developed commarginal ribs close to ventral margin.

Materials.—Three specimens, one in shell preservation and two composite molds (BSPG 2014V 240/1–3) from the middle–late Bathonian Kehailia Formation of Gebel Mowerib, Sinai.

Measurements.—See Table 9.

Remarks.—*Dacryomya diana* (d'Orbigny, 1850) can be distinguished from other Jurassic nuculanids by having a triangular valve, strongly rounded anterior and ventral margins, a well-defined and ornamented escutcheon, a slightly rostrate and narrow posterior end, and a well-developed posterior umbonal ridge with a deep sulcus located anterior of it (Fig. 16.34, 16.35). d'Orbigny (1850) had regarded *Nucula mucronata* as figured and described by Goldfuss (1837, p. 156, pl. 126, figs. 9a–d; non J. Sowerby, 1825) from the Lower Jurassic of Germany as the holotype of his new species *Leda diana* from the Lower Jurassic (Toarcian) of France [lectotype and lectostratotype: Goldfuss' material, E stratis Lias dictis Franconiae et Württembergiae, Germany]. *Nucula mucronata* J. de. C. Sowerby (1825, p. 120, pl. 476, fig. 4) from the Bajocian of England has a sub-rhombohedral valve, a narrower rostrum, a strongly convex ventral margin (sinuate posteriorly), well-developed commarginal ribs between posterior umbonal ridge and anterior margin, and is less elongated and less inflated than the present material. Quenstedt (1884) suggested that *D. diana* is a juvenile form of *N. rostralis* (Lamarck, 1819). As long as no intermediate forms are recorded from Jurassic strata, the suggestion of Quenstedt is not acceptable. In addition, *N. rostralis* has a much longer rostrum than *D. diana*, well-developed ridges bordering the deep escutcheon (see Goldfuss, 1837, pl. 125, fig. 8c), and an elongated shallow lanceolate lunule. Klöcker (1966, p. 220) regarded *Nucula claviformis* J. de C. Sowerby, 1825 (p. 119, pl. 476, fig. 2) from the Upper Jurassic of England as a synonym of *N. rostralis*. Although the two species are very similar, *N. claviformis* has a shorter rostrum, a deeper posterior sulcus, lacks a lunule, and its posterior umbonal ridge is less developed and concave posterodorsally (straight in *N. rostralis*). Another very similar species is *Leda medusa* Borissjak, 1904, from the Callovian–Oxfordian of Russia (Borissjak, 1904, p. 43, pl. 3, figs. 2a–e, 3a–e, 4a–e). The latter species can be distinguished by its large and thick valve, smooth escutcheon and lunule, a strongly inflated umbo with well-developed beak, and irregular commarginal growth lines. *Nuculana* (*Dacryomya*) *lacryma* (J. de. C. Sowerby, 1825) figured by Cox (1940, p. 29, pl. 2, figs. 2–5) and Jaitly et al. (1995, p. 161, pl. 2, figs. 21–23) from the Middle Jurassic of western India resembles the present species in having a well-developed posterior umbonal ridge, a posterior sulcus, and fine commarginal ribs, but differs in having a more rostrate posterior elongation, a deep escutcheon (delimited by a blunt ridge; e.g., Cox, 1940, pl. 2, fig. 2b; Jaitly et al., 1995, pl. 2, figs. 21b, 23b), and a strongly convex anterodorsal margin.

Dacryomya lacryma (J. de C. Sowerby, 1824)
Figures 16.39–16.43, 18.1–18.7

*1824 *Nucula lacryma* J. de. C. Sowerby, p. 119, pl. 476, fig. 3.
.1857 *Nucula lacryma*; Quenstedt, p. 505, pl. 67, figs. 18–21.
.1867 *Nucula lacryma*; Ogérien, p. 775, fig. 426.
.1899 *Leda lacryma*; Greppin, p. 97, pl. 9, figs. 1, 1a.
.1912 *Leda lacryma*; Cossmann, p. 7, pl. 3, figs. 11–13.
.1936 *Leda lacryma*; Marzloff et al., p. 108, pl. 12, figs. 9, 10a, b.
.1938 *Leda lacryma*; Kuhn, p. 132, pl. 5, fig. 6.
.1940 *Nuculana* (*Dacryomya*) *lacryma*; Cox, p. 29, pl. 2, figs. 2–5.
.1956 *Nuculana* (*Dacryomya*) *lacryma*; Agrawal, p. 55, pl. 7, fig. 3c.
?1967 *Nuculana* (*Dacryomya*) cf. *lacryma*; Mongin, p. 41, pl. 1, figs. 15, 16.
.1973 *Leda lacryma*; Romanov, p. 35, pl. 2, figs. 8–12.
.1995 *Dacryomya lacryma*; Jaitly et al., p. 161, pl. 2, figs. 21–23, text-fig. 13.
v1989 *Nuculana rostrata* Ali, p. 89, pl. 24, figs. 1–7. [Homonym of the type species of *Nuculana*, viz. *N. rostrata* (Gmelin, 1791)]
v2002 *Nuculana rostrata*; Abdelhamid, pl. 5, figs. 7, 8. [= *Dacryomya lacryma* (J. de C. Sowerby, 1824)]
v2003 *Cuspidaria* sp., Khalil, pl. 1, figs. 18, 19. [= *D. lacryma* (J. de C. Sowerby, 1824)]

Holotype.—*Nucula lacryma* J. de. C. Sowerby, 1824, pl. 476, fig. 3, from the "Great Oolite" (Bathonian) of Ancliff, southern England.

Occurrence.—Bajocian–Bathonian of England, Germany, France, USSR, Bajocian of Switzerland, upper Bajocian–lower Kimmeridgian of western India, ?Bathonian of Morocco, and Bajocian–Callovian of Gebel Maghara (first record).

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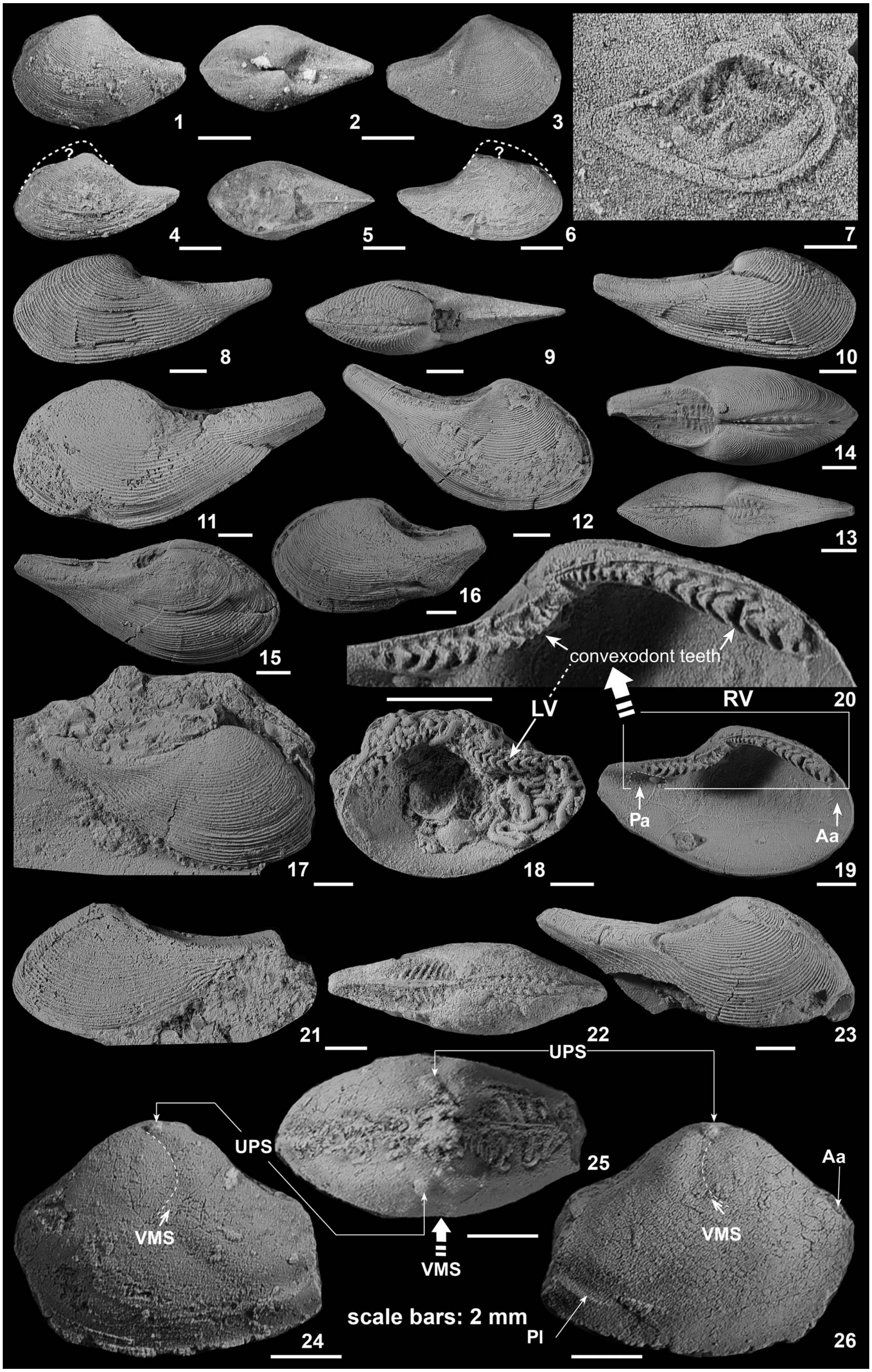

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Figure 18. (**1–7**) *Dacryomya lacryma* (J. de C. Sowerby, 1824) from the Lower–Middle Jurassic of Gebel Maghara. (**1–6**) Shusha Formation, western Bir Maghara; (**1–3**) BSPG 2014V 417/1, left valve, dorsal view showing deep escutcheon, and right lateral view, respectively, (**4–6**) BSPG 2014V 417/2, left lateral, dorsal, and right lateral views, respectively, (**7**) BSPG 2014V 245/1, Kehailia Formation, Gebel Arousiah, left valve interior showing the gradidentate convexodont teeth. (**8–26**) *Ryderia decorata* (Douvillé, 1916) from the Jurassic (Toarcian–lower Kimmeridgian) rocks of Gebel Maghara; (**8–10**) BSPG 2014V 416/1, Masajid Formation, western Bir Maghara, left lateral, dorsal, and right lateral views, respectively, (**11–14**) Kehailia Formation, Gebel Homayir; (**11**) BSPG 2014V 243/1, left lateral view, (**12**) BSPG 2014V 243/2, right lateral view, (**13**) BSPG 2014V 243/3, dorsal view; (**14**) BSPG 2014V 342/1, dorsal view showing a wide, cordate-shaped, ornamented escutcheon; (**15**) BSPG 2014V 343/1, Kehailia Formation, Gebel Mowerib, right lateral view; (**16**) BSPG 2014V 345/1, Masajid Formation, western Bir Maghara, left lateral view; (**17, 18**) Kehailia Formation, Gebel Engabashi; (**17**) BSPG 2014V 3/1, right lateral view, (**18**) BSPG 2014V 3/2, interior of right valve showing the convexodont teeth and sockets with serpulid encrustations; (**19, 20**) BSPG 2014V 342/2, Kehailia Formation, Gebel Homayir; (**19**) left valve interior showing anterior (Aa) and posterior muscle scars (Pa), (**20**) close-up showing slightly convex anterior hinge with convexodont teeth and slightly concave posterior hinge; (**21**) BSPG 2014V 341/1, Kehailia Formation, Gebel Homayir, left lateral view; (**22**) BSPG 2014V 416/2, Masajid Formation, western Bir Maghara, dorsal view; (**23**) BSPG 2014V 342/3, Kehailia Formation, Gebel Homayir, right valve; (**24–26**) BSPG 2014V 242/1, Kehailia Formation, Gebel Homayir; (**24**) left valve, internal mold showing well-developed visceral muscle scar (VMS) and umbonal pedal muscle scars (UPS), (**25**) dorsal view showing the well-preserved (UPS), (**26**) right lateral view showing anterior muscle scar (Aa), part of the pallial line (Pl), (UPS), and VMS (arrowed). Scale bars = 2 mm.

Description.—Small nuculaniform shell, elongated-ovate, very inequilateral, longer than high (H/L: 0.62–?0.67; Table 10), moderately inflated, slightly rostrate. Anterior margin strongly convex, meeting ventral margin in rounded curve. Posterodorsal margin slightly concave. Ventral margin moderately convex anteriorly, becoming straight towards posterior end. Umbo inflated, triangular, and located slightly anterior of mid-length of valve. Beak prominent, slightly opisthogyrate, elevated above dorsal margin. Escutcheon well impressed, smooth, and bordered by a well-defined rounded ridge. Hinge not well preserved, gradidentate with convexodont teeth (Figs. 16.42, 18.7). Anterior and posterior rows of teeth decreasing in size towards umbo. Ornamentation consisting of fine irregular commarginal growth lines.

Materials.—Eight specimens, in shell preservation, from upper Toarcian to upper Bathonian strata of Gebel Maghara; four specimens from the upper Toarcian Shusha Formation (BSPG 2014V 417/1–4), western Bir Maghara; two incomplete specimens from the upper Bajocian Bir Maghara Formation, Gebel Arousiah (BSPG 2014V 339/1–2); a single specimen from the middle–upper Bathonian Kehailia Formation, Gebel Mowerib (BSPG 2014V 340/1); and a single specimen from the same formation of Gebel Arousiah (BSPG 2014V 245/1).

Measurements.—See Table 10.

Remarks.—Ali (1989) erected *Nuculana rostrata* from the Lower Bathonian Safa Formation of Gebel Maghara. Later on, Abdelhamid (2002) recorded that species from the same area, but from a younger stratigraphic level (upper Bathonian–Callovian Kehailia member, Masajid Formation). According to the ICZN (1999), Ali's *N. rostrata* is invalid, because the species name is preoccupied by the type species of genus *Nuculana*—*N. rostrata* (Gmelin, 1791). Moreover with respect to shell outline and size and length of rostrum, the Egyptian material is identical to *Dacryomya lacryma* (J. de C. Sowerby, 1824; Fig. 19.1–19.3, 19.9) as figured and described by other authors (e.g., J. de C. Sowerby, 1824, pl. 476, fig. 3, from the Middle Jurassic Great Oolite of England; Quenstedt, 1857, pl. 67, figs. 18–21, from the Middle Jurassic of Germany; Cox, 1940, pl. 2, figs. 2–5, from the Middle Jurassic [Bathonian–Oxfordian] of western India; and Jaitly et al., 1995, pl. 2, figs. 21–23, from the Middle Jurassic [Bathonian–Oxfordian] of western India). The specimens figured by Khalil (2003, pl. 1, figs. 18, 19) as *Cuspidaria* sp. from the upper Bathonian rocks of Gebel Maghara show a taxodont hinge, a shallow posterior umbonal sulcus, a narrow rostrate posterior end, and a strongly convex anterodorsal and anterior margin (Fig. 19.5–19.7). These features closely fit *Dacryomya* and there is no doubt

Table 10. Measurements (in mm) of *Dacryomya lacryma* (J. de C. Sowerby, 1824).

Specimens	L	H	Iav	Isv	H/L	Iav/L	Isv/L
BSPG 2014V 339/1	?7.2	4.8	—	2.2	?0.67	—	?0.30
BSPG 2014V 417/1	6.5	4.2	3.2	—	0.65	0.49	—
BSPG 2014V 417/2	8.1	?5.0	3.7	—	0.62	0.46	—

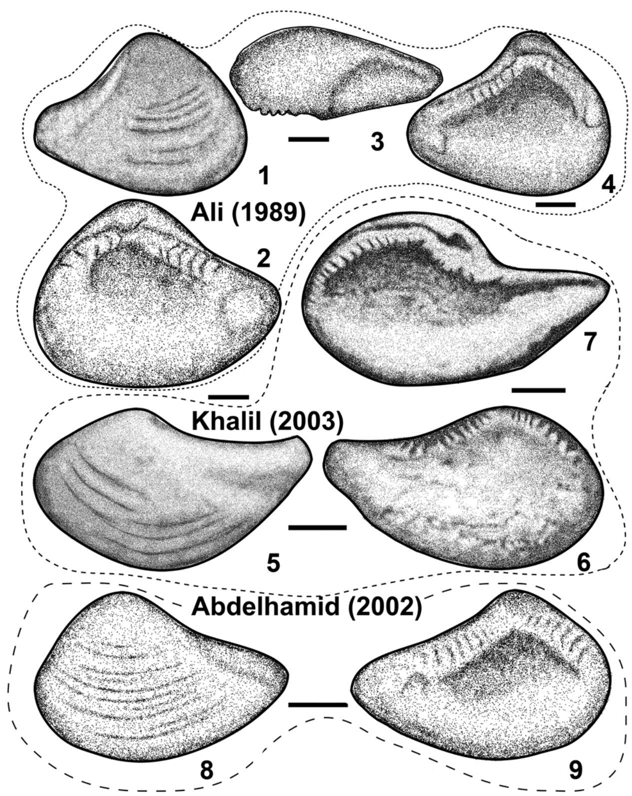

Figure 19. (**1–4**) Sketches of *Nuculana rostrata* Ali, 1989, from the lower Bathonian Safa Formation, Gebel Maghara (homonym of the type species of *Nuculana*, viz. *N. rostrata* [Gmelin, 1791] = *Dacryomya lacryma* [J. de C. Sowerby, 1824]). (**5–7**) *Cuspidaria* sp., Khalil, 2003, from upper Bathonian rocks, Gebel Maghara (= *D. lacryma* [J. de C. Sowerby, 1824]). (**8, 9**) *Nuculana rostrata* Ali et al., 1997, of Abdelhamid (2002) from the upper Bathonian–Callovian of Gebel Maghara (= *Dacryomya lacryma* [J. de C. Sowerby, 1824]). Scale bars = 2 mm.

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that the specimens of Khalil (2003) clearly fall into the range of variation of *D. lacryma* (J. de C. Sowerby, 1824) as documented by Cox (1940) and Jaitly et al. (1995). Therefore, the specimens of Ali (1989), Abdelhamid (2002), and Khalil (2003) have been included as junior synonyms of *D. lacryma*.

Nuculana (*Dacryomya*) cf. *D. lacryma* (Sowerby) of Choubert and Faure-Muret (1967) from the Middle Jurassic of Morocco differs from the holotype of Sowerby in having strong commarginal ribs, a shorter rostrum, and much greater inflation. *Dacryomya lacryma* differs from *D. diana* (d'Orbigny, 1850) in having a longer rostrum, a deep escutcheon delimited by a sharp ridge, and a strongly convex anterodorsal margin. *Dacryomya heberti* (Martin, 1860) of Hodges (2000, p. 22, pl. 1, figs. 31–43, 46, 48–50, aff. fig. 30, text-figs. 16–23) from the Lower Jurassic (Pliensbachian) of England differs from the present species in being less elongated, lacking the umbonal posterior ridge, and in having a more posteriorly placed umbo. A strongly inflated valve and a short rostrum distinguish the Toarcian *Nuculana* (*Dacryomya*) *thompsoni* Cox (1965, p. 26, pl. 1, figs. 4a–c) from Kenya from the present species. The figured specimens of *N.* (*D.*) *dodsoni* Cox (1965, p. 27, pl. 1, figs. 2a–c) from Bathonian−Callovian rocks of the same area are internal molds and differ from *D. lacryma* in being more rostrate.

Genus *Ryderia* Wilton, 1830

Type species.—*Leda renevieri* Oppel, 1856, from the Lower Lias of Awre, Gloucester, southern England; subsequent designation by Cox (1936).

Remarks.—Douvillé (1916) erected *Leda decorata* from Middle Bathonian rocks of Gebel Maghara, Egypt. Later on, Abdelhady and Fürsich (2014, fig. 6E, F) assigned *Leda decorata* to *Ryderia*. According to Damborenea and Pagani (2019), the records of *Ryderia* from the Middle Jurassic of Egypt are doubtful and, therefore, they suggested that Douvillé's species probably belongs to the genus *Nuculana*. Based on the diagnostic features of *Ryderia* (a very long, narrow rostrum, a well-developed umbonal ridge, a well-developed corselet, an entire pallial line, and fine commarginal striae; Hodges, 2000, p. 40, 45), the present material (138 well-preserved specimens) can be placed in *Ryderia* without any doubt (Fig. 18.8–18.23). The genus *Ryderia* has been recorded from Rhaetian–Toarcian strata (Cox, 1965; Liu, 1995; Ivimey-Cook et al., 1999; Fürsich et al., 2001; Yin and McRoberts, 2006; Mander et al., 2008; Ros et al., 2014). According to Hodges (2000, p. 40), *Ryderia* extends from the Carboniferous to the Lower Jurassic (upper Pliensbachian) of Europe, South America, Mexico, Afghanistan, Japan, China, and New Zealand. Ros et al. (2014, p. 19) did not agree with Hodges, because he did not provide references to confirm his statement. In addition, the oldest well-documented records of *Ryderia* are from Rhaetian beds (e.g., Ivimey-Cook et al., 1999) and it extends to the lower Toarcian (e.g., Fürsich et al., 2001). Damborenea and Pagani (2019, p. 934) pointed out that Middle Jurassic records of *Ryderia* are doubtful. The latter view is not accepted here, because Dietze et al. (2021, p. 48, pl. 27, fig. 6) recorded *Ryderia doris* (d'Orbigny, 1849) from the early Middle Jurassic (Aalenian, ammonite *Opalinum* Zone) of southwestern Germany. In the present study, the occurrence of

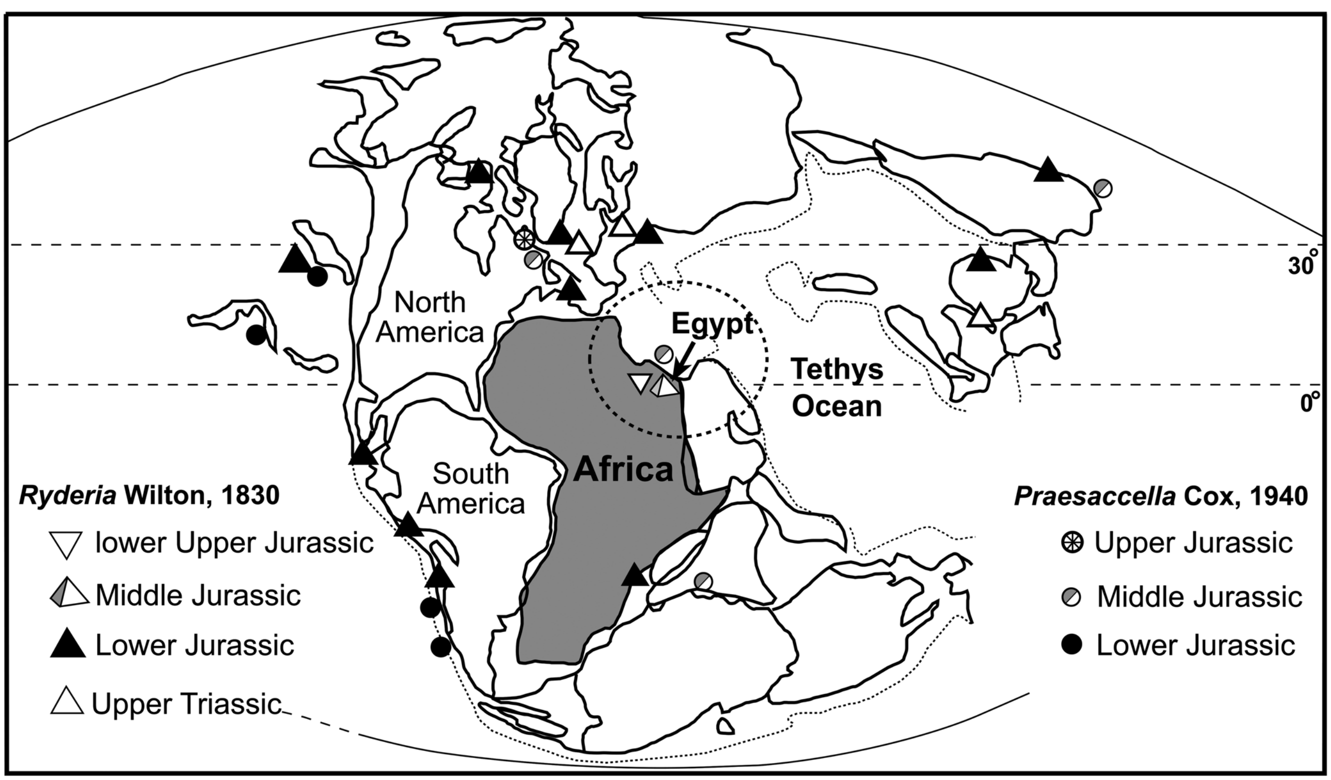

Figure 20. Paleogeographic distribution of *Ryderia* Wilton, 1830, and *Praesaccella* Cox, 1940, during Upper Triassic and Jurassic time. See Figure 15 for references.

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Ryderia is extended to the lower Upper Jurassic of Egypt (Fig. 20). It has been recorded from the Toarcian Shusha Formation, middle–upper Bathonian Kehailia Formation, and from the Lower Kimmeridgian Masajid Formation of Gebel Maghara. Because there are no previous records of *Ryderia* from Africa (Ros et al., 2014, fig. 4; Fig. 20), this is also the first record of the genus from Africa.

Ryderia decorata (Douvillé, 1916)
Figures 18.8–18.26, 21.1–21.3

*1916 *Leda Decorata* Douvillé, p. 61, pl. 5, figs. 56–62.
.1980 *Nuculana decorata*; Hirsch, p. 130, pl. 1, fig. 9.
non 1981 *Ryderia* sp. cf. *R. decorata*; Parnes, p. 27, pl. 3, figs. 27–28.
.2002 *Nuculana decorata*; Abdelhamid, p. 337, pl. 5, figs. 5, 6.
v.2014 *Ryderia decorata*; Abdelhady, p. 72, fig. 5.4E, F.
v.2014 *Ryderia decorata*; Abdelhady and Fürsich, p. 181, fig. 6E, F.

Holotype.—*Leda decorata* Douvillé, 1916, pl. 5, figs. 56–62, from the Middle Jurassic (Bathonian) of Gebel Maghara, Sinai Peninsula, Egypt.

Occurrence.—Toarcian–lower Kimmeridgian of Gebel Maghara (Douvillé, 1916; present study).

Description.—Shell small, elongated-ovate, distinctly longer than high (H/L: ?0.41–0.49; Table 11), very inequilateral, equivalved, moderately inflated. Posterior end tapering, forming a narrow and long rostrum (complete rostra not preserved in all specimens). Anterior margin strongly convex, meeting ventral margin in rounded curve. Ventral margin convex, becoming straight to slightly concave posteriorly. Posterodorsal margin straight to slightly concave, anterodorsal margin slightly convex. Beak hardly prominent, small, opisthogyrate, located anteriorly. Escutcheon (Esc) wide, elongated-cordate, rounded at umbonal end, tapering towards posterior, located within corselet (Ct), ornamented with fine ribs, occasionally producing a chevron pattern (Fig. 21.1–21.3). Corselet elongated-cordate in outline, slightly concave, separated from main valve by rounded posterior ridge, extending from umbo to a position approximately one-third along posterodorsal margin. Posterior umbonal sulcus (ventral of posterior ridge) narrow, deep, gradually widening towards ventral margin (Fig. 18.14). Lunule distinct, shallow, lanceolate, sharply pointed at extremities with two rows of teeth-like granules (external projections of anterior teeth; Fig. 22), arranged parallel to anterodorsal margins of both valves. Posterior adductor muscle scar sub-ovate, more elongated than anterior one, located close to posterodorsal margin. Anterior adductor muscle scar sub-rounded, located at anterior end. Visceral muscle scar (VMS) preserved on few internal molds as grooves extending from umbo towards ventral margin, fading approximately at the mid-height of shell (Fig. 18.24–18.26). Umbonal pedal muscle scars (UPS) well preserved, located dorso-ventrally below umbo (Fig. 18.25). Hinge taxodont, slightly gradidentate. Anterior part of hinge slightly convex dorsally with 17 convexodont teeth and sockets, gradually decreasing in size towards umbo (Fig. 18.18–18.20). Posterior part of hinge dorsally concave with ∼10 chevron-like teeth and sockets, pointing and decreasing in size towards umbo. Chondrophore small, triangular, shallow, located below the smallest five anterior teeth below umbo (Fig. 18.20). Ornament consisting of numerous, regular, fine commarginal ribs (Fig. 18.17, 18.23).

Materials.—One hundred and thirty-seven specimens, mostly articulated and in shell preservation, from the Toarcian–lower Kimmeridgian strata of the Maghara area: three specimens from the marl beds of the Toarcian Shusha Formation (BSPG 2014V 418/1–3); 63 specimens from the middle–upper Bathonian Kehailia Formation, Gebel Homayir (BSPG 2014V 242/1–3; 243/1–31; 341/1–6; 342/1–14; 347/1–4; 348/1–2; 350/1–3); 11 specimens from the same formation, Gebel Mowerib (BSPG 2014V 343/1; 346/1; 349/1–9); seven specimens from the Kehailia Formation, Gebel Arousiah (BSPG 2014V 320/1–4; 321/1–2; 344/1); two specimens from the Kehailia Formation, Gebel Engabashi (BSPG 2014V 3/1–2); 37 specimens from the basal part (marl and bioclastic marl beds) of the lower Kimmeridgian Masajid Formation, western Bir Maghara (BSPG 2014V 345/1–19; 415/1–5; 416/1–13); and 14 specimens from the upper part of the same formation, western Bir Maghara (BSPG 2014V 414/1–4; 423/1–10).

Measurements.—See Table 11.

Remarks on measurements.—In agreement with Hodges (2000, p. 42), measuring the length of the species is often difficult, because the rostrum, being so long and thin, is commonly broken and often appears shorter than it actually was. Therefore, the H/L (shell outline) and Iav/L (shell inflation) ratios are not accurate. In the present study, the lengths of nearly complete specimens have been measured, but marked with a question mark.

Remarks.—Douvillé (1916) erected *Leda decorata* from the middle Bathonian rocks of Gebel Maghara on the basis of a well-ornamented deep escutcheon, numerous fine commarginal ribs, and a large and moderately inflated valve (L >21.0 mm; Iav/L: ?0.31–0.36; Table 11). In addition, the lunule of *R. decorata* is narrow, shallow, and lanceolate with two rows of tubercles or granules arranged along the anterodorsal margins of both valves. According to Cox (1940, p. 31), the "row of pearls of lunule" described by Douvillé (1916) is due to some abnormal development of hinge-teeth, the positions of which are indicated by a series of projections on the exterior of the shell. This view is followed here, because the number of granules (external projections of teeth) are nearly the same as that of the anterior teeth. In addition, the external projections have the same arrangement as the anterior teeth in the two valves (tooth in left valve located opposite to socket in the right one), and occasionally have the same orientation as the anterior teeth (Fig. 22). Cox (1940) suggested that *Leda decorata* Douvillé is probably a junior synonym of *Nuculana* (*Dacryomya*) *lacryma* (J. Sowerby) from the Lower Callovian of India (Cox, 1940, p. 29, pl. 2, figs. 2–5). Later, Jaitly et al. (1995, p. 161) accepted Cox's view, which is not followed here. Some similarities exist

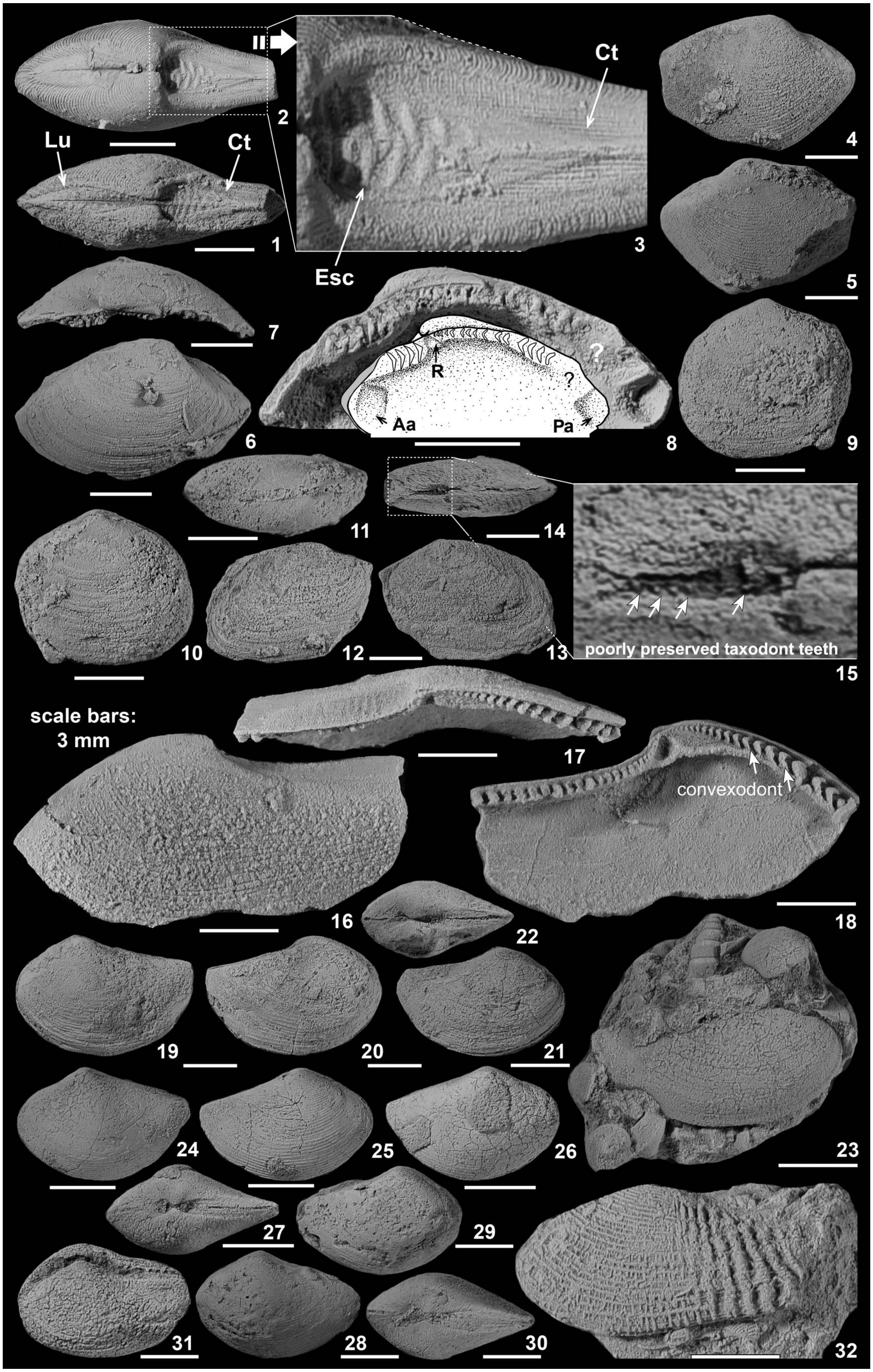

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Figure 21. (**1–3**) *Ryderia decorata* (Douvillé, 1916) from the Jurassic (Toarcian–lower Kimmeridgian) rocks of Gebel Maghara; (**1**) BSPG 2014V 414/1, Masajid Formation, western Bir Maghara, dorsal view showing a well-developed corselet (Ct), (**2, 3**) BSPG 2014V 243/4, Kehailia Formation, Gebel Homayir; dorsal view and close-up, respectively, showing a well-ornamented escutcheon (Esc), located within corselet (Ct), and separated from main valve by corselet ridge. (**4–8**) *Rollieria*? sp. cf. *Rollieria aequilateralis* (Roemer, 1836) from the Middle–Upper Jurassic of Gebel Maghara. (**4, 5**) BSPG 2014V 324/1, Bir Maghara Formation, Gebel Arousiah, right lateral and left lateral views, respectively; (**6–8**) BSPG 2014V 351/1, Safa Formation, Bir Maghara, right valve exterior, dorsal view, and close-up and sketch, respectively, showing the convexodont teeth, a small resilifer (R), and rectangular anterior and posterior muscle scars (Aa, Pa). (**9–15**) *Rollieria*? sp. indet. from the Middle Jurassic of Gebel Maghara. (**9–11**) BSPG 2014V 352/1, Bir Maghara Formation, Gebel Arousiah, incomplete left lateral view, right valve, and dorsal view, respectively, (**12–15**) BSPG 2014V 353/1, Kehailia Formation, Gebel Homayir, right lateral view, left lateral view, dorsal view, and close-up showing the poorly preserved taxodont hinge (arrowed), respectively. (**16–18**) *Nuculana* (*Nuculana*) sp. indet., BSPG 2014V 322/1, middle−upper Bathonian Kehailia Formation, Gebel Mowerib, left lateral view, dorsal view, and left valve interior, respectively. (**19–31**) *Praesaccella juriana* Cox, 1940, from the Middle Jurassic of Gebel Maghara. (**19, 20**) BSPG 2014V 355/1, Bir Maghara Formation, Gebel Arousiah, left valve and right valve, respectively, (**21–30**) Kehailia Formation, Gebel Mowerib; (**21, 22**) BSPG 2014V 218/1, right valve and dorsal views, respectively, (**23**) BSPG 2014V 218/2, exterior view of right valve with gastropod and bivalve encrustations, (**24, 25**) BSPG 2014V 218/3, left valve and right valve, respectively, (**26, 27**) BSPG 2014V 218/4, right valve and dorsal views, respectively, (**28–30**) BSPG 2014V 218/5, left valve, right valve, and dorsal view, respectively; (**31**) BSPG 2014V 354/1, Kehailia Formation, Gebel Homayir, left lateral view showing the taxodont hinge. (**32**) *Costinuculana magharensis* Ayoub-Hannaa, Fürsich, and Abdelhamid, 2017, BSPG 2014V 356/1, Kehailia Formation, Gebel Homayir, left lateral view. Scale bars = 3 mm.

between the two species, but also some differences. *R. decorata* has a long and narrow rostrum (rapidly narrowing posterior rostrum in *D. lacryma*), numerous fine commarginal ribs, well-ornamented escutcheon (smooth in *D. lacryma*), a well-developed umbonal posterior sulcus, extending from umbo to posteroventral corner, a shallow lanceolate lunule, a well-developed corselet (absent in *D. lacryma*), and is larger (L_{max}> 21.0 mm as opposed to 13.5 mm in Cox, 1940), less inflated, and more elongated (H/L: ?0.41–0.49 as opposed to 0.60; Cox, 1940, p. 30). The most closely related species is *R. doris* (d'Orbigny, 1849) figured and described, for example, by Hodges (2000, p. 40, pl. 3, figs. 1–4, 6–7, text-figs. 40–45) from the Lower Sinemurian of southeastern England and by Karapunar et al. (2020, p. 15, pl. 2, figs. 9–19, pl. 3, figs. 1–8, pl. 10, fig. 12) from the Pliensbachian of southern Germany. *Ryderia doris* differs from *R. decorata* in having a very long, narrow rostrum (H/L = 0.26–0.37; Hodges, 2000, as opposed to 0.41–0.49), a shallow, smooth escutcheon (strongly ornamented in *R. decorata*), a well-developed rostral groove, and in being less inflated (Iav/L = 0.13–0.22; Karapunar et al., 2020, as opposed to ?0.30–0.36). In addition, *R. decorata* is stratigraphically younger (Toarcian–lower Kimmeridgian) than *R. doris*. *Ryderia* sp. cf. *R. decorata* (Douvillé, 1916) of Parnes (1981) from the Bajocian of Negev, southern Israel, has a strong posterior ridge extending from the umbo to the ventral end of the rostrum, a smooth shell surface, compressed valves particularly along the posterior area, and a narrower and much more elongated valve than *Ryderia decorata*.

Another very closely related species is *N. rostrialis* (Lamarck, 1819), figured and described by some authors, including Goldfuss (1837, p. 155, pl. 125, figs. 8a–c) and Klöcker (1966, p. 220, fig. 1) from the Lower Jurassic of Germany, Bronn (1836, p. 371, pl. 20, figs. 6a, b) from the Lower Jurassic of France, and Etter (1990, pl. 3, fig. 7) from the Lower Jurassic of Switzerland. Although the latter two species have the same shell outline, size and ornamentation, *N. rostrialis* differs in having a narrow, smooth escutcheon, a strong posterior ridge extending from the umbo to the ventral end of the rostrum, a smooth and sharply demarcated lunule, sharply pointed, slightly opisthogyrate beaks, and a slightly concave posterodorsal margin. *Nuculana* sp. figured by Hirsch (1980, p. 130, pl. 1, fig. 10) from the middle Callovian of Makhtesh Hatira, Israel, has a wider rostrum, faint radial ribs close to the ventral margin, and is larger (L = ?46.0 mm). The poorly preserved *Nuculana* (*Ryderia*) *kenyana* Cox, 1965 (p. 27, pl. 1, figs. 6a–c) from the upper Toarcian of Kenya differs from the present species in having compressed valves, an angulated anterior margin, and lacks a lunule. With respect to general outline, *Nuculana numismalis* (Tate, 1870) figured by Chen (1987, p. 40, pl. 2, fig. 1) from the Lower Jurassic of China is similar to the present species, but has a slightly concave posterodorsal margin, thick commarginal ribs, a less-convex ventral margin, and is much smaller than the present species. *Ryderia texturata* (Terquem and Piette, 1865) (p. 89, pl. 11, figs. 5, 6) from the Toarcian of France and *Ryderia tehuelchana* Damborenea and Pagani, 2019 (p. 934, figs. 5.1–5.5, 5.18, 7.4) from the Lower Jurassic

Table 11. Measurements (in mm) of *Ryderia decorata* (Douvillé, 1916).

Specimens	L	H	Iav	Al	H/L	Iav/L	Al/L
BSPG 2014V 243/1	>15.7	7.7	5.3	7.5	?0.49	?0.34	?0.48
BSPG 2014V 243/2	>20.5	9.0	7.5	8.8	?0.44	?0.36	?0.43
BSPG 2014V 341/1	>13.6	6.7	4.3	5.5	?0.49	?0.32	?0.40
BSPG 2014V 341/2	>14.5	6.4	4.3	5.4	?0.44	?0.30	?0.37
BSPG 2014V 341/3	>12.1	6.2	3.6	5.5	?0.51	?0.30	?0.45
BSPG 2014V 342/1	>17.5	8.0	5.3	6.7	?0.46	?0.30	?0.38
BSPG 2014V 349/1	>15.5	6.8	4.8	6.1	?0.44	?0.31	?0.39
BSPG 2014V 349/2	>16.0	7.2	—	6.3	?0.45	—	?0.39
BSPG 2014V 414/1	>14.5	6.4	4.3	5.4	?0.44	?0.30	?0.37

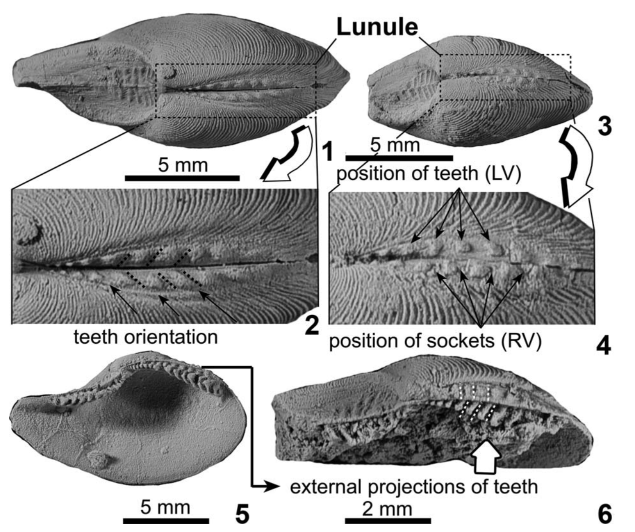

Figure 22. Relationships between the two rows of tubercles or granules on the lunule and development of anterior teeth in *Ryderia decorata* (Douvillé, 1916) from the Jurassic of Gebel Maghara.

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of Chubut (Argentina) display a different ornamentation, particularly on the rostrum.

Family Sareptidae Stoliczka, 1870
Subfamily Yoldiinae Dall, 1908
Genus *Rollieria* Cossmann, 1920

Type species.—*Nucula palmae* J. de C. Sowerby, 1824, "Mountain Limestone" (Carboniferous) of Derbyshire, England; subsequent designation by Rollier, 1923.

Remarks.—*Rollieria* was regarded as a subgenus of *Nuculana* by some workers (e.g., Cox et al., 1969, p. N237; Liu, 1995). Hodges (2000, p. 35) placed *Rollieria* as a separate genus within the subfamily Yoldiinae (family Yoldiidae) on the basis of a sub-central, slightly prosogyrate umbo, a shallow pallial sinus, an elongated valve, and the lack of an escutcheon and lunule. Later, Carter et al. (2011) assigned the subfamily Yoldiinae Dall, 1908, to the family Sareptidae Stoliczka, 1870. The type species of J. Sowerby was collected from Carboniferous rocks of England. Hodges (2000, p. 35–36) doubted the presence of *Rollieria* at that time because this is the only occurrence of the genus in strata older than Jurassic. He pointed out that, apart from its questionable occurrence in the Carboniferous, *Rollieria* has a stratigraphic range from the Lower Jurassic–Lower Cretaceous of Europe and India. In the present study, *Rollieria* is recorded from Middle–Upper Jurassic strata of Gebel Maghara for the first time.

Rollieria? sp. cf. Rollieria aequilateralis (Roemer, 1836)
Figure 21.4–21.8

cf. 1836 *Nucula aequilateralis* Roemer, p. 101, pl. 6, fig. 13a–c.

Occurrence.—Middle Jurassic of Germany and probably from the Middle–Upper Jurassic of Gebel Maghara (first record).

Description.—Shell small, elongated-ovate, longer than high (H/L: ?0.60–0.62; Table 12) slightly equilateral, equivalved, and moderately inflated. Posterodorsal margin slightly convex to straight. Anterodorsal margin straight, meeting anterior margin at nearly a right angle. Anterior margin blunt, meeting ventral margin in rounded curve. Posterior margin broken off. No lunule and escutcheon (Fig. 21.7). Umbo low, moderately inflated, located slightly anterior of mid-length of valve. Beaks hardly prominent, prosogyrate. Anterior and posterior muscle scars partly preserved, subquadrate in outline, located close to anterior and posterior margin, respectively. Hinge taxodont with unequal teeth and sockets. Anterior and posterior hinge teeth meeting in an obtuse angle (125°), separated by small triangular resilifer, directed slightly posteriorly (Fig. 21.8). Posterior part of hinge longer than anterior one with ~17 convexodont teeth, decreasing in size towards beak. Anterior convexodont teeth larger and fewer (~7) than posterior ones. Shell surface with fine growth lines.

Table 12. Measurements (in mm) of *Rollieria*? sp. cf. *Rollieria aequilateralis* (Roemer, 1836).

Specimens	L	H	Iav	Al	H/L	Iav/L	Al/L
BSPG 2014V 324/1	?12.5	7.7	5.3	5.5	?0.62	?0.42	0.44
BSPG 2014V 351/1	12.3	?7.4	—	5.7	?0.60	—	0.46

Materials.—Four specimens, three composite molds and two in shell preservation, from the Middle–Upper Jurassic of Gebel Maghara, a single specimen from the upper Bajocian Bir Maghara Formation, Gebel Arousiah (BSPG 2014V 324/1), a single left valve from the upper third part of the lower Bathonian Safa Formation, Bir Maghara (BSPG 2014V 351/1), and two specimens from the lower marl beds of the early Kimmeridgian Masajid Formation, western Bir Maghara (BSPG 2014V 412/1–2).

Measurements.—See Table 12.

Remarks.—Based on the diagnostic features of *Rollieria* mentioned by Hodges (2000, p. 35) the present specimens might well be *Rollieria*. Due to the missing posterior area (incomplete shell outline), however, the generic assignment is somewhat doubtful. Therefore, the material is assigned to the genus with question mark. *Nucula aequilateralis* Roemer (1836, p. 101, pl. 6, figs. 13a–c) from the Upper Jurassic of Germany, which is comparable in shape and size, is elongated subtriangular, has a narrow, blunt anterior margin, a smooth shell surface, and lacks escutcheon and lunule. The incomplete preservation makes it difficult to place the present specimens in this species with certainty.

Rollieria? sp. indet.
Figure 21.9–21.15

Description.—Shell small (L >9.0 mm; H = 6.7 mm), incomplete, outline apparently subovate, equivalved, inequilateral, and moderately inflated (Iav/H = 0.52). Posterior margin convex, meeting ventral margin in rounded curve. Anterior margin broken off. Ventral margin strongly rounded. Beaks small, slightly prosogyrate, located approximately anterior of mid-length. No lunule or escutcheon (Fig. 21.11, 21.14). Hinge taxodont with numerous teeth and sockets (Fig. 21.15). Shell surface with irregular commarginal growth lines.

Materials.—Four incomplete composite molds from the Middle Jurassic of Gebel Maghara; a single specimen from the Bajocian Bir Maghara Formation, Gebel Arousiah (BSPG 2014V 352/1) and three specimens from the middle–upper Bathonian Kehailia Formation, Gebel Homayir (BSPG 2014V 353/1–3).

Remarks.—None of the present specimens is complete. This incomplete preservation makes it difficult to place them in any of the known species. However, they are somewhat similar to *Rollieria bronni* (Andler, 1858) of Hodges (2000, pl. 2, figs. 31–35, text-figs. 35–38) from the Lower Jurassic of England in having rounded margins and a smooth surface, but the latter is more elongated. Recently, Karapunar et al. (2020) regarded *Rollieria bronni* as a synonym of their new species *R. goldfussi* (Karapunar et al., 2020, p. 16, pl. 13, figs. 9–12, pl. 4, figs. 1, 2, text-figs. 10–12), which has been recorded from the Pliensbachian of southern Germany. Another closely similar species is *R. aequilatera* (Koch and Dunker, 1837) of Cox (1965, p. 29, pl. 1, fig. 5a–c) from the Toarcian of Kenya, but the latter has strongly rounded margins and compressed valves.

Family Nuculanidae Adams and Adams, 1858
Genus *Nuculana* Link, 1807
Subgenus *Nuculana* Link, 1807

Type species.—*Arca rostrata* Chemnitz, 1774 (= *Arca pernula* Müller, 1779) by original designation (Link, 1807, p. 155).

Nuculana (*Nuculana*) sp. indet.
Figure 21.16–21.18

Description.—Shell small (L = ?17.5 mm), longer than high, inequilateral, weakly inflated, with a long posterior rostrum. Posterodorsal margin slightly concave. Anterodorsal margin slightly convex. Ventral margin broken off. Beak less prominent, opisthogyrate, and located anteriorly. Escutcheon less distinct, shallow, and ornamented (Fig. 21.17). Lunule narrow, shallow, lanceolate. Hinge gradidentate with convexodont teeth. Anterior part of hinge dorsally convex, posterior hinge dorsally concave, both separated by triangular, narrow, deep resilifer with slightly concave and smooth area located anterior of resilifer (Fig. 21.18). Anterior teeth strong, convexodont, sharply pointed, and decreasing in size towards umbo. Ornamentation consisting of faint commarginal striae (Fig. 21.16).

Materials.—A single incomplete specimen from the middle–upper Bathonian Kehailia Formation, Gebel Mowerib, Gebel Maghara (BSPG 2014V 322/1).

Remarks.—Structure of the teeth and general outline allow assignment of the present specimen to the genus *Nuculana*. It can be distinguished from other Jurassic *Nuculana* species by having a shallow and ornamented escutcheon, a very narrow lanceolate lunule, and a resilifer bordered anteriorly by a slightly concave, smooth area (Fig. 21.18). Because only an incomplete left valve is available, identification at the species level is not possible. The valve resembles *Leda alpina* d'Orbigny figured by Cottreau (1925, p. 143, pl. 17, fig. 3) from the Callovian of France in general outline, but the latter differs in being smaller and in having more-inflated umbones.

Genus *Praesaccella* Cox, 1940

Type species.—*Nuculana* (*Praesaccella*) *juriana* Cox, 1940, from the Callovian of Kachchh, India, by original designation.

Remarks.—*Praesaccella* was erected as a subgenus of *Nuculana* by Cox (1940, p. 32) based on an entire pallial line and relatively few hinge teeth. Recently, Damborenea and Pagani (2019, p. 933) regarded *Praesaccella* as a separate genus when describing *P. ovum* (J. de C. Sowerby, 1824) from the Lower Jurassic of Argentina. Most Jurassic *Praesaccella* species, such as *Nuculana* (*Praesaccella*) *camelorum* Cox, 1965 (p. 28, pl. 2, fig. l0a, b) from the Toarcian or Bajocian of East Africa, *N.* (*P.*) *juriana* Cox, 1940 (p. 33, pl. 2, figs. 6–9), and *N.* (*P.*) *calloviensis* (Kanjilal and Singh, 1973) (p. 469, pl. 1, figs. a–f) from Callovian–Oxfordian rocks of western India have an acutely pointed posterior end, which is almost at mid-height or slightly above the mid-height of the valve. The latter feature, therefore, should be included as diagnostic of the genus.

Praesaccella has a wide geographic distribution; it has been recorded from the Lower Jurassic of Chile (Aberhan, 1994, p. 10), Argentina (Damborenea, 1987; Damborenea and Pagani, 2019), Middle Jurassic of western India (Cox, 1940; Kanjilal and Singh, 1973; Jaitly et al., 1995), Spain (Delvene, 2001), Japan (Hayami, 1961), and Toarcian or Bajocian of East Africa (Cox, 1965). The species is recorded from Middle Jurassic rocks (upper Bajocian–Bathonian) of Egypt for the first time (Fig. 20).

Praesaccella juriana Cox, 1940
Figure 21.19–21.31

*1940 *Nuculana* (*Praesaccella*) *juriana* Cox, p. 33, pl. 2, figs. 6–9.
.1995 *Nuculana* (*Praesaccella*) *juriana*; Jaitly et al., p. 159, pl. 2, figs. 9–12, text-fig. 12.

Holotype.—*Nuculana* (*Praesaccella*) *juriana* Cox, 1940, pl. 2, fig. 7, from the Callovian of Kachchh, western India.

Occurrence.—Callovian–Oxfordian of India and Bajocian to late Bathonian of Gebel Maghara (present study, first record).

Description.—Shell small, subtriangular, longer than high (H/L: 0.65–0.70; Table 13), inequilateral, equivalved, moderately inflated, and posteriorly elongated into short rostrum. Anterior margin strongly convex meeting ventral margin in rounded angle. Posterior end of rostrum narrowly rounded, occasionally angulated, and located slightly above mid-height of valve (Fig. 21.19, 21.23). Ventral margin regularly rounded. Posterodorsal margin slightly concave, gradually sloping posteriorly. Umbones triangular, depressed, and located anterior of mid-length. Beak sharply pointed, orthogyrate to slightly prosogyrate. Escutcheon lanceolate, narrow, shallow, and delimited by a moderately well-developed ridge extending from umbo to end of rostrum (Fig. 21.22, 21.27). No lunule. Anterior part of hinge dorsally convex, posterior one slightly concave and carries numerous teeth and sockets (Fig. 21.14). Ornamentation consisting of numerous very fine commarginal striae except for posterodorsal and umbonal areas (Fig. 21.19, 21.25).

Materials.—Seventeen articulated specimens with shell preservation, from the Middle Jurassic of Gebel Maghara: a

Table 13. Measurements (in mm) of *Praesaccella juriana* Cox, 1940.

Specimens	L	H	Iav	Al	H/L	Iav/L	Al/L
BSPG 2014V 218/1	8.0	5.3	4.1	3.7	0.66	0.51	0.46
BSPG 2014V 218/2	7.8	5.5	4.1	3.6	0.70	0.52	0.46
BSPG 2014V 218/3	9.3	6.1	5.0	4.5	0.65	0.54	0.48
BSPG 2014V 218/4	7.3	4.8	3.7	3.8	0.66	0.51	0.52
BSPG 2014V 218/5	8.6	5.7	4.8	4.3	0.66	0.56	0.50
BSPG 2014V 355/1	10.2	6.7	?4.8	4.7	0.66	?0.47	0.46

single specimen from the upper Bajocian Bir Maghara Formation, Gebel Arousiah (BSPG 2014V 355/1), 14 specimens from the middle–upper Bathonian Kehailia Formation, Gebel Mowerib (BSPG 2014V 218/1–14), and two specimens from the Kehailia Formation, Gebel Homayir (BSPG 2014V 354/1–2).

Measurements.—See Table 13.

Remarks.—With respect to general outline, size, and ornamentation, the present specimens fit very well with the specimens of *Nuculana* (*Praesaccella*) *juriana* described and figured by Cox (1940) from the Middle–Upper Jurassic of India. The present species differs from the very similar *Leda argoviensis* Moesch, 1867 (p. 302, pl. 4, fig. 12a–c) from the Oxfordian of the Swiss Jura Mountains by having a longer rostrum, a depressed umbo (triangular in *L. argoviensis*), and a broadly convex anterior margin. The strongly convex posterior margin of *L. dewalquei* Terquem and Piette, 1865, figured by Stefanini (1939, p. 141, pl. 16, figs. 3–6) from the Lower Jurassic of Somalia distinguishes it from the present species. *Praesaccella ovum* (J. de C. Sowerby, 1824) of Damborenea and Pagani (2019, p. 9, figs 6.1–6.6, 7.5) from the Lower Jurassic of Argentina has a rounded posterior end, a strongly opisthogyrate umbo, regular commarginal lines, and its shell is less elongated than the present species. *Nuculana* (*P.*) *camelorum* Cox, 1965 (p. 28, pl. 2, fig. 10a, b) from Toarcian or Bajocian strata of Kenya is more rostrate, more inflated, and has a well-developed umbonal posterior carina.

Subfamily Veteranellinae Chen, Liu, and Lan, 1983
Genus *Costinuculana* Ayoub-Hannaa, Abdelhady, and Fürsich, 2017

Type species.—*Costinuculana magharensis* Ayoub-Hannaa, Abdelhady, and Fürsich, 2017, from the middle Bathonian of Gebel Maghara, North Sinai, Egypt, by monotypy.

Diagnosis.—See Ayoub-Hannaa et al. (2017, p. 435–437).

Remarks.—The genus *Costinuculana* and the species *C. magharensis* have been described, figured, and discussed in detail by Ayoub-Hannaa et al. (2017).

Costinuculana magharensis Ayoub-Hannaa, Abdelhady, and Fürsich, 2017
Figure 21.32

v.2014 *Nuculoidea* n. sp. Abdelhady, p. 72, fig. 5.4A, B.
v.2014 *Nuculoidea* n. sp. Abdelhady and Fürsich, p. 181, fig. 6a, b.
*2017 *Costinuculana magharensis* Ayoub-Hannaa, Abdelhady, and Fürsich, p. 437, figs. 4.1–4.9, 5.1–5.21, 6, 7.2.

Holotype.—Articulated specimen BSPG 2014V 1 (Ayoub-Hannaa et al., 2017, fig. 5.13–5.17) from the middle Bathonian of Gebel Maghara, Egypt.

Table 14. Measurements (in mm) of *Costinuculana magharensis* Ayoub-Hannaa, Abdelhady, and Fürsich, 2017.

Specimens	L	H	Isv	H/L	Isv/L
BSPG 2014V 356	?11.2	5.8	3.2	?0.52	?0.28

Occurrence.—Middle Bathonian Kehailia Formation, Gebel Maghara (Ayoub-Hannaa et al., 2017; present study).

Description.—Shells small, elongated-ovate in outline, strongly inequilateral, posteriorly elongated with ribbed rostrum. Anterodorsal margin slightly convex, meeting anterior margin in strongly rounded curve. Posterodorsal margin long, slightly concave. Anterior margin narrow and strongly convex. Posterior margin broken off. Ventral margin broad, irregular, slightly convex towards anterior margin, slightly concave posteriorly. Umbones broad, strongly convex, and located anteriorly. Beak sharply pointed and strongly incurved posteriorly. Escutcheon wide, moderately deep, and well ornamented with fine riblets. Surface with well-developed sub-vertical ribs, asymmetrical in cross-section, covering an area ∼45% of total valve length from posterior end, and separated by deep, narrow interspaces. Area between these radial ribs and anterior margin covered by reticulate ornamentation (Fig. 21.32).

Materials.—A single specimen from the Middle Jurassic (Bathonian) of Gebel Maghara, Kehailia Formation, Gebel Homayir (BSPG 2014V 356/1).

Measurements.—See Table 14.

Remarks.—According to Ayoub-Hannaa et al. (2017), the taxonomic characters of *Costinuculana* (type species: *Costinuculana magharensis*) are not present in the majority of Jurassic nuculanid genera that have been identified from different areas (e.g., Pandey and Singh, 1981; Fürsich, 1982; Aberhan, 1994, 1998; Jaitly et al., 1995; Sha et al., 1998). *Costinuculana* can be distinguished from other Jurassic nuculanids by having strong, rounded, and oblique radial ribs on the rostrum (occasionally bifurcated ventrally), a wide and deep escutcheon, which is delimited by blunt ridges and ornamented by fine riblets, and a narrow, lanceolate, sharply demarcated lunule. In the present material, the area between the oblique radial ribs and anterior margin is covered by reticulate ornamentation (Fig. 21.32). For more details concerning diagnosis, description, and comparison with closely related taxa, see Ayoub-Hannaa et al. (2017).

According to Damborenea and Pagani (2019), *Costinuculana* is closely related to *Ryderia*. Actually, *Ryderia* has a very narrow and much more elongated rostrum, a narrow and smooth escutcheon (deep, ornamented, and delimited by blunt ridges in *Costinuculana*, see Ayoub-Hannaa et al., 2017, figs. 4.1, 4.5, 4.7, 5.17), a less-distinct lunule (sharply demarcated in *Costinuculana*), and is less inflated (moderately to strongly inflated in the present material). In addition, the strength, number, and development of ribs on the rostrum of *Costinuculana* are quite different from those of species of *Ryderia*.

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Conclusions

Based on detailed analyses of several thousand specimens and on multivariate analyses of morphological features, the Jurassic protobranch bivalves from Gebel Maghara (northern Sinai, Egypt) were systematically described, and the genus and species boundaries were clearly defined. In addition, the paleobiogeographic patterns of some Jurassic protobranch genera were mapped (Figs. 15, 20). Due to the excellent preservation of many specimens, morphological features could be described in great detail. Among the sixteen taxa, three species were new—*Nuculoma douvillei* n. sp., *N. sinaiensis* n. sp., and *Palaeoneilo aegyptiaca* n. sp. In addition, five species—*Palaeonucula cuneiformis* (J. de C. Sowerby), *P. muensteri* (Goldfuss), *Dacryomya diana* (d'Orbigny), *D. lacryma* (J. de. C. Sowerby), and *Praesaccella juriana* Cox—had not been recorded from the Jurassic rocks of Egypt before. In the past, Middle and Upper Jurassic records of the genus *Palaeoneilo* have not been accepted due to insufficient knowledge of morphological details. Based on well-preserved internal and external characters, the occurrence of *Palaeoneilo* in Middle Jurassic (Bajocian−Bathonian) strata of Gebel Maghara can be confirmed. Similarly, Bathonian−Kimmeridgian records of *Dacryomya* and *Ryderia* from the Gebel Maghara area considerably extend the ranges of these genera. The wide geographic distribution of the identified taxa suggests that they were not influenced to a great extent by latitudinal climate gradients.

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Author contributions

The material for this study was collected by AAA and FTF and identified by WA-H, AAA, and FTF. The manuscript was largely written by WA-H. FTF extensively discussed taxonomic problems with WA-H and improved the manuscript. All authors read and commented on the final version of the manuscript.

Declaration of competing interests

The authors declare none.

References

Abdel-Gawad, G.I., and Gameil, M., 1999, Middle Jurassic fauna from El Minshera area, north Central Sinai, Egypt: Proceedings of the 4th International Conference of Geology of the Arab World, GAW4, Cairo University, 31 March 1998, p. 767–789.

Abdelhady, A.A., 2014, Palaeoenvironments and Palaeoecology of the Middle and Upper Jurassic Succession of Gebel Maghara (Sinai) [Ph.D. dissertation]: Erlangen-Nürnberg, Germany, Friedrich-Alexander Universität, 125 p.

Abdelhady, A.A., and Fürsich, F.T., 2014, Macroinvertebrate palaeocommunities 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 eustacy and basin topography: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 417, p. 261–273.

Abdelhamid, M.A.M., 2002, Some Middle–Upper Jurassic macrofauna from Gebel El-Maghara, northern Sinai, Egypt: Egyptian Journal of Paleontology, v. 2, p. 319–343.

Aberhan, M., 1994, Early Jurassic Bivalvia of northern Chile. Part I. Subclasses Palaeotaxodonta, Pteriomorphia, and Isofilibranchia: Beringeria, v. 13, p. 3–115.

Aberhan, M., 1998, Early Jurassic Bivalvia of western Canada. Part I. Subclasses Palaeotaxodonta, Pteriomorphia, 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., 1853–1858, The genera of Recent Mollusca; arranged according to their organization: London, John van Voorst, v. 1 (1853−1854), 484 p.; v. 2 (1854−1858), 661 p.; v. 3 (1858), 136 pls.

Agassiz, L.J.R., 1840, Mémoire sur les moules de mollusques vivans et fossils. Première partie: moules d'acephales vivans: Mémoires de Société des Sciences Naturelles de Neuchâtel, v. 2, p. 1−48.

Agrawal, S.K., 1956, Contribution a l'étude stratigraphique et paléontologique du Jurassique du Kutch (Inde): Annales du Centre d'Études et de Documentation Paléontologiques, v. 19, p. 1–188.

Agrawal, S.K., and Kachhara, R.P., 1977, Habo Beds near Ler (Kutch): Succession and fossil molluscs of the beds on the east of Ler: Recent Researches in Geology, v. 3, p. 495–503.

Agrawal, S.K., and Kachhara, R.P., 1980, *Nuculoma wynnei* Cox from the Jurassic of Kutch (Gujarat): Proceedings of the National Academy of Sciences, India, Section B: Biological Sciences, v. 46, p. 474–478.

Al Far, D.M., 1966, Geology and coal deposits of Gebel Al Maghara, North Sinai, Egypt: U.A.R. Geologic Survey Report, v. 37, p. 1–59.

Ali, M.H., 1989, Paleontological studies on the Jurassic macrofauna at Gebel Maghara area, northern Sinai Egypt [Ph. D. dissertation]: Minya, Egypt, El-Minia University, 241 p.

Ali, M.S.M., Azab, M.M., and Hussain, A.M., 1997, Some Bathonian brachiopods and bivalves, and their paleoecological significance at Gabal El-Maghara, northern Sinai, Egypt: El Minia Faculty of Science Bulletin, v. 10, n. 2, p. 1–28.

Andler, D., 1858, Über die Angulaten-Schichten in der Würtembergischen Jura-Formation: Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde, v. 1858, p. 641−645.

Arkell, W.J., 1952, Jurassic ammonites from Jebel Tuwayq, central Arabia: Philosophical Transactions of the Royal Society of London, Series B, v. 236, p. 241–313.

Ayoub-Hannaa, W.S., Abdelhady, A.A., and Fürsich, F.T., 2017, *Costinuculana magharensis* n. gen. n. sp. (Bivalvia, Nuculanidae) from the Middle Jurassic of Gebel Maghara, North Sinai, Egypt: Journal of Paleontology, v. 91, p. 434–443.

Ayyad, M.H., Darwish, M., and Sehim, A., 1998, Introducing a new structural model for north Sinai with its significance to petroleum exploration: Egyptian General Petroleum Corporation 14th Petroleum Conference, Egypt, v. 1, p. 101–117.

Babin, C., 1966, Mollusques Bivalves et Céphalopodes du Paléozoïque Armoricain. Étude Systematique. Essai sur la Phylogénie des Bivalves. Esquisse Paléoécologique. Brest, France, Imprimerie Commerciale et Administrative, 470 p.

Bengtson, P., 1988, Open nomenclature: Palaeontology, v. 31, p. 223–227.

Biju-Duval, B., Letouzey, J., and Montadert, L., 1979, Variety of margins and deep basins in the Mediterranean, *in* Watkins, J.S., Montadert, L., and Dickerson, P.W., eds., Geological and Geophysical Investigations of Continental Margins: American Association of Petroleum Geologists Memoir, v. 29, p. 293–317.

Borissjak, A., 1904, Die Pelecypoden der Jura-Ablagerungen im Europaeischen Russland. I. Nuculidae: Mémoires du Comité Géologique, Nouvelle Série, v. 11, p. 1–49.

Bronn, H., 1834–1837, Lethaea Geognostica oder Abbildungen und Beschreibungen der für die Gebirgs-Formationen bezeichnendsten Versteinerungen: Stuttgart, Schweizerbart, v. 1, 544 p.

Carter, J.G., 1990, Evolutionary significance of shell microstructure in the Palaeotaxodonta, Pteriomorphia and Isofilibranchia (Bivalvia: Mollusca), *in* Carter, J.G., ed., Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends: New York, Van Nostrand Reinhold, p. 136–296.

Carter, J.G., 2001, Shell and ligament microstructure of selected Silurian and Recent palaeotaxodonts (Mollusca: Bivalvia): American Malacological Bulletin, v. 16, p. 217−238.

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: 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., et al., 2011, A synoptical classification of the Bivalvia (Mollusca): Paleontological Contributions, v. 4, p. 1–47.

Carter, J.G., Harries, P.J., Malchus, N., Sartori, A.R., Anderson, L.C., Bieler, R., Bogan, A. E., et al., 2012, Chapter 31: Illustrated Glossary of the Bivalvia: Treatise Online no. 48: Part N, Revised, Volume 1. https://doi.org/10.17161/to.v0i0.4322.

Carter, J.G., Altaba, C.R., Anderson, L.C., Campbell, D.C., Fang, Z., Harries, P.J., and Skelton, P. W., 2015, The paracladistic approach to phylogenetic taxonomy: Paleontological Contributions, v. 12, p. 1–9.

Chavan, A., 1946, L'évolution des faunes marines de Mollusques dans le nord-ouest de l'Europe, de la fin du Crétacé à celle de l'Éocène: Bulletin de la Société Géologique de France, ser. 5, v. 16, p. 193−212.

Chavan, A., 1952, Les pélécypodes des sables astartiens de Cordebugle (Calvados): Mémoire de la Société Paléontologique Suisse, v. 69, p. 1−132.

Chemnitz, J.H., 1774, Neues Systematisches Conchilien-Cabinet, Volume 7: Nürnberg, Germany, Raspische Buchhandlung, 356 p.

Chen, J.H., 1987, Early Jurassic marine bivalves from Quangdong-Nanling district, southern China: Bulletin of the Nanjing Institute of Geology and Palaeontology, Academia Sinica, v. 12, p. 23–94.

Chen, J.-H., Liu, L., and Lan, X., 1983, [Veteranellinae, a new subfamily of Nuculanidae (Bivalvia) with classificatory significance of ornamentations in Palaeotaxodonta]: Acta Palaeontologica Sinica, v. 22, p. 616–627. [in Chinese with English summary]

Choubert, G., and Faure-Muret, A., 1967, Le Jurassique de la région d'El Mers-Skoura: Notes et Mémoires du Service Géologique du Maroc, v. 200, p. 1–32.

Conrad, T.A., 1842, Observations of the Silurian and Devonian systems of the United States, with descriptions of new species of organic remains: Journal of the Academy of Natural Sciences of Philadelphia, v. 8, p. 228–280.

Cossmann, M., 1907, Description de quelques Pélécypodes Jurassiques de France. 2ème article. Association Française pour l'Avancement des Sciences, Congrès de Lyon, p. 273–283.

Cossmann, M., 1912, Quelques Pelécypodes Jurassiques recueillis en France: Comptes Rendus, Association Française pour l'Avancement des Sciences, p. 1–11.

Cossmann, A.E.M., 1920, Rectifications de nomenclature: Revue Critique de Paléozoologie, v. 24, p. 81−83.

Cossmann, M., 1924, Extension dans les Deux-Sèvres de la Faune du Callovien de Montreuil-Bellay, avec un aperçu stratigraphique par l'Abbé Boone: Mémoires de la Societé Géologique et Minéralogique de Bretagne, v. 1, p. 1–53.

Cottreau, J., 1925, Types du Prodrôme de paléontologie stratigraphique universelle de d' Orbigny (1). Tome II. Callovien−Portlandien: Annales de Paléontologie, v. 14, p. 133–164.

Cox, L.R., 1936, The Gastropoda and Lamellibranchia of the Green Ammonite Beds of Dorset: Quarterly Journal of the Geological Society, London, v. 92, p. 456–471.

Cox, L.R., 1937, Notes on Jurassic Lamellibranchia. I. On the occurrence of the genus *Palaeoneilo* in the Jurassic of Great Britain: Proceedings of the Malacological Society of London, v. 22, p. 190–193.

Cox, L.R., 1940, The Jurassic lamellibranch fauna of Kachh (Cutch): Memoirs of the Geological Survey of India, Palaeontologica Indica, n. ser. 9, v. 3, no. 3, p. 1–157.

Cox, L.R., 1965, Jurassic Bivalvia and Gastropoda from Tanganiyka and Kenya: Bulletin of the British Museum of Natural History (Geology), Supplement, v. 1, p. 1–213.

Cox, L.R., 1969, General features of Bivalvia, *in* Moore, R.C., and Teichert, C., eds., Treatise on Invertebrate Paleontology, Part N, Mollusca 6, Bivalvia, Volume 1: Boulder, Colorado and Lawrence, Kansas, Geological Society of America and The University of Kansas Press, p. N2–N129.

Cox, L.R., Newell, N.D., Branson, C.C., Casey, R., Chavan, A., Coogan, A.H., Dechaseaux, C., et al., 1969, Systematic descriptions, *in* Moore, R.C., and Teichert, C., eds., Treatise on Invertebrate Paleontology, Part N, Mollusca 6, Bivalvia, Volume 1: Boulder, Colorado and Lawrence, Kansas, Geological Society of America and The University of Kansas Press, p. N225–N489.

Dall, W.H., 1889, On the hinge of pelecypods and its development, with an attempt toward a better subdivision of the group: American Journal of Science, ser. 3, v. 38, p. 445−462.

Dall, W.H., 1908, Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission steamer „Albatross", during 1891, Lieut. Commander Z.L. Tanner, U.S.N., commanding. XXXVII. Reports on the scientific results of the expeditions to the eastern tropical Pacific, in charge of Alexander Agassiz, by the U.S. Fish Commission steamer „Albatross", from October, 1904, to March, 1905, Lieut. commander L.M. Garrett, U.S.N., commanding. XIV. The Mollusca and the Brachiopoda: Bulletin of the Museum of Comparative Zoology at Harvard College, v 43, p. 205−487.

Damborenea, S.E., 1987, Early Jurassic Bivalvia of Argentina. Part 1: stratigraphical introduction and superfamilies Nuculanacea, Arcacea, Mytilacea and Pinnacea: Palaeontographica Abteilung A, v. 199, p. 23–111.

Damborenea, S.E., and Pagani, M.A., 2019, Early Jurassic protobranch bivalves from Chubut, Argentina: Journal of Paleontology, v. 93, p. 925–944.

Defrance, M.J.L., 1825, Nucule (Fossiles): Dictionnaire des Sciences Naturelles, v. 35, p. 216–219.

de Loriol, P., 1899, Étude sur les mollusques et brachiopodes de l'Oxfordien inférieur du zone à du Jura bernois, accompagnee d'une notice stratigraphique par M. le professeur Koby, E: Mémoires de la Societé Paléontologique Suisse, v. 26, p. 119–220.

de Loriol, P., 1901, Etude sur les mollusques et brachiopodes de l'Oxfordien supérieur et moyen du Jura bernois: Mémoires de la Société Paléontologique Suisse, v. 28, p. 1−119.

Delvene, G., 2001, Middle and Upper Jurassic bivalves from the Iberian Range (Spain): Beringeria, v. 28, p. 43–104.

Deshayes, G.P., 1839−1858, Traité Élémentaire de Conchyliologie [avec les applications de cette science sur la géologie]: Paris, Crochard & Cie., v. 1, pt. 1, p. 1−368 (1839); v. 1, pt. 2, p. 1−128 (1839), 129−824 (1850); v. 2, p. 1−192 (1857), 193−384 (1858); explication des planches, p. 1−24 (1839), 25−48 (1850), 49−80 (1853); appendice à explication des planches, i−iv (1850), v−xi (1857).

Dietze, V., Gräbenstein, S., Franz, M., Schweigert, G., and Wetzel, A., 2021, The Middle Jurassic Opalinuston Formation (Aalenian, Opalinum Zone) at its type locality near Bad Boll and adjacent outcrops (Swabian Alb, SW Germany): Palaeodiversity, v. 14, p. 15–113.

d´Orbigny, A., 1849–1852, Prodrome de paléontologie stratigraphique universelle des Animaux Mollusques et Rayonnés. Faisant Suite au Cours Élémentaire de Paléontologie et de Géologie Stratigraphique: Paris, Victor Masson, v. 1 (1849 [1850]), 394 p.; v. 2 (1850), 428 p.; v. 3 (1852), 387 p.

Douvillé, H., 1916, Les terrains secondaires dans le Massif de Moghara à l'Est de l'Isthme Suez: Mémoire de l'Académie des Sciences de Paris, v. 54, p. 1–184.

Duff, K.L., 1978, Bivalvia from the English Lower Oxford Clay (Middle Jurassic): Palaeontographical Society Monographs, No. 553, p. 1–137.

Dumortier, V.E., 1869, Études Paléontologiques sur les Dépôts Jurassiques du Bassin du Rhône. Troisième Partie. Lias Moyen: Paris, F. Savy, 348 p.

Dumortier, V.E., 1874, Études Paléontologiques sur les Dépôts Jurassiques du Bassin du Rhône. Quatrième Partie. Lias Supérieur: Paris, F. Savy, 335 p.

Etter, W., 1990, Paläontologische Untersuchungen im Unteren Opalinuston der Nordschweiz [Inaugural-Dissertation]: Zürich, Universität Zürich, 151 p.

Farag, I.A.M., and Gatinaud, W., 1960, Un nouveau genre de Terebratulides dans le Bathonien d'Egypte: Journal of Geology of the United Arab Republic, v. 4, p. 77–79.

Feldman, H.R., Owen, E.F., and Hirsch, F., 1991, Brachiopods from the Jurassic of Gebel El-Maghara, northern Sinai: American Museum Novitates, v. 3006, p. 1–28.

Feldman, H.R., Radulovic, V.J., Hegab, A.A., and Radulovic, B., 2012, Taxonomy and paleobiogeography of late Bathonian brachiopods from Gebel Engabashi, northern Sinai: Journal of Paleontology, v. 86, p. 238–252.

Fischer, P.H., 1880–1887, Manuel de Conchyliologie et de Paléontologie Conchyliologique, ou Histoire Naturelle des Mollusques Vivants et Fossils suivi d'un Appendice sur les Brachiopods par D.P. Oehlert. Avec 23 planches contenant 600 figures dessinées par S.P. Woodward: Paris, Savy, 1369 p.

Flamand, G.B.M., 1911, Recherches Géologiques et Géographiques sur le Haut-Pays de l'Oranie (Algérie et Territoires du Sud) [Thèses-Sciences]: Lyon, France, Université de Lyon, 1001 p.

Fourtau, R., 1924, Catalogue des invertébrés fossiles de l'Égypte: Geological Survey of Egypt, Palaeontology Series, v. 6, p. 1–27.

Fraas, O., 1877, Juraschichten am Hermon: Neues Jahrbuch für Mineralogie, Geologie and Palaeontologie, v. 1877, p. 17–30.

Frebold, H., 1929, Die Schichtenfolge des Jura und der Unterkreide an der Ostküste Südwest-Spitzbergens: Abhandlungen des Naturwissenschaftlichen Vereins, Hamburg, v. 22, p. 255–292.

Fürsich, F.T., 1982, Upper Jurassic bivalves from Milne Land, East Greenland: Bulletin, Grønlands Geologiske Undersøgelse, v. 144, p. 1−126.

Fürsich, F.T., and Pan, Y.H., 2014, Callovian−Oxfordian (Jurassic) bivalves from the Kamar-e-Mehdi Formation of east-central Iran: Beringeria, v. 44, p. 3–50.

Fürsich, F.T., and Werner, W., 1987, The Upper Jurassic Bivalvia of Portugal. Part I. Palaeotaxodonta and Pteriomorphia (Arcoida and Mytiloida): Comunicações dos Serviços Geológicos de Portugal, v. 73, p. 103–144.

Fürsich, F.T., Berndt, R., Scheuer, T., and Gahr, M., 2001, Comparative ecological analysis of Toarcian (Lower Jurassic) benthic faunas from southern France and east-central Spain: Lethaia, v. 34, p. 169–199.

Fürsich, F.T., Heinze, M., and Ayoub-Hannaa, W.S., 2019, Middle to Upper Jurassic bivalves of the southwestern Morondava Basin (Madagasca): Zitteliana, v. 93, p. 143–203.

Fürsich, F.T., Alberti, M., Pandey, D.K., and Ayoub-Hannaa, W.S., 2022, Jurassic bivalves from the Spiti area of the Himalayas, northern India: Zitteliana, v. 96, p. 153–178.

Garfunkel, Z., 1998, Constrains on the origin and history of the Eastern Mediterranean Basin: Tectonophysics, v. 298, p. 5–35.

Garfunkel, Z., and Derin, B., 1984, Permian−early Mesozoic tectonism and continental margin formation in Israel and its implications for the history of the Eastern Mediterranean, *in* Dixon, J.E., and Robertson, A.H.F., eds., The Geological Evolution of the Eastern Mediterranean: Geological Society, London, Special Publications, v. 17, p. 187–201.

Girty, G.H., 1911, On some new genera and species of Pennsylvanian fossils from the Wewoka Formation of Oklahoma: Annals of the New York Academy of Sciences, v. 21, p. 99−156.

Gmelin, J.F., 1791, Caroli a Linné, Systema Naturae: Tomus I, Pars VI, p. 3021–3910, Lipsiae, Georg. Emanuel. Beer.

Goldfuss, F.A., 1837–1841, Petrefacta Germaniae tam ea, quae in Museo Universitatis Regiae Borussicae Fridericiae Wilhelmiae Rhenanae Servantur quam alia Quaecunquae in Museis Hoenighusiano Muensteriano Aliisque Extant, Iconibus et Descriptionibus Illustrata. Abbildungen und Beschreibungen der Petrefacten Deutschlands und der Angrenzender Länder unter Mitwirkung des Herrn Grafen Georg zu Münster. Zweiter Theil [Bivalvia]: part 3, p. 141–224 (1837); part 4, p. 225–312 (1841), Düsseldorf, Arnz & Co.

Gray, J.E., 1824, Shells, *in* Parry W.E., ed., Supplement to Appendix, Parry's Voyage for the Discovery of a north-west passage in the years 1819–1820, containing an account of the subjects of Natural History: London, John Murray, Appendix 10, Zoology, p. 240–246.

Greppin, E., 1899, Description des fossiles du Bajocian supérieur des environs de Bâle: Mémoires de la Société Paléontologique Suisse, v. 26, p. 53–126.

Hall, J., 1885, Lamellibrachiata II, descriptions and figures of the Dimyaria, of the upper Helderberg, Hamilton, Portage and Chemung groups: Geological Survey of the State of New York, v. 5, p. 269–562.

Hall, J., and Whitfield, R.P., 1869, Preliminary notice of the Lamellibranchiata shells of the upper Helderberg, Hamilton and Chemung groups with others from the Waverly sandstones, part 2: Albany, New York, New York State Museum, 96 p.

Hallam, A., 1976, Stratigraphic distribution and ecology of European Jurassic Bivalves: Lethaia, v. 9, p. 245–259.

Hallam, A., 1977, Jurassic bivalve biogeography: Paleobiology, v. 3, p. 58–73.

Hammer, Ø., Harper, D.A.T., and Ryan, P.D., 2001, PAST: paleontological statistics software package for education and data analysis: Palaeontologia Electronica, v. 4. http://palaeo-electronica.org/2001_1/past/issue1_01.htm.

Hayami, I., 1961, On the Jurassic pelecypod faunas in Japan: Journal of the Faculty of Science, University of Tokyo, Section II, Geology, Mineralogy, Geography, Geophysics, v. 13, p. 243–343.

Hayami, I., 1975, A systematic survey of the Mesozoic Bivalvia from Japan: The University Museum, The University of Tokyo, Bulletin, v. 10, p. 1–249.

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., 1991a, New genus *Praeudesia* (Brachiopoda) from the Jurassic outcrops of Gebel El-Maghara, northern Sinai, Egypt: Bulletin of the Faculty of Science, Assiut University, v. 20, p. 1–17.

Hegab, A.A., 1991b, The occurrence of genus *Flabellothyris* (Brachiopoda) from the Jurassic of northern Sinai: Bulletin of the Faculty of Science, Assiut University, v. 20, p. 39–49.

Herrmannsen, A.N., 1846, Indices Generum Malacozoorum Primordia. Nomina Subgenerum, Generum, Familiarum, Tribuum, Ordinum, Classium; Adjectis Auctoribus, Temporibus, Locis Systematicis Atque Literariis, Etymis, Synonymis. Praetermittuntur Cirripedia, Tunicata et Rhizopoda: v. 1, p. 1–637, Cassellis, Fischer.

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: The Palaeontographical Society (London), Monographs, no. 614, p. 1–64.

Holdhaus, K., 1913, Fauna of the Spiti Shales (Lamellibranchiata and Gastropoda): Memoirs of the Geological Survey of India, Palaeontologica Indica, ser.15, pt. 2, v. 4, p. 397–456.

Holzapfel, S., 1998, Palökologie benthischer Faunengemeinschaften und Taxonomie der Bivalven im Jura Südtunesien: Beringeria, v. 22, p. 3–199.

Hryniewicz, K., Little, C.T.S., and Nakrem, H.A., 2014, Bivalves from the latest Jurassic–earliest Cretaceous hydrocarbon seep carbonates from central Spitsbergen, Svalbard: Zootaxa, v. 3859, 66 p.

ICZN, 1999, International Code of Zoological Nomenclature, 4th Edition: The International Trust for Zoological Nomenclature, London, 306 p.

Ivimey-Cook, H.C., Hodges, P., Swift, A., and Radley, J.D., 1999, Bivalves, *in* Swift, A., and Martill, D.M., eds., Fossils of the Rhaetian Penarth Group: The Palaeontological Association Field Guides to Fossils, v. 9, p. 83–127.

Jaboli, D., 1959, Fossili giurassici dell' Harar (Africa Orientale). Brachiopodi, Lamellibranchi e Gasteropodi. Missione Geologica dell' Azienda Generale Italiana Petroli (A.G.I.P.) nella Dancalia Meridionale e sugli Altipiani Hararini (1936–1938), vol. 4, Documentazione Paleontologica, parte prima: Roma, Accademia Nazionale dei Lincei, 100 p.

Jaitly, A.K., 2017, Implication of the Middle Jurassic pholadomyoids of Kachchh in the palaeobiogeography of the Middle East and South Asia: a review: Journal of the Geological Society of India, v. 90, p. 41–50.

Jaitly, A.K., Fürsich, F.T., and Heinze, M., 1995, Contributions to the Jurassic of Kachchh, western India. IV. The bivalve fauna. Part I. Subclasses Palaeotaxodonta, Pteriomorphia, and Isofilibranchia: Beringeria, v. 16, p. 147–257.

Kanjilal, S., 1980, Studies on Jurassic nuculids (Bivalvia) from the Habo Hill, District Kutch, Gujarat: Proceedings of the 3rd Indian Geological Congress, Poona, p. 331–346.

Kanjilal, S., 1985, On some species of *Palaeoneilo* Hall & Whitfield, 1869, from the Jurassic rocks of Habo Hill, district Kutch (Gujarat): Journal of Molluscan Studies, v. 51, p. 69–72.

Kanjilal, S., and Pathak, D.B., 1998, Spiti Shale bivalves from Chichim and Gate, Himachal Pradesh, India: Himalayan Geology, v. 19, p. 29–37.

Kanjilal, S., and Singh, G.S.P., 1973, A new nuculanid genus from the Callovian of Kutch (Gujarat), India: Proceedings of the Malacological Society of London, v. 40, p. 469–471.

Karapunar, B., Werner, W., Fürsich, F.T., and Nützel, A., 2020, Taxonomy and palaeoecology of the Early Jurassic (Pliensbachian) bivalves from Buttenheim, Franconia (southern Germany): Palaeontographica, Abteilung A, v. 318, p. 1–127.

Keeley, M.L., 1994, Phanerozoic evolution of the basins of northern Egypt and adjacent areas: Geologische Rundschau, v. 83, p. 728–742.

Kelly, S.R.A., 1984, Bivalvia of the Spilsby Sandstone and Sandringham sands (Late Jurassic−Early Cretaceous) of eastern England; Part 1: Monograph of the Palaeontographical Society, no. 566, p. 1–94.

Khalil, H., 2003, Late Bajocian–early Bathonian (Jurassic) molluscs from Gabal El-Maghara, northern Sinai, Egypt: Egyptian Journal of Paleontology, v. 3, p. 305–329.

Klöcker, P., 1966, Faunistische und feinstratigraphische Untersuchungen an der Lias-Dogger-Grenze am Schönberg bei Freiburg i. Br. 1. Teil: Profil und Fauna (Lamellibranchiata und Gastropoda): Berichte der Naturforschenden Gesellschaft zu Freiburg im Breisgau, v. 56, p. 209–248.

Koch, C.L., and Dunker, W., 1837, Beiträge zur Kenntnis des Norddeutschen Oolithgebildes und dessen Versteinerungen: Braunschweig, Germany, Oehme & Müller, 64 p.

Korobkov, I.A., 1954, [Spravochnik i Metodicheskoe Rukovodstvo po Tretichnym Molliuskam. Plastinchatozhabernye]: Leningradskoe Otdelenie, Gosudarstvennoe Nauchno-Tekhnicheskoe Izdatel'stvo Neftyanoĭ i Gorno-toplivnoĭ Literatury, 444 p. [in Russian]

Kuhn, O., 1935, Revision der Opalinuston (Dogger Alpha) -Fauna in Franken, mit Ausschluss der Cephalopoden: Palaeontologische Zeitschrift, v. 17, p. 109–158.

Kuhn, O., 1936, Die Fauna des Amaltheentons (Lias δ) in Franken: Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilageband, v. 75, p. 231–311.

Kuhn, O., 1938, Die Fauna des Dogger Delta der Frankenalb (Mit Nachträgen zum übrigen Jura): Nova Acta Leopoldina, Neue Folge, v. 6, p. 123–170.

Kumpera, O., Prantl, F., and Růžička, B., 1960, Revision of the Nuculanidae from the Ostrava-Karviná District (Pelecypoda): Acta Musei Nationalis Pragae (ser. B) Historia Naturalis, v. 16, p. 17−80.

Lamarck, J.B. de, 1819, Histoire Naturelle des Animaux sans Vertèbres. Vol. 6, 1ère partie: Paris, Deterville, 232 p.

Leanza, A.F., 1942, Los pelecïpodos del Lías de Piedra Pintada en el Neuquén: Revista del Museo de La Plata, Nueva Serie, Paleontología, v. 2, p. 143–208.

Link, H.F., 1806–1808, Beschreibung der Naturalien-Sammlung der Universität zu Rostock: v. 1, p. 1–160 (1806 [1807]); v. 2, p. 1–30 (1807); v. 3, p. 1–38 (1808); Rostock.

Linnaeus, C.A., 1758, Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Editio Decima, reformata. Tomus I, Regnum Animale: Holmiae, L. Salvvi, 823 p.

Liu, C., 1995, Jurassic bivalve palaeobiogeography of the Proto-Atlantic and the application of multivariate analysis methods to palaeobiogeography: Beringeria, v. 16, p. 3–123.

McAlester, A.L., and Rhoads, D.C., 1967, Bivalves as bathymetric indicators: Marine Geology, v. 5, p. 383–388.

Makowski, H., 1952, La faune Callovienne de Lukow en Pologne: Palaeontologica Polonicia, v. 4, p. 1–64.

Mander, L., Twitchett, R., and Benton, M.J., 2008, Palaeoecology of the Upper Triassic extinction event in the SW UK: Journal of the Geological Society of London, v. 165, p. 319–332.

Mart, Y., 1987, Superpositional tectonic patterns along the continental margin of the southeastern Mediterranean: a review: Tectonophysics, v. 140, v. 213–232.

Martin, J., 1860, Paléontologie stratigraphique de Infra-Lias du Département de la Côte-d'Or: Mémoires de la Société Géologique de France, sér. 2, v. 7, p. 1−101.

Marzloff, D., Dareste De La Chavanne J., and Moret, J., 1936, Étude sur la faune du Bajocien supérieur du Mont d'Or Lyonnais (Ciret). Gastéropodes, Lamellibranches, Brachiopodes, Echinodermes, Anthozoaires, Spongiaires (suite et fin): Travaux du Laboratoire de Géologie de la Faculté des Sciences de Lyon, v. 28, p. 57–147.

Matthews, S.C., 1973, Notes on open nomenclature and on synonymy lists: Palaeontology, v. 16, p. 713–719.

Ménégaux, A., 1889, Sur la branchie des lamellibranches et sur sa comparaison avec celle des scutibranches: Bulletin de la Société Philomatique de Paris, sér. 8, v. 1, p. 137−144.

Moesch, C., 1867, Geologische Beschreibung des Aargauer Jura und der nördlichen Gebiete des Kantons Zürich: Beiträge zur Geologischen Karte der Schweiz, v. 4, p. 1–319.

Mongin, D., 1967, Les Mollusques du Bathonien saumatre du Moyen Atlas: Notes et Mémoires de Service Géologique du Maroc, v. 200, p. 37–94.

Monke, H., 1888, Die Liasmulde von Herford in Westfalen: Verhandlungen des Naturhistorischen Vereins, Bonn, v. 45, p. 125–238.

Morris, J., and Lycett, J., 1853–1854, A monograph of the Mollusca from the Great Oolite, chiefly from Minchinhampton and the Coast of Yorkshire: Monographs of the Palaeontographical Society, part II, Bivalves, v. 7, p. 1–80 (1853); part III, Bivalves, v. 8, p. 81−148 (1854).

Moustafa, A.R., El-Badrawy, R., and Gibali, H., 1998, Pervasive E-ENE oriented faults in the northern Egypt and their relationship to Late Cretaceous petroliferous basins in the northern Western Desert: Proceedings of 14th Egyptian General Petroleum Corporation Exploration and Production Conference, Cairo, v. 1, p. 51– 67.

Müller, J.M., 1847, Monographie der Petrefacten der Aachener Kreideformation: Bonn, Henry and Cohen, 48 p.

Müller, O.F., 1779, Von zwoen wenig bekannten Muscheln, der Schinkenarche und der gerunzelten Mahlermuschel: Beschäftigungen der Berlinischen Gesellschaft, v. 4, p. 55–59.

Nicol, D., 1969, Deposit-feeding pelecypods in Recent marine faunas: Transactions of Gulf Coast Association of Geological Societies, v. 19, p. 423–424.

Nicol, D., 1972, Geological history of deposit-feeding pelecypods: The Nautilus, v. 86, p. 11–15.

Noetling, F., 1887, Der Jura am Hermon eine Geognostische Monographie: Stuttgart, Schweizerbart, 46 p.

Ogérien, F., 1867, Histoire Naturelle du Jura et des Départements Voisins. Tome I. Géologie, 2e Fascicule: Géologie proprement dite, appliquée aux Arts, à l'Industrie et surtout à l'Agriculture: Paris, Victor Masson, 945 p.

Oppel, A.C., 1856, Die Juraformation Englands, Frankreichs und des südwestlichen Deutschlands: Jahrbuch des Vereins für vaterländische Naturkunde in Württemberg, v. 12, p. 121–556.

Palmer, C.P., 1973, The palaeontology of the Liassic (Lower Jurassic) clay pits at Stonehouse and Tuffley in Gloucestershire: Geological Magazine, v. 110, p. 249–263.

Pandey, D.K., and Agrawal, S.K., 1984, Bathonian−Callovian molluscs of Gora Dongar, Pachchham "Island" (District Kahchh, Gujarat): Quarterly Journal of the Geological, Mining and Metallurgical Society of India, v. 56, p. 176–196.

Pandey, D.K., and Singh, C.S.P., 1981, A new species of *Indoculana* Kanjilal & 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., 1981, Biostratigraphy of the Mahmal Formation (middle and upper Bajocian) in Makhtesh Ramon, Negev, southern Israel: Bulletin of the Geological Survey of Israel, v. 74, p. 1–55.

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.

Pelseneer, P., 1889, Sur la classification phylogenetique de pelecypods: Bulletin Scientifique de la France et de la Belgique, sér. 3, no. 2, v. 20, p. 27−52.

Phillips, J., 1829, Illustrations of the Geology of Yorkshire: York, UK, Wilson and Sons, 192 p.

Picard, L., and Hirsch, F., 1987, The Jurassic Stratigraphy in Israel and the Adjacent Countries: Jerusalem, Israel Academy of Sciences and Humanities, 106 p.

Piette, E., 1856, Notice sur les Grès d´Aiglemont et de Rimogne: Bulletin de la Societé Géologique de France, sér. 2, v. 13, p. 188–207.

Pugaczewska, H., 1986, Bivalvia of the Polish Middle Jurassic and remarks on their paleoecology: Acta Palaeontologica Polonica, v. 31, p. 27–83.

Quenstedt, F.A., 1851–1852, Handbuch der Petrefaktenkunde, 1st Edition: Tübingen, Laupp and Siebeck, p. 1–528 (1851); p. 529–792 (1852).

Quenstedt, F.A., 1856–1857, Der Jura: Tübingen, Laupp and Siebeck, p. 1–368 (1856); p. 369–842 (1857).

Quenstedt, F.A., 1884, Handbuch der Petrefaktenkunde (3. Aufl.): Tübingen, H. Laupp, 1230 p.

Quenstedt, W., 1930, Die Anpassung an die grabende Lebensweise in der Geschichte der Solenomyiden, und Nuculaceen: Geologische und Palaeontologische Abhandlungen, Neue Folge, v. 18, p. 5–119.

Roemer, F.A., 1835–1839, Die Versteinerungen des Norddeutschen Oolithen Gebirges: Hannover, Hahn'sche Hofbuchhandlung, v. 2, p. 1–74 (1835); v. 3, p. 75–218 (1836); Nachtrag, p. 1–59 (1839).

Rollier, L., 1923, Rectification de nomenclature: Revue Critique de Paléozoologie et de Paléophytologie, 27, p. 67.

Romanov, L.F., 1973, Yurskie Morskie Dvustvorchateie Molliuski Mezhdurechia Dnestr-Prut [Jurassic Marine Bivalves of the Dniester-Prut Interfluve]: Chisinau, Moldova, Shtiintsa, 227 p. [in Russian]

Ros, S., Márquez-Aliaga, A., and Damborenea, S., 2014, Comprehensive database on Induan (Lower Triassic) to Sinemurian (Lower Jurassic) marine bivalve genera and their paleobiogeographic record: University of Kansas Paleontological Contributions, v. 8, p. 1–219.

Sanin, V.R., 1976, Rannemelovye ktenodoitidy Sibiri [Early Cretaceous ctenodontids (Bivalvia) from northern Siberia]: Trudy Instituta Geologii i Geofiziki (Novosibirsk), v. 310, p. 1–70. [in Russian]

Schenck, H.G., 1934, Classification of nuculid pelecypods: Bulletin du Musée Royal d´Histoire Naturelle de Belgique, v. 10, p. 1–78.

Scholz, A., Aberhan, M., and González-León, C.M., 2008, Early Jurassic bivalves of the Antimonio terrane (Sonora, NW Mexico): taxonomy, biogeography, and paleogeographic implications: Geological Society of America, Special Paper, v. 442, p. 269–312.

Scotese, C.R., 2001, Atlas of Earth History. Volume 1, Paleogeography: Arlington, Texas, PALEOMAP Project, 58 p.

Sha, J.-G., and Fürsich, F.T., 1994, Bivalve faunas from eastern Heilongjiang, northeastern China. II. The Late Jurassic and Early Cretaceous buchiid fauna: Beringeria, v. 12, p. 3−93.

Sha, J.-G., Fürsich, F.T., Smith, P.L., and Wang, L.-J., 1998, Palaeotaxodonta, Pteriomorphia and Isofilibranchia (Bivalvia) from the Jurassic of the main ridge of the Tanggula Mountains, Qinghai-Xizang Plateau, China: Beringeria, v. 21, p. 3−55.

Singh, C.S.P., and Kanjilal, S., 1977, *Habonucula*, a new nuculid (Bivalvia) genus from Jurassic rocks of Kutch (Gujarat), W. India: Journal of the Geological Society of India, v. 18, p. 189–193.

Sowerby, J. de C., 1823–1846, The Mineral Conchology of Great Britain: v. 4, p. 115–151, pls. 384–407 (1823); v. 5, p. 1–64, pls. 408–443 (1823); p. 65–138, pls. 444–485 (1824 [1825]); p. 139–171, pls. 486–503 (1825); v. 6, p. 1–86, pls. 504–545 (1826); p. 87–156, pls. 546–580 (1827); p. 157–200, pls. 581–597 (1828); p. 201–235, pls. 598–609 (1829); Preface to the General Indexes and Systematik Index to the six volumes, p. 239–250 (1835); Alphabet Index to volumes 1–6, p. 1–8, pls. 610–618 (1840); p. 9–16, pls. 619–623 (1841); p. 17–24, pls. 624–628 (1843); p. 25–56, pls. 629–643 (1844); p. 57–80, pls. 644–648 (1846), London, J. de C. Sowerby.

Sowerby, J. de C., 1840, Description of fossils from the Upper Secondary Formation of Cutch collected by C. W. Grant: Transactions of the Geological Society of London, ser. 2, v. 5, explanation of pl. 21–23 and figs. 8–17.

Stefanini, G., 1939, Molluschi del Giuralias della Somalia: Palaeontographia Italica, v. 3, p. 103–270.

Stephenson, L.W., 1953, Larger invertebrate fossils of the Woodbine Formation (Cenomanian) of Texas: U.S. Geological Survey Professional Paper, v. 242, p. 1–211, 219–225. [for 1952]

Stoliczka, F., 1870–1871, Cretaceous fauna of southern India. The Pelecypoda, with a review of all known genera of this class, fossil and Recent: Memoirs of the Geological Survey of India, Palaeontologica Indica, ser. 6, v. 3, p. 1−538.

Tate, R., 1870, On the palaeontology of the junction beds of the Lower and Middle Lias in Gloucestershire: Quarterly Journal of the Geological Society of London, v. 26, p. 394–408.
Terquem, O., and Jourdy, E., 1871, Monographie de l'etage Bathonien dans le département de la Moselle: Mémoires de la Société Géologique de France, ser. 2, v. 9, p. 1–175.
Terquem, O., and Piette, E., 1865, Le Lias inférieur de l'Est de la France comprénant la Meurthe, la Moselle, le Grand-Duché de Luxembourg, la Belgique et la Meuse: Mémoires de la Societé Géologique de France, ser. 2, v. 8, p. 1–175 p.
Thevenin, A., 1906–1923, Types du Prodrome de Paléontologie stratigraphique universelle d'Alcide d'Orbigny. Tome I. Silurien–Bathonien: Annales de Paléontologie, v. 1, p. 97–100, 165–172, 193–196 (1906); v. 2, p. 89–96, 161–172 (1907); v. 3, p. 25–40, 189–200 (1908); v. 4, p. 109–124, 153–164 (1909); v. 5, p. 65–88 (1910); v. 6, p. 65–92 (1911) , v. 8, p. 73–104 (1913); v. 12, p. 149–176 (1923).
Thiéry, P., and Cossmann, M., 1907, Note sur la Callovien de la Haute-Marne et spécialement sur un gisement situé dans la commune de Bricon: Bulletin de la Société d'Agriculture, Lettres, Sciences et Arts du Département de la Haute-Saône, Vesoul, L. Bon, 79 p.
Troedsson, G., 1951, On the Höganäs Series of Sweden (Rhaeto-Lias): Skrifter från Mineralogisk-och Paleontologisk-Geologiska Institutionerna, Lund, v. 7, p. 1–269.
von Seebach, K., 1865, Beiträge zur Geologie der Insel Bornholm: Zeitschrift der Deutschen Geologischen Gesellschaft, v. 17, p. 338–347.
Wasmer, M.S., Hautmann, M., Hermann, E., Ware, D., Roohi, Gh., Ur-Rehman, Kh., Yaseen, A., and Bucher, H., 2012, Olenekian (Early Triassic) bivalves from the Salt Range and Surghar Range, Pakistan: Palaeontology, v. 55, p. 1043–1073.
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. 1830, p. 64–73.
Woods, H., 1899, A monograph of the Cretaceous Lamellibranchia: Monographs of the Palaeontographical Society, no. 53, p. 1–72.
Yin, J., and McRoberts, C.A., 2006, Latest Triassic–earliest Jurassic bivalves of the Germig Formation from Lanongla (Tibet, China): Journal of Paleontology, v. 80, p. 104–120.
Zieten, C.H.V., 1830–1833, Die Versteinerungen Württembergs: Stuttgart, Verlag und Lithographie der Expedition des Werkes unserer Zeit, 102 p.

Appendix A

Dimensions of *Nuculoma douvillei* n. sp. See Figure 3 for explanation of measurements and ratios; measurements in mm.

Morphotype (*Nuculoma douvillei* n. sp.)	L	H	Iav	AL	H/L	Iav/L	Al/L
BSPG 2014V 4/1	10	8.8	8.2	8.5	0.88	0.82	0.85
BSPG 2014V 4/2	8.8	7.3	7.5	7.2	0.83	0.85	0.82
BSPG 2014V 4/3	7.9	7	6.2	7.2	0.89	0.78	0.91
BSPG 2014V 4/4	8.7	6.4	8.1	7.5	0.74	0.93	0.86
BSPG 2014V 4/5	9.1	7.8	7.5	6.9	0.86	0.82	0.76
BSPG 2014V 4/6	6.5	5.8	5.5	5.2	0.89	0.85	0.80
BSPG 2014V 4/7	6.9	7.2	6	6.2	1.04	0.87	0.90
BSPG 2014V 167/1	4.7	5	4	4.3	1.06	0.85	0.91
BSPG 2014V 173/1	8	8.5	8.5	6.5	1.06	1.06	0.81
BSPG 2014V 173/2	10.5	9.3	8.5	8.5	0.89	0.81	0.81
BSPG 2014V 173/3	7	7.8	6.9	6.2	1.11	0.99	0.89
BSPG 2014V 173/4	9.2	8.5	8.4	8.8	0.92	0.91	0.96
BSPG 2014V 173/5	8.2	8.6	7.5	6.8	1.05	0.91	0.83
BSPG 2014V 173/6	8.7	9.2	7.5	8	1.06	0.86	0.92
BSPG 2014V 173/7	8.2	8.5	7.3	7.5	1.04	0.89	0.91
BSPG 2014V 173/8	7.7	8.4	7.5	7	1.09	0.97	0.91
BSPG 2014V 173/9	8.2	8.8	7.3	7	1.07	0.89	0.85
BSPG 2014V 173/10	7	8.3	7.3	6.5	1.19	1.04	0.93
BSPG 2014V 173/11	9.5	9.3	7.3	8.4	0.98	0.77	0.88
BSPG 2014V 173/12	8.2	8.5	7.9	7.5	1.04	0.96	0.91
BSPG 2014V 173/13	9.7	8.3	8.4	9.1	0.86	0.87	0.94
BSPG 2014V 173/14	7	7.1	6.6	6.5	1.01	0.94	0.93
BSPG 2014V 173/15	8.3	8.8	7.5	7.5	1.06	0.90	0.90
BSPG 2014V 174/1	7.1	7.4	6.9	6.8	1.04	0.97	0.96
BSPG 2014V 175/1	6.3	6.8	6.2	6.2	1.08	0.98	0.98
BSPG 2014V 175/2	5.8	6.2	4.9	5	1.07	0.84	0.86
BSPG 2014V 175/3	6.5	6.8	6.5	6.3	1.05	1.00	0.97
BSPG 2014V 175/4	6.1	5.2	5.2	5.6	0.85	0.85	0.92

Continued.

Morphotype (*Nuculoma douvillei* n. sp.)	L	H	Iav	AL	H/L	Iav/L	Al/L
BSPG 2014V 175/5	5.5	6	4.5	4.3	1.09	0.82	0.78
BSPG 2014V 175/6	7.2	6.1	5.5	6.5	0.85	0.76	0.90
BSPG 2014V 175/7	6.9	5.4	5.7	6.2	0.78	0.83	0.90
BSPG 2014V 175/8	6.1	5.2	5.3	5.8	0.85	0.87	0.95
BSPG 2014V 175/9	6.5	5.5	5.3	6.1	0.85	0.82	0.94
BSPG 2014V 175/10	6.5	5.8	5.7	5.2	0.89	0.88	0.80
BSPG 2014V 175/11	5.9	5	4.3	5.3	0.85	0.73	0.90
BSPG 2014V 178/1	7.9	8	7	7.1	1.01	0.89	0.90
BSPG 2014V 178/2	5.7	5.5	5.1	5.1	0.96	0.89	0.89
BSPG 2014V 178/3	8.7	7.5	7.2	8.1	0.86	0.83	0.93
BSPG 2014V 178/4	6	5.8	5.5	5.3	0.97	0.92	0.88
BSPG 2014V 178/5	6.3	5.8	5.8	5.7	0.92	0.92	0.90
BSPG 2014V 178/6	7.1	6.5	6.5	6.5	0.92	0.92	0.92
BSPG 2014V 178/7	6	6.5	5.7	4.8	1.08	0.95	0.80
BSPG 2014V 178/8	10.7	9	9.5	9.5	0.84	0.89	0.89
BSPG 2014V 178/9	7.5	6.3	6	6	0.84	0.80	0.80
BSPG 2014V 178/10	9	7.2	8.2	7.2	0.80	0.91	0.80
BSPG 2014V 178/11	6.5	7.7	6.3	6.1	1.18	0.97	0.94
BSPG 2014V 178/12	9	7.5	7.5	7.7	0.83	0.83	0.86
BSPG 2014V 178/13	6.8	7.3	6	5.7	1.07	0.88	0.84
BSPG 2014V 178/14	9	7.5	7.5	7.8	0.83	0.83	0.87
BSPG 2014V 178/15	6.7	6	5.8	5.8	0.90	0.87	0.87
BSPG 2014V 178/16	7.7	6.5	6.3	6.8	0.84	0.82	0.88
BSPG 2014V 178/17	5.5	6.7	6	5.2	1.22	1.09	0.95
BSPG 2014V 178/18	8.2	7.7	7.5	7.4	0.94	0.91	0.90
BSPG 2014V 178/19	6.6	7.8	6.2	6.2	1.18	0.94	0.94
BSPG 2014V 178/20	7.3	7.8	6.2	6.7	1.07	0.85	0.92
BSPG 2014V 178/21	5.9	6.2	5.5	5.5	1.05	0.93	0.93
BSPG 2014V 178/22	7.2	7.7	6.5	6.8	1.07	0.90	0.94
BSPG 2014V 178/23	7.8	8.2	7.2	6.5	1.05	0.92	0.83
BSPG 2014V 178/24	8.2	8.5	7.5	6.8	1.04	0.91	0.83
BSPG 2014V 178/25	7.7	8.5	7	7	1.10	0.91	0.91
BSPG 2014V 178/26	6.5	6.9	6	5.7	1.06	0.92	0.88
BSPG 2014V 178/27	6.9	7.3	6.2	6.3	1.06	0.90	0.91
BSPG 2014V 178/28	7.2	6.4	6.5	6.8	0.89	0.90	0.94
BSPG 2014V 178/29	5.5	5.8	5.3	4.8	1.05	0.96	0.87
BSPG 2014V 178/30	5	5.3	4.4	4.5	1.06	0.88	0.90
BSPG 2014V 178/31	5	5.2	5	4.3	1.04	1.00	0.86
BSPG 2014V 178/32	5.5	5.8	4.5	4.8	1.05	0.82	0.87
BSPG 2014V 178/33	5.4	5.9	4.8	5.1	1.09	0.89	0.94
BSPG 2014V 178/34	9	7.5	7.5	6.8	0.83	0.83	0.76
BSPG 2014V 178/35	5.3	5.8	4.7	4.4	1.09	0.89	0.83
BSPG 2014V 178/36	7.2	7.8	7	7	1.08	0.97	0.97
BSPG 2014V 308/1	9.5	9.2	7.8	8.5	0.97	0.82	0.89
BSPG 2014V 308/2	8.3	9	8.4	7.3	1.08	1.01	0.88
BSPG 2014V 308/3	9.2	9.5	8.7	8.3	1.03	0.95	0.90
BSPG 2014V 308/4	8.4	8.8	7.9	7.3	1.05	0.94	0.87
BSPG 2014V 308/5	7.7	9.2	8.1	7	1.19	1.05	0.91
BSPG 2014V 308/6	8.2	8.1	8.1	7.5	0.99	0.99	0.91
BSPG 2014V 308/7	8.5	8.3	7	7	0.98	0.82	0.82
BSPG 2014V 308/8	6	5.7	5.2	5.5	0.95	0.87	0.92
BSPG 2014V 308/9	8.3	7.5	7.7	7.8	0.90	0.93	0.94
BSPG 2014V 308/10	8.7	8.5	8.3	7.6	0.98	0.95	0.87
BSPG 2014V 308/11	10	8.5	8.1	9	0.85	0.81	0.90
BSPG 2014V 308/12	8.3	8.3	8	7.3	1.00	0.96	0.88
BSPG 2014V 308/13	9.3	8.3	7.8	8.3	0.89	0.84	0.89
BSPG 2014V 308/14	9	9	8.2	8.3	1.00	0.91	0.92
BSPG 2014V 308/15	9	9	8.3	8.3	1.00	0.92	0.92
BSPG 2014V 308/16	9	9.5	8.3	8.2	1.06	0.92	0.91
BSPG 2014V 308/17	9	9.4	8.3	8.2	1.04	0.92	0.91
BSPG 2014V 308/18	8.4	9.6	8.4	8	1.14	1.00	0.95
BSPG 2014V 308/19	6.8	8	6.6	6.2	1.18	0.97	0.91
BSPG 2014V 308/20	8.6	9.2	8	7.5	1.07	0.93	0.87
BSPG 2014V 308/21	9	8.8	7.6	8.1	0.98	0.84	0.90
BSPG 2014V 308/22	8.1	7	6.4	7.5	0.86	0.79	0.93
BSPG 2014V 308/23	8.1	8.5	7.5	7.3	1.05	0.93	0.90
BSPG 2014V 308/24	7.3	8	6.1	6.9	1.10	0.84	0.95
BSPG 2014V 308/25	7.8	6.8	6.5	7	0.87	0.83	0.90
BSPG 2014V 308/26	6.8	7.2	6.2	6.5	1.06	0.91	0.96
BSPG 2014V 308/27	5.8	6.3	5.5	4.8	1.09	0.95	0.83
BSPG 2014V 308/28	7.4	8	7	6.5	1.08	0.95	0.88
BSPG 2014V 309/1	9	8.8	7.6	7.5	0.98	0.84	0.83
BSPG 2014V 309/2	8.4	8.8	8	7	1.05	0.95	0.83
BSPG 2014V 309/3	7.6	8	7.4	6.2	1.05	0.97	0.82
BSPG 2014V 309/4	7.8	7.8	7.2	6.4	1.00	0.92	0.82
BSPG 2014V 309/5	6.3	7	5.7	5.8	1.11	0.90	0.92

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Continued.

Morphotype (*Nuculoma douvillei* n. sp.)	L	H	Iav	AL	H/L	Iav/L	Al/L
BSPG 2014V 309/6	6.6	7	5.9	5.5	1.06	0.89	0.83
BSPG 2014V 309/7	7.8	7.5	7	7	0.96	0.90	0.90
BSPG 2014V 310/1	6.4	6.8	5.5	5.8	1.06	0.86	0.91
BSPG 2014V 310/2	7.5	8.8	7.1	6.8	1.17	0.95	0.91
BSPG 2014V 310/3	5.2	5.5	4.8	4.2	1.06	0.92	0.81
BSPG 2014V 310/4	8.3	6.8	6.8	6.8	0.82	0.82	0.82
BSPG 2014V 310/5	8.1	6.8	7.2	6.1	0.84	0.89	0.75
BSPG 2014V 310/6	7.1	6	6.2	5.3	0.85	0.87	0.75
BSPG 2014V 310/7	9	7.5	7.5	7.2	0.83	0.83	0.80
BSPG 2014V 310/8	7.6	6.8	7.1	6	0.89	0.93	0.79
BSPG 2014V 310/9	7.5	6.5	7	6.2	0.87	0.93	0.83
BSPG 2014V 311/1	7.5	7.8	6.8	7	1.04	0.91	0.93
BSPG 2014V 311/2	7.2	7.8	7.3	6.8	1.08	1.01	0.94
BSPG 2014V 311/3	4.8	5	4.5	3.7	1.04	0.94	0.77
BSPG 2014V 311/4	6	6.3	4.7	5.2	1.05	0.78	0.87
BSPG 2014V 311/5	6.5	6.8	5.7	5.5	1.05	0.88	0.85

Appendix B

Dimensions of *Nuculoma wynnei* Cox, 1940, and *Nuculoma sinaiensis* n. sp. See Figure 3 for explanation of measurements and ratios; measurements in mm.

Nuculoma wynnei (Kachchh, India)	L	H	Iav	H/L	Iav/L
PIW 1991 III10/1	16.7	14.7	11.3	0.88	0.68
PIW 1991 III11/1	12.8	10.75	6.8	0.84	0.53
PIW 1991 III12/1	17.7	14.5	12.1	0.82	0.68
PIW 1991 III12/2	18.4	16.1	13	0.88	0.71
PIW 1991 III12/3	21	17.45	13.7	0.83	0.65
PIW 1991 III12/4	18	16	13.2	0.89	0.73
PIW 1991 III12/5	18	16.2	11.3	0.90	0.63
PIW 1991 III15/1	17.65	15.5	13.8	0.88	0.78
PIW 1991 III15/2	18.7	16.8	13.4	0.90	0.72
PIW 1991 III15/3	18.2	16.2	12.4	0.89	0.68
PIW 1991 III15/4	17.5	15.4	11.5	0.88	0.66
PIW 1991 III20/1	18.7	15.6	14	0.83	0.75
PIW 1991 III20/2	23	19.7	17.2	0.86	0.75
PIW 1991 III20/3	20.5	17.7	15	0.86	0.73
PIW 1991 III23/1	13.9	12.4	9	0.89	0.65
PIW 1991 III23/2	17	14.6	11.9	0.86	0.70
PIW 1991 III23/3	17.8	15.3	12.8	0.86	0.72
PIW 1991 III23/4	14.3	13	10.5	0.91	0.73
PIW 1991 III23/5	14.6	12.7	10	0.87	0.68
PIW 1991 III23/6	16.8	13.5	12	0.80	0.71
PIW 1991 III23/7	17.5	15.5	12.7	0.89	0.73
PIW 1991 III24/1	22.4	18	15	0.80	0.67
PIW 1991 III24/2	24	18.8	16.5	0.78	0.69
PIW 1991 III25/1	17	15	11.7	0.88	0.69
PIW 1991 III25/2	18.3	15.8	12.9	0.86	0.70
PIW 1991 III25/3	18	15.5	12.5	0.86	0.69
PIW 1991 III25/4	17.2	15.3	11.3	0.89	0.66
PIW 1991 III28/1	19.2	15.8	12.8	0.82	0.67
PIW 1991 III28/2	17.85	15.7	12.8	0.88	0.72
PIW 1991 III28/3	16.9	15.3	11.5	0.91	0.68
PIW 1991 III28/4	19.1	18	12.5	0.94	0.65
PIW 1991 III29/1	17.5	14.2	12	0.81	0.69
PIW 1991 III29/2	17	13.8	12.3	0.81	0.72
PIW 1991 III30/1	21.3	18.5	15.4	0.87	0.72
PIW 1991 III30/2	15.6	14	12.1	0.90	0.78
PIW 1991 III33/1	16.8	16.3	11.5	0.97	0.68
PIW 1991 III34/1	24.4	19	16	0.78	0.66
PIW 1991 III34/2	19.6	18	12.3	0.92	0.63
PIW 1991 III38/1	13.7	10.8	9.5	0.79	0.69
PIW 1991 III45/1	20.5	16.8	12.5	0.82	0.61
PIW 1991 III45/2	18	13.8	12.2	0.77	0.68
PIW 1991 III45/3	17.7	15.9	12.5	0.90	0.71
PIW 1991 III46/1	18.3	13.5	12.2	0.74	0.67
PIW 1991 III46/2	17.3	14.2	11.5	0.82	0.66

Continued.

Nuculoma wynnei (Kachchh, India)	L	H	Iav	H/L	Iav/L
PIW 1991 III46/3	16.5	13.7	12.3	0.83	0.75
PIW 1991 III46/4	16.8	13.5	11.4	0.80	0.68
PIW 1991 III46/5	15.2	12.2	11.5	0.80	0.76
PIW 1991 III46/6	16.9	14.2	12.5	0.84	0.74
PIW 1991 III46/7	15.2	12.23	11	0.80	0.72
PIW 1991 III46/8	14.8	12.5	9.5	0.84	0.64
PIW 1991 III46/9	16.4	12.8	9.7	0.78	0.59
PIW 1991 III46/10	13.3	10.5	7.6	0.79	0.57
PIW 1991 III46/11	14.7	12	8.2	0.82	0.56
PIW 1991 III46/12	18	16	14	0.89	0.78
PIW 1991 III46/13	17.8	14.8	11	0.83	0.62
PIW 1991 III46/14	19.6	16.3	13.2	0.83	0.67
PIW 1991 III46/15	12.5	10	7.3	0.80	0.58
PIW 1991 III970/1	21	17	14	0.81	0.67
PIW 1991 III971/1	28.5	24.3	18.3	0.85	0.64
PIW 1991 III971/2	19.7	15.5	13	0.79	0.66
Nuculoma sinaiensis n. sp. (Sinai, Egypt)					
BSPG 2014V 303/1	10	7.5	6.8	0.75	0.68
BSPG 2014V 303/2	10.8	7.8	6.75	0.72	0.63
BSPG 2014V 303/3	10.5	7.5	7.4	0.71	0.70
BSPG 2014V 303/4	8.7	6.5	5.7	0.75	0.66
BSPG 2014V 303/5	9.25	6.7	6.5	0.72	0.70
BSPG 2014V 303/6	10.5	7.45	6.7	0.71	0.64
BSPG 2014V 303/7	13.9	8.5	8	0.61	0.58
BSPG 2014V 303/8	10.7	7.7	6.35	0.72	0.59
BSPG 2014V 304/1	10.5	7.9	7.1	0.75	0.68
BSPG 2014V 305/1	12.85	9.25	8.2	0.72	0.64
BSPG 2014V 305/2	12.55	9	8.5	0.72	0.68
BSPG 2014V 305/3	11.5	8.5	7.8	0.74	0.68
BSPG 2014V 305/4	12.25	9.35	8	0.76	0.65
BSPG 2014V 305/5	11	8	7.5	0.73	0.68
BSPG 2014V 305/6	12.2	8	7.7	0.66	0.63
BSPG 2014V 306/1	11	7.4	7	0.67	0.64
BSPG 2014V 306/2	9.75	7	6.8	0.72	0.70
BSPG 2014V 306/3	11.2	7.6	7	0.68	0.63
BSPG 2014V 312/1	7.25	5.2	4.65	0.72	0.64
BSPG 2014V 312/2	9	6.15	5.4	0.68	0.60
BSPG 2014V 312/3	10.85	7.5	6.5	0.69	0.60
BSPG 2014V 312/4	6.7	4.25	4.25	0.63	0.63
BSPG 2014V 312/5	14	9.6	8.5	0.69	0.61
BSPG 2014V 312/6	14.4	9	8.7	0.63	0.60
BSPG 2014V 313/1	12.85	9	8.45	0.70	0.66
BSPG 2014V 313/2	13.5	8.65	8.8	0.64	0.65
BSPG 2014V 313/3	12.9	9.5	8.35	0.74	0.65
BSPG 2014V 313/4	10.5	8	8	0.76	0.76
BSPG 2014V 313/5	12.4	9	7.5	0.73	0.60
BSPG 2014V 313/6	10.25	7.8	7.4	0.76	0.72
BSPG 2014V 313/7	10.4	8	7.55	0.77	0.73
BSPG 2014V 313/8	11.05	7.2	6.35	0.65	0.57
BSPG 2014V 313/9	11.05	7.5	6.5	0.68	0.59
BSPG 2014V 314/1	13.25	9.45	8.4	0.71	0.63
BSPG 2014V 314/2	8.3	6.4	5.5	0.77	0.66
BSPG 2014V 314/3	6.6	4.3	4.2	0.65	0.64
BSPG 2014V 314/4	11.55	8.5	7.6	0.74	0.66
BSPG 2014V 314/5	10	7.1	6.5	0.71	0.65
BSPG 2014V 314/6	12.5	8	8.5	0.64	0.68
BSPG 2014V 315/1	11.85	8.8	7.5	0.74	0.63
BSPG 2014V 315/2	12.7	9.58	8.1	0.75	0.64
BSPG 2014V 315/3	10.4	7.8	7	0.75	0.67
BSPG 2014V 315/4	14	9.1	9	0.65	0.64
BSPG 2014V 316/1	5.65	4	3.7	0.71	0.65
BSPG 2014V 316/2	12.5	9	9	0.72	0.72
BSPG 2014V 316/3	10.2	7.5	6.35	0.74	0.62
BSPG 2014V 316/4	5.35	3.8	3.5	0.71	0.65
BSPG 2014V 316/5	9.3	6.8	6.7	0.73	0.72
BSPG 2014V 316/6	7.1	5.2	4.3	0.73	0.61
BSPG 2014V 316/7	8.3	6	5	0.72	0.60
BSPG 2014V 316/8	6.6	4.8	5	0.73	0.76
BSPG 2014V 317/1	11.5	8.5	8	0.74	0.70
BSPG 2014V 317/2	12.35	8.6	8.2	0.70	0.66
BSPG 2014V 317/3	10.35	7.5	6.85	0.72	0.66
BSPG 2014V 318/1	10.8	8.5	6.5	0.79	0.60
BSPG 2014V 318/2	10.7	7.6	6.5	0.71	0.61
BSPG 2014V 327/1	6.3	4.2	3.8	0.67	0.60

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