


Jurassic Trigoniida (Bivalvia) from Gebel Maghara, northern Sinai, Egypt

Wagih S. Ayoub-Hannaa,^{1,2} Michael R. Cooper,³ Ahmed A. Abdelhady,⁴ and Franz T. Fürsich^{2*} 

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

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

³Honorary Curator at Natural Science Museum, Durban, South Africa <mikecooper2646@gmail.com>

⁴Geology Department, Faculty of Science, Minia University, 61519 Minia, Egypt <ahmed.abdelhady@mu.edu.eg>

Non-technical Summary.—On the Sinai Peninsula, a thick pile of terrestrial to shallow-marine sediments accumulated during the Jurassic period. The sea floor at that time was colonized chiefly by brachiopods and bivalves. Among the latter, trigoniids were a comparatively rare but diverse faunal element, represented by very small to small individuals. They belong to 14 species and nine genera. One of these species is new to science, but five genera with species occurring also elsewhere in Jurassic seas were recognized as new, all of them characterized by a very small to small size.

Abstract.—The Jurassic trigoniid bivalves of Gebel Maghara, northern Sinai, Egypt are described and figured. They belong to 14 species, nine genera, and two families. The identified taxa occur in rocks ranging in age from the Toarcian (Lower Jurassic) to the lower Kimmeridgian (Upper Jurassic). Five genera and one species are new: *Magharitrigonia asymmetrica* new genus new species; *Cotswoldella* aff. *C. hemisphaerica* (Lycett, 1853); *Cornbrashella pullus* (J. de C. Sowerby, 1826); *Parorthotrigonia lepidomorpha* (Abdallah and Fahmy, 1969); and *Retetrigonia imbricata* (J. de C. Sowerby, 1826). Five species, *Trigonia reticulata* Agassiz, 1840, *T. cf. T. castor* d’Orbigny, 1849, *Promyophorella tuberculata* (Agassiz, 1840), *Orthotrigonia exortiva* (Kitchin, 1903), and *O. gracilis* (Kitchin, 1903) are recorded from the Jurassic rocks of Gebel Maghara for the first time.

UUID: <http://zoobank.org/4dc3cc67-6bc3-406f-a022-6a05ed97efc6>

Introduction

Although trigoniid bivalves reached their greatest diversity during the Cretaceous period, they steadily increased in species richness during the Jurassic (Stanley, 1977; Kelly, 1995). Trigoniids became widely dispersed during the late Early Jurassic to early Middle Jurassic (Echevarría et al., 2021), reaching the European Tethys (Francis, 2000; Francis and Hallam, 2003) and the southeast Asian Tethys (Wandel, 1936; Hayami, 1972) by the Toarcian, the high latitudes of Antarctica by the Pliensbachian–Toarcian (Kelly, 1995), New Zealand by the Aalenian (Fleming, 1987), and eastern Africa by the Bajocian (Cox, 1965).

The Jurassic succession of Gebel Maghara is the thickest and most complete Jurassic succession not only of northern Sinai but also of the African–Arabian Plate (1800 m thick; Al Far, 1966; Hirsch, 1980; Keeley, 1994). Bivalves are the most abundant group in the Jurassic strata of Gebel Maghara, followed by gastropods, ammonites, brachiopods, corals, and echinoids. Ayoub-Hannaa et al. (2023) pointed out that the bivalves

and gastropods of Gebel Maghara have been neglected from a taxonomic point of view since the pioneering study of Douvillé in the early twentieth century (Douvillé, 1916). Hirsch (1980), Abdelhamid (2002), and Khalil (2003) illustrated some bivalve and gastropod taxa from the area, but without a comprehensive taxonomic study. Abdelhady (2014) and Abdelhady and Fürsich (2014, 2015a–c) listed 232 benthic and nektonic macrofaunal taxa from Gebel Maghara but did not perform a taxonomic analysis. The faunas are dominated by bivalves (60 species) and gastropods (52 species) (Abdelhady, 2014, appendix B). Therefore, Ayoub-Hannaa et al. (2017, 2023) began a detailed taxonomic revision of the bivalve fauna, dealing with proto-branches. The present study on the trigoniids is the second part of the comprehensive taxonomic study on the Jurassic bivalves of Gebel Maghara. In addition, the revision of the trigoniid fauna from the Jurassic of Egypt fills a gap in our knowledge of the Jurassic paleobiogeography of the region.

Geologic setting

The Levant region was strongly affected by Neo-Tethys rifting that resulted in the formation of intracratonic graben and horst systems, possibly starting as early as late Permian (e.g., Keeley,

*Corresponding author



1994). In northern Sinai, Jurassic strata crop out at Gebel Maghara, situated 50 km south of the Mediterranean shoreline, in an anticlinal structure that covers an area of about 400 km², and represents the fill of a half-graben (Al Far, 1966; Keeley, 1994; Fig. 1.1–1.3). The oldest Jurassic rocks (Mashabba Formation) at Gebel Maghara are Pliensbachian to Toarcian in age and represent fluvial, marginal-marine, and shallow-marine environments (e.g., Ghandour and Fürsich, 2022). Subsequently, shallow-marine and carbonate sediments deposited on a homoclinal ramp prevailed up to the Kimmeridgian, except during the global early Bathonian sea-level fall (Haq et al., 1987) during which deltaic sandstones and coals of the Safa Formation (Al Far, 1966; Abdelhady and Fürsich, 2015a) accumulated. The basin was closed by compressional forces due to convergence between Eurasia and Africa at the Jurassic-Cretaceous transition (Abd El-Motaal and Kusky, 2003).

Bivalve specimens have been collected from four sections, from west to east: Gebel Homayir, Gebel Arousiah, western Bir Maghara, and Gebel Mowerib (Fig. 1.2, 1.3). The first three sections belong to the western flank of the anticline with the strata dipping 15–30°, while the Gebel Mowerib section is exposed on the eastern flank dipping at angles exceeding 60° in some parts. Al Far (1966) subdivided the succession into seven formations, which were revised in detail by Abdelhady (2014). These formations are, in stratigraphic order, the Mahl, Bir Maghara, Safa, Kehailia, Arousiah, Tauriat, and Masajid formations (Fig. 1.5, 1.6). For more details concerning the litho- and biostratigraphy, faunal content, and lateral facies changes see Abdelhady (2014) and Abdelhady and Fürsich (2015a–c).

Material and methods

The studied trigonioid bivalve fauna consists of specimens collected by F.T. Fürsich in 1993 with complementary sampling by A.A. Abdelhady and F.T. Fürsich in 2012 from the Jurassic succession of Gebel Maghara, northern Sinai. Specimens were recovered from three sections: Gebel Homayir, Gebel Arousiah, and Gebel Mowerib. F.T. Fürsich collected additional specimens from the Toarcian Rajabiah and Shusha formations and the lower Kimmeridgian Masajid Formation of western Bir Maghara (section 4; Fig. 1.2). Abdelhady (2014) and Abdelhady and Fürsich (2015a–c) studied the litho- and biostratigraphy of the four sections, made taphonomic observations, and collected macrofossils bed by bed. Primary identification of the collected fossils took place during 2012–2014 as a part of a Ph.D. project by A.A. Abdelhady (2014). Faunal identification was greatly aided by the Jurassic bivalve catalogue at the GeoZentrum Nordbayern of Friedrich-Alexander-Universität, Erlangen. This catalogue contains photocopies of about 95% of all figured Jurassic bivalves worldwide. The trigonioid bivalves are mostly preserved with shell, are disarticulated, incomplete, and are small (H = 10 to < 20 mm) to very small (H < 10 mm) in size. Few specimens are preserved as composite molds. The hinge and other internal structures are usually covered with poorly indurated matrix, which was removed using diluted hydrogen peroxide (H₂O₂). Specimens were cleaned in the laboratory and prepared mechanically using steel needles under a binocular microscope. In addition, an air abrasive was used to clean the flank costae, area, and teeth. The specimens were photographed after having

been coated with ammonium chloride to enhance details of ornamental features.

The systematic classification of the bivalves is that of Carter et al. (2011). The morphological terminology follows Carter et al. (2012). As in Ayoub-Hannaa et al. (2023), the synonymy lists contain only references, which have been carefully checked by the authors, beginning with the original description of the particular taxon, and followed by literature records from the Jurassic of Egypt. More comprehensive synonymies can be found in the references cited. For abbreviations in synonymy lists and open nomenclature to indicate the degree of confidence in allocation of each entry see Matthews (1973) and Bengtson (1988). Using “cf.” for some specimens refers to a provisional identification due to poor preservation, whereas a question mark indicates uncertain identification at the species level.

Linear measurements (taken with a Vernier caliper, accurate to 0.1 mm) are in millimeters. Measured dimensions, general morphologic terminology, teeth, and orientation are given in Figure 2. Abbreviations for dimensions are: L = length, H = height, I = inflation of articulated valves, and D = distance between umbo and anterior margin with the posterodorsal margin horizontal.

Repository and institutional abbreviation.—All specimens are housed in the collections of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich under the prefix BSPG 2014 V.

Systematic paleontology

Infraclass Heteroconchia Hertwig, 1895
 Cohort Uniomorphi J. Gray, 1854
 Megaorder Unionata J. Gray, 1854
 Order Trigoniida Dall, 1889
 Superfamily Trigonioidea Lamarck, 1819
 Family Trigoniidae Lamarck, 1819
 Subfamily Trigoniinae Lamarck, 1819
 Genus *Magharitrigonia* new genus

Type species.—*Magharitrigonia asymmetrica* n. gen. n. sp., by original designation herein. Lower Toarcian Rajabiah Formation, western Bir Maghara, Sinai, Egypt.

Referred species.—*Magharitrigonia senex* (Kobayashi and Mori, 1954) n. gen. n. comb. (Kobayashi and Mori, 1954, p. 167, pl. 16, fig. 8) from the Hettangian of Japan; *Magharitrigonia brevicostata* (Kitchin, 1903) n. gen. n. comb. (Kitchin, 1903, p. 23, pl. 2, figs. 4, 5) from the Middle Jurassic of Kachchh, western India; *Magharitrigonia cristagalli* (Bigot, 1893) n. gen. n. comb. (Bigot, 1893, p. 290, pl. 2, fig. 3) from the Bathonian of France.

Diagnosis.—Very small to small, subtrigonal, moderately to strongly inflated with orthogyrate to slightly opisthogyrate beak, a wide and smooth antecarinal sulcus, coarsely nodate escutcheon and marginal carinae; escutcheon small, cordate, and smooth; right and left valves of some species differently ornamented on areas; LV with narrow and shallow area, bipartite, divided into two unequal halves by a distinctly

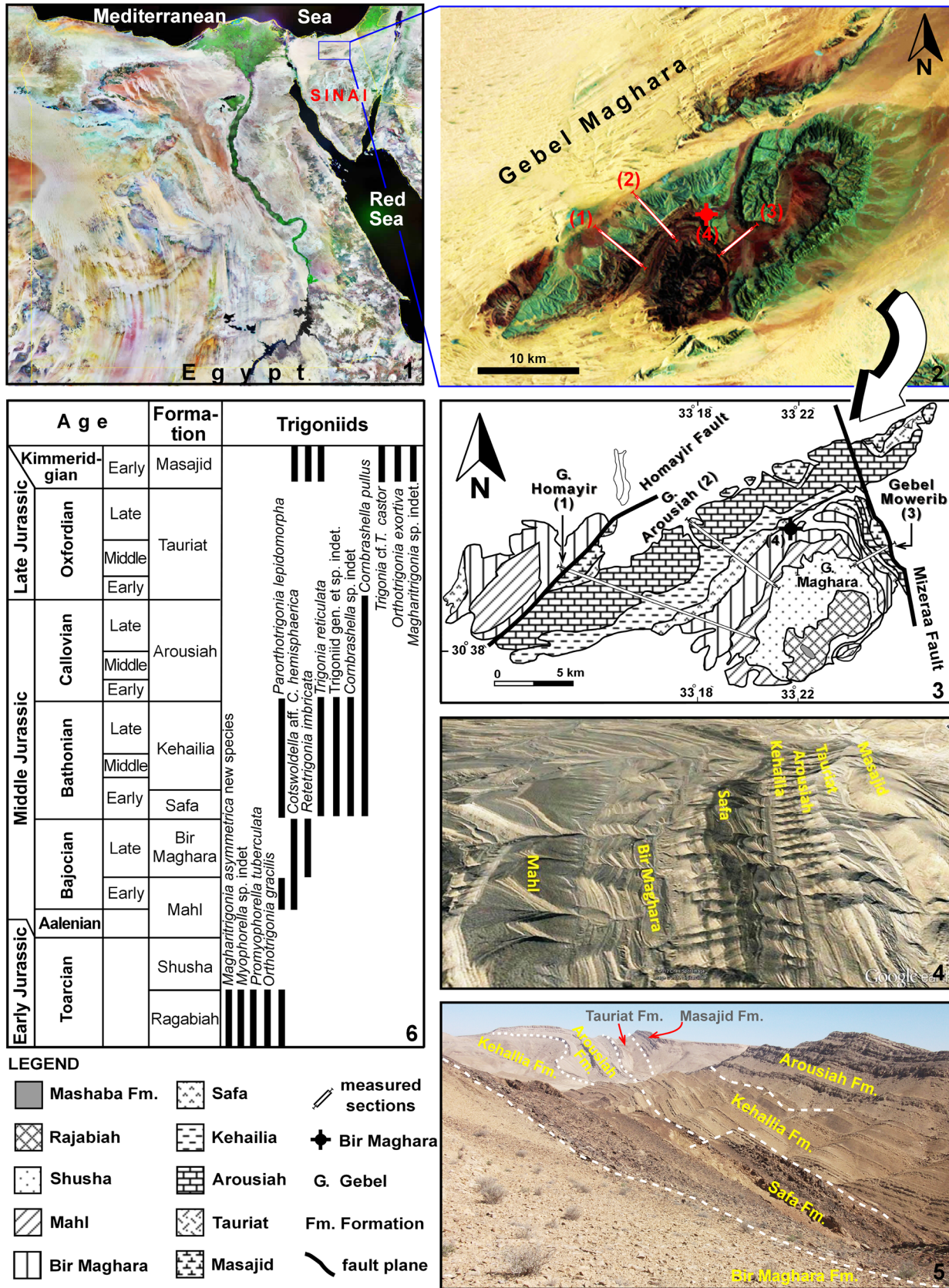


Figure 1. (1) Locality map of Gebel Maghara. (2) Landsat image of the Gebel Maghara area showing positions of the three sections (numbered 1–3). (3) Geologic map (modified after Al Far, 1966; Hirsch, 1980) with positions of the investigated sections. (4) Satellite image of the Middle–Upper Jurassic succession; width of photograph corresponds to 1600 m. (5) Field photograph of the Middle to Upper Jurassic formations, exposed in the eastern saddle of the anticline of Gebel Maghara; thickness of Kehailia Formation is 250 m. (6) Jurassic subdivision and equivalent formations from older to younger (after Abdelhady and Fürsich, 2015a) with stratigraphic ranges of the trigoniid taxa. New genera are *Magharitrigonia*, *Cotswoldella*, *Cornbrashella*, *Parorthotrigonia*, and *Retetrigonia*.

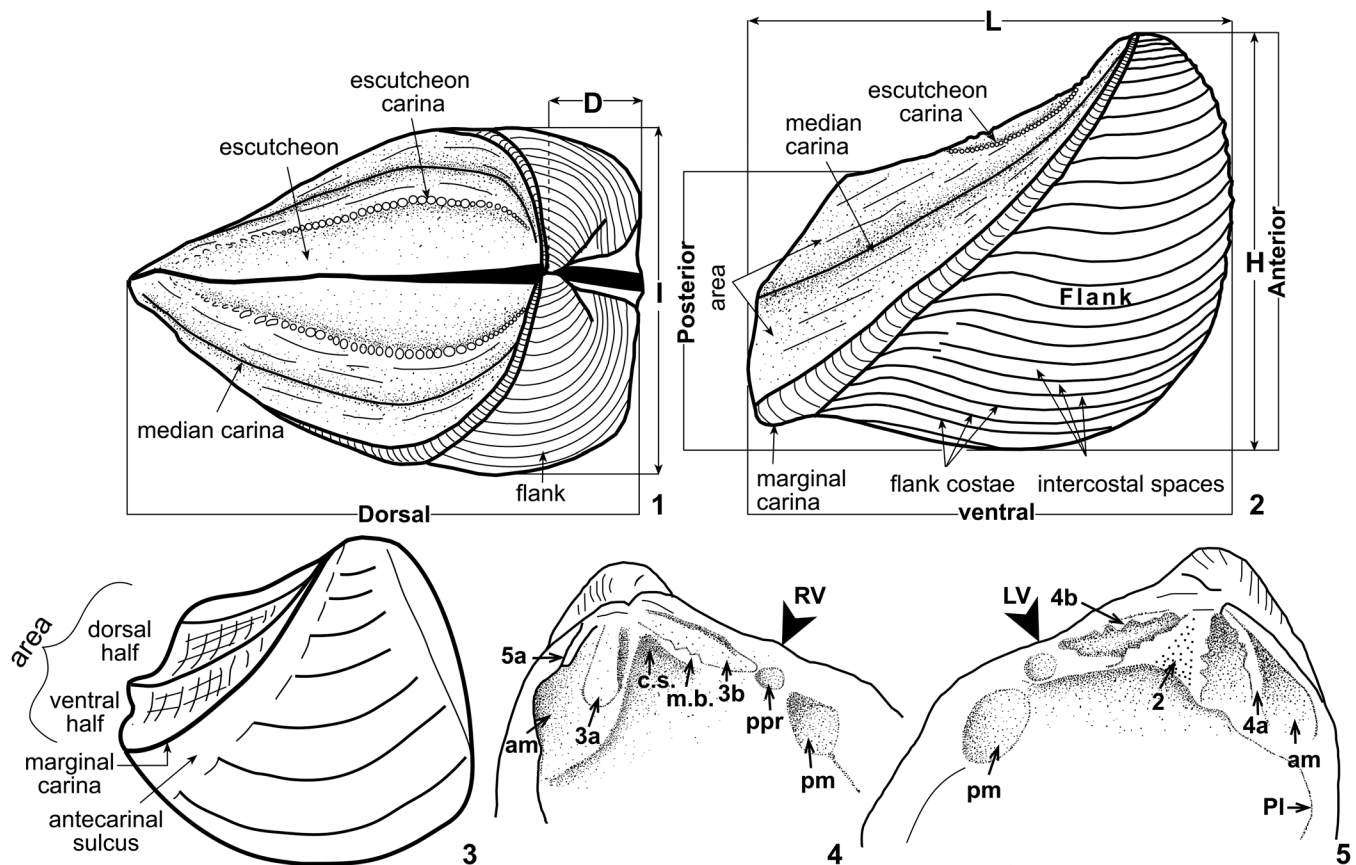


Figure 2. (1–3) Descriptive terminology and orientation of trigoniid shell, (4, 5) hinge structure of left and right trigoniid valves. RV = right valve; LV = left valve; m.b. = myophoric buttress; c.s. = cardinal socket; am = anterior adductor muscle scar; pm = posterior adductor muscle scar; PI = pallial line; ppr = posterior pedal retractor muscle scar; L = length; D = length between umbo and anterior end; H = height; I = inflation of articulated valves; 2, 4 = cardinal teeth of left valve; 3, 5 = cardinal teeth of right valve; a, b = anterior and cardinal teeth, respectively.

crenulated median carina, the dorsal half with tuberculated radial costellae in later growth, its ventral half with reticulate ornament; RV with narrow, deep area, tripartite, divided into three unequal parts by well-developed tuberculated median and additional carinae, all parts covered with widely spaced sharp commarginal costellae; few and widely spaced commarginal flank costae (7–10), terminating in nodes close to the antecarinal sulcus, and separated by smooth and wide intercostal spaces (1.5–3.2 mm).

Occurrence.—Upper Lower Jurassic (lower Toarcian) of Sinai, Egypt.

Etymology.—Combination of the type locality Gebel Maghara (Sinai, Egypt) and the genus *Trigonia*.

Remarks.—*Magharitrigonia* n. gen. is established largely on the basis of the different ornamentation of the areas of the two valves but, where only one valve is available, the genus can be easily distinguished from other Jurassic trigoniid genera by its small to very small size, low number of widely spaced commarginal costae terminating in nodes close to the antecarinal sulcus, orthogyrate to slightly opisthogyrate beak, smooth escutcheon and cordate escutcheon carina, and wide and smooth antecarinal sulcus. *Trigonia* Bruguière, 1789 (type

species: *Venus sulcata* Hermann, 1781, pl. 4, figs. 2–4, 9, 10) resembles *Magharitrigonia* n. gen. in having a trigonal outline and commarginal flank costae, but differs in being much larger ($L = 75$ mm), with reticulate ornament to the entire area that has a broader lower area with at least 12 radial costellae, and a higher number of commarginal flank costae that curve downwards posteriorly and do not terminate in nodes.

Magharitrigonia asymmetrica new species

Figures 3, 4.1, 4.2

Type material.—Holotype: BSPG 2014V 317/4, Lower Jurassic (Lower Toarcian), Rajabiah Formation, western Bir Maghara. Paratypes: eight specimens, BSPG 2014V 317/5–317/12, with shell preservation, mostly articulated, from the same formation and locality.

Diagnosis.—Small to very small, outline trigonal; beak orthogyrate to slightly opisthogyrate; commarginal flank costae widely spaced, terminating in nodes close to antecarinal sulcus, and separated by smooth and wide intercostal spaces; escutcheon small, smooth; area of left valve bipartite with different ornamentation patterns; area of right valve tripartite with widely spaced commarginal costellae; antecarinal sulcus wide, smooth.

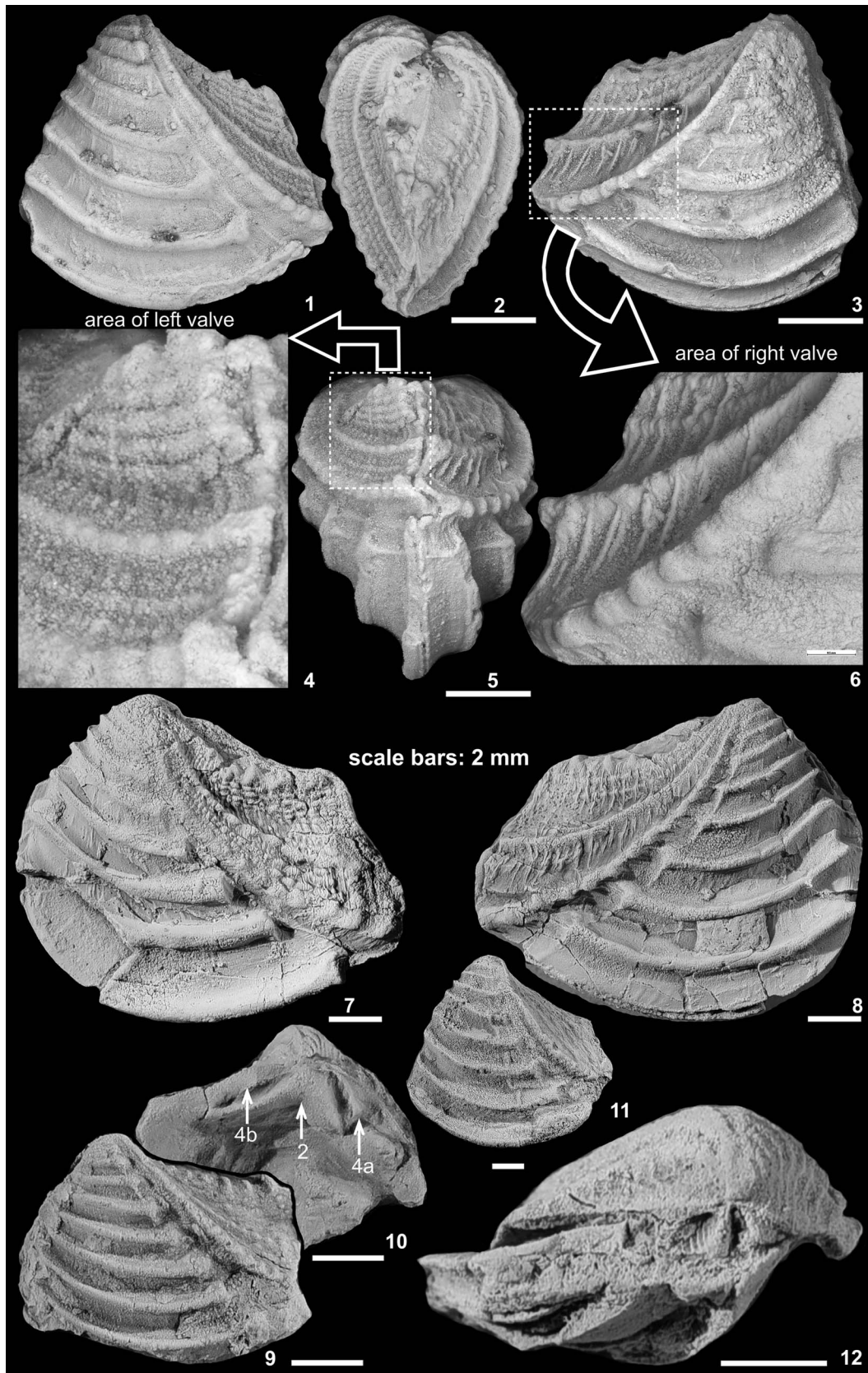


Figure 3. *Magharitrigonia asymmetrica* n. gen. n. sp. from the lower Toarcian Rajabiah Formation, western Bir Maghara. (1–6) Holotype, articulated specimen BSPG 2014V 317/4; (1) left valve view showing smooth and wide intercostal sulcus, (2) dorsal view, (3) right valve view, (4) close-up showing bipartite area of left valve differing in ornamentation, (5) posterior view showing deep area of left valve, (6) close-up showing tripartite area of right valve with widely spaced commarginal costellae. (7, 8) Paratype, articulated specimen BSPG2014V 317/5, showing the differently ornamented area of left (7) and right (8) valve. (9, 10) Paratype, left valve, BSPG2014V 317/6; (9) exterior view with tuberculated escutcheon carina, (10) interior view showing hinge. (11) Paratype, left valve, BSPG2014V 317/7, with few and widely spaced commarginal costae of area. (12) Paratype, left valve, BSPG2014V 317/8, dorsal view. Scale bars = 2 mm.

Description.—Shell small to very small, outline trigonal, inequilateral, equivalved, slightly longer than high (Table 1), and moderately inflated. Maximum inflation slightly below umbo. Anterior margin slightly convex, meeting ventral margin in rounded angle. Posterior margin oblique, subtruncated, narrow, forming angle with ventral margin. Posterodorsal margin slightly concave, meeting posterior margin at obtuse angle. Ventral margin irregularly convex. Umbo triangular, inflated, located at about one-third of total valve length from anterior end. Beak orthogyrate to slightly opisthogyrate. Marginal carina distinct, sharp in early growth, thicker and tuberculated towards posteroventral corner (Fig. 3.1). Escutcheon carina slightly tuberculated in early growth, later with prominent oblique nodes. Escutcheon small, elongated-cordate in outline, smooth (Fig. 3.2). Antecarinal sulcus of left valve wide, smooth, broadening gradually towards posteroventral corner, with faint intercalatory radial riblet (Fig. 3.1). Area of left valve narrow, shallow, divided into two unequal parts by distinctly tuberculate median carina; dorsal half ornamented with commarginal costae in early growth followed by faint tuberculated radial costellae running parallel to posterodorsal margin; ventral half with reticulate ornament (Fig. 3.4, 3.5). Area of right valve wider and deeper than that of left valve, tripartite with well-developed tuberculated median carina and additional carina in dorsal half (Fig. 4.1, 4.2), covered with widely spaced commarginal costellae (Fig. 3.6). Flank inflated, triangular, occupying about two-thirds of shell surface, ornamented with 8–10 widely spaced commarginal costae (0.5–0.8 mm), asymmetrical in profile (steepest dorsally), terminating in node close to antecarinal sulcus and separated by very wide and smooth intercostal spaces (1.5–3.2 mm). Terminal nodes with distinct ventral extensions that are connected by thin radial riblet. Hinge of left valve wide, with large triangular cardinal tooth (2) separated from anterior and posterior teeth (4a, 4b) by anterior and posterior sockets, respectively (Fig. 3.10). Posterior tooth (4b) narrower than anterior one and running parallel to posterodorsal margin.

Etymology.—Asymmetricus (Latin) = asymmetric; after the differently ornamented areas of the right and left valves.

Measurements.—See Table 1.

Remarks.—*Magharitrigonia asymmetrica* n. gen. n. sp. is easily distinguished from other trigoniid species identified herein by its small to very small size (Table 1), a smooth and elongated-cordate escutcheon, a flank with few and widely spaced commarginal costae terminating in nodes close to

antecarinal sulcus, a bipartite area to the left valve differing in ornamentation, and a tripartite area to the right valve with widely spaced commarginal costellae.

The most closely related species is *Magharitrigonia senex* (Kobayashi and Mori, 1954) n. gen. n. comb. (Kobayashi and Mori, 1954, p. 167, pl. 16, fig. 8) from the Hettangian of Japan in having widely spaced commarginal costae with small spines close to the antecarinal sulcus, and a bipartite area of the left valve with reticulate ornamentation but differs in being larger and in having strongly convex anterior and ventral margins, a narrower antecarinal sulcus and a rounder valve.

Like *M. asymmetrica* n. gen. n. sp., *Magharitrigonia brevicostata* (Kitchin, 1903) n. gen. n. comb. (Kitchin, 1903, p. 23, pl. 2, figs. 4, 5) from the Middle Jurassic of Kachchh, western India, has widely spaced commarginal costae, a tuberculated marginal carina, and a wide antecarinal sulcus, but differs in being larger (L = 23–28 mm, H = 20–23 mm as opposed to L = 6.5–15.2 mm, H = 6.1–13.5 mm), less inflated, and in having a higher number of commarginal flank costae, which do not terminate in nodes close to the marginal carina. In addition, the ornamentation of the areas (right and left valves) of *M. brevicostata* n. gen. n. comb. are similar (reticulated).

Magharitrigonia cristagalli (Bigot, 1893) n. gen. n. comb. (Bigot, 1893, p. 290, pl. 2, fig. 3) from the Bathonian of France differs in being more elongated (higher than long) and in having a narrower antecarinal sulcus, and its commarginal costae are straight.

In *Trigonia stelzneri* Gottsche (1878, p. 24, pl. 6, fig. 1a–d) from the Bajocian and Callovian of Argentina (Weaver, 1931, p. 240, pl. 20, figs. 103, 104), the ornamentation of the area of the left valve resembles that of the present species. However, that species differs from *M. asymmetrica* n. gen. n. sp. in having a wider area, a narrow antecarinal sulcus, a blunt and tuberculated marginal carina, a higher number of commarginal flank costae, and in being larger (L = 58 mm, H = 52 mm; Weaver, 1931, p. 241, as opposed to L = 6.5–15.2 mm, H = 6.1–13.5 mm). Similarly, *T. (Lyriodon) sumiyagura* Kobayashi and Kaseno (1947, p. 42, pl. 10, figs. 1a–2b) from the Lower Jurassic of Japan has a higher number of commarginal flank costae and is larger than the present species.

Trigonia (Trigonia) patchamensis Fürsich and Heinze (1998, p. 155, pl. 2, figs. 6–10) from the Middle Jurassic strata of Kachchh, India, has an ornamented escutcheon, strongly rounded anterior and ventral margins, a smaller area that is divided into two parts by a median groove, and is less inflated.

With respect to shell outline and size, *T. costata* J. Sowerby (1815), which was described and figured by Pugaczewska (1976, p. 83, pl. 17, figs. 1–3, pl. 20, figs. 3, 4, pl. 21, figs. 2, 3) from the Middle Jurassic of Poland and by Francis (2000, p. 62, pl. 1, figs. a–f, pl. 2, figs. a–f, pl. 3, figs. a–e) from the Middle Jurassic of Europe, differs in having a strongly rounded posterior margin, a tripartite area in each valve, a very narrow antecarinal sulcus, and a greater number of commarginal flank costae.

Trigonia triangularis (Goldfuss, 1837), figured by the same authors (Pugaczewska, 1976, p. 85, pl. 26, figs. 1–5, pl. 20, figs. 1–2, 6–7, pl. 21, figs. 1, 4, 10) from the Middle Jurassic of Poland, and by Francis (2000, p. 84, pl. 7, figs. e–h) from the Bajocian of Germany is similar to the present species with

Table 1. Measurements (in mm) of *Magharitrigonia asymmetrica* n. gen. n. sp. *Holotype; all other specimens are paratypes; see Figure 2 for measurement key.

| Specimen | L | H | I | D | H/L | I/L | D/L |
|-------------------|------|------|-----|-----|------|------|------|
| *BSPG 2014V 317/4 | 7.3 | 6.7 | 5.0 | 3.2 | 0.92 | 0.68 | 0.44 |
| BSPG 2014V 317/5 | 11.7 | 10.5 | 6.5 | 3.8 | 0.90 | 0.55 | 0.32 |
| BSPG 2014V 317/6 | 6.5 | 6.1 | 5.0 | 2.7 | 0.94 | 0.76 | 0.41 |
| BSPG 2014V 317/7 | 15.2 | 13.5 | 8.2 | 5.5 | 0.89 | 0.53 | 0.36 |
| BSPG 2014V 317/8 | 11.0 | 9.2 | — | 3.7 | 0.83 | — | 0.34 |
| BSPG 2014V 317/9 | 9.7 | 8.0 | — | 3.2 | 0.82 | — | 0.33 |

respect to shell outline. Like *M. asymmetrica* n. gen. n. sp., it also has a wide and smooth antecarinal sulcus, widely spaced commarginal flank costae, and a small cordate and smooth escutcheon, but differs in having a blunt and strongly tuberculated marginal carina, the areas of the two valves having the same ornamentation (reticulated pattern), and in being larger than the present species. In addition, the ventral margin of *T. triangularis* is concave below the antecarinal sulcus, and strongly convex anteroventrally.

Trigonia interlaevigata Quenstedt (1857, p. 503, pl. 67, figs. 7–8) from the Middle Jurassic of Germany differs in having strongly convex anterior and ventral margins, a truncated anterodorsal margin, a wider antecarinal sulcus, and in being larger.

A higher number of commarginal flank costae and a wide area distinguish *T. castor* d'Orbigny, 1850, figured by Thevenin (1913, p. 74, pl. 27, fig. 19) from the Bathonian of France from the present species.

Another related species is *T. similis* Agassiz (1840, p. 36, pl. 2, figs. 18–21, pl. 3, fig. 7) from the Lower Jurassic of France. However, that species is larger and has a higher number of commarginal flank costae.

Magharitrigonia n. gen. sp. indet.

Figure 4.3

Description.—Shell very small, sub-triangular in outline, strongly inequilateral, slightly longer than high (Table 2). Posterodorsal margin slightly concave. Anterior margin strongly convex, meeting ventral margin in rounded angle. Umbo inflated and located one-third of total valve length from anterior end. Beak sharply pointed and orthogyrate. Marginal carina distinct, blunt, smooth. Escutcheon carina slightly tuberculated in early growth, later with strong nodes. Antecarinal sulcus smooth, widening gradually towards posteroventral corner. Area wide, deep, tripartite with well-developed median and additional carina, and covered by faint commarginal costellae. Flank inflated, triangular, ornamented with nine widely spaced commarginal costae terminating in nodes close to antecarinal sulcus (Fig. 4.3), and separated by very wide, smooth intercostal spaces.

Materials.—A single right valve, with shell preserved, from the lower marl beds of the lower Kimmeridgian Masajid Formation, western Bir Maghara (BSPG 2014V 312/23).

Measurements.—See Table 2.

Remarks.—The present material is somewhat similar to *Magharitrigonia asymmetrica* n. gen. n. sp. from the Lower Jurassic of Gebel Maghara in having a small triangular shell, tripartite area with faint commarginal costellae, widely spaced commarginal flank costae, terminating in nodes close to antecarinal sulcus, and on tuberculated escutcheon carina, but differs in having a blunt, smooth marginal carina and in being

more elongated (H/L=0.78). Moreover, *Magharitrigonia* n. gen. sp. indet. is stratigraphically distinctly younger (lower Kimmeridgian) than *M. asymmetrica* n. gen. n. sp., which is from the lower Toarcian.

Genus *Cotswoldella* new genus

Type species.—*Trigonia hemisphaerica* Lycett, 1853 (p. 231, pl. 11, fig. 2); by original designation herein. Inferior Oolite (Bajocian) of England.

Other species.—*Cotswoldella culleni* (Lycett, 1877) n. gen. n. comb. (Lycett, 1877, p. 173, pl. 31, fig. 9), *C. elegantissima* n. gen. n. comb. (Meek, 1873, p. 474; Imlay, 1964, p. C29, pl. 3, figs. 1–7), *C. kidugalloensis* (Cox, 1965) n. gen. n. comb. (Cox 1965, p. 75, pl. 2, fig. 3a–c), *C. densestriata* (Behrendsen, 1892) n. gen. n. comb. (Behrendsen, 1892, p. 12, pl. 1, fig. 8), *C. gadoisi* (Cossmann, 1911) n. gen. n. comb., (Cossmann, 1911, p. 8, pl. 1, figs. 6–8), *C. langrunensis* (Bigot, 1893) n. gen. n. comb. (Bigot, 1893, p. 287, pl. 1, figs. 10–12, pl. 2, fig. 10), *C. parva* (Kitchin, 1903) n. gen. n. comb. (Kitchin, 1903, p. 37, pl. 3, figs. 7, 8), *C. ranvilliana* (Bigot, 1893) n. gen. n. comb. (Bigot, 1893, p. 290, pl. 9, fig. 8), *C. hemisphaerica*, race *asiatica* (Douvillé, 1916) n. gen. n. comb. (Douvillé, 1916, p. 29, pl. 4, fig. 9), and *C. asiatica* (Douvillé, 1916) n. gen. n. comb. of Hirsch (1980, pl. 4, figs. 13, 14) from the upper Bajocian of Gebel Maghara.

Diagnosis.—Small, moderately inflated, trigonal-ovate to subquadratic, with opisthogyrate beak, low inconspicuous umbo, slightly depressed escutcheon, fine escutcheon carina, and sharp marginal carina; area with feeble to obsolete median carina, with or without longitudinal furrow; ventral part of area with reticulate ornament, dorsal part with radial costellae predominant; antecarinal sulcus narrow; commarginal flank costae numerous (50 or more in large specimens), fine, as narrow as or narrower than interspaces, coarsening ventrally. Upper Sinemurian-lower Kimmeridgian.

Etymology.—From the Cotswolds, the rolling hills of central-southwest England, mainly in Gloucestershire and Oxfordshire, from where the type species was collected.

Remarks.—In the past, species of *Cotswoldella* n. gen. have been assigned to the genus *Trigonia* but differ from it in being smaller, possessing an ovate shape and an almost straight posterodorsal margin, lacking a sinus at the posteroventral margin, having fewer (5–9) radial costellae in the ventral part of the area as opposed to 14 in the type species of *Trigonia*, which are reticulate only in the lower part, and in having a narrower antecarinal sulcus and denser, more numerous flank costellae that barely curve downwards posteriorly, if at all. Except for the areal ornament, which is rarely described in the older literature, these are the characters of the referred species.

Cotswoldella aff. *C. hemisphaerica* (Lycett, 1853)
n. gen. n. comb.
Figure 4.4–4.8

Table 2. Measurements (in mm) of *Magharitrigonia* n. gen. sp. indet. See Figure 2 for measurement key.

| Specimen | L | H | I | D | H/L | I/L | D/L |
|-------------------|-----|-----|---|-----|------|-----|------|
| BSPG 2014V 312/23 | 5.5 | 4.3 | — | 1.8 | 0.78 | — | 0.33 |

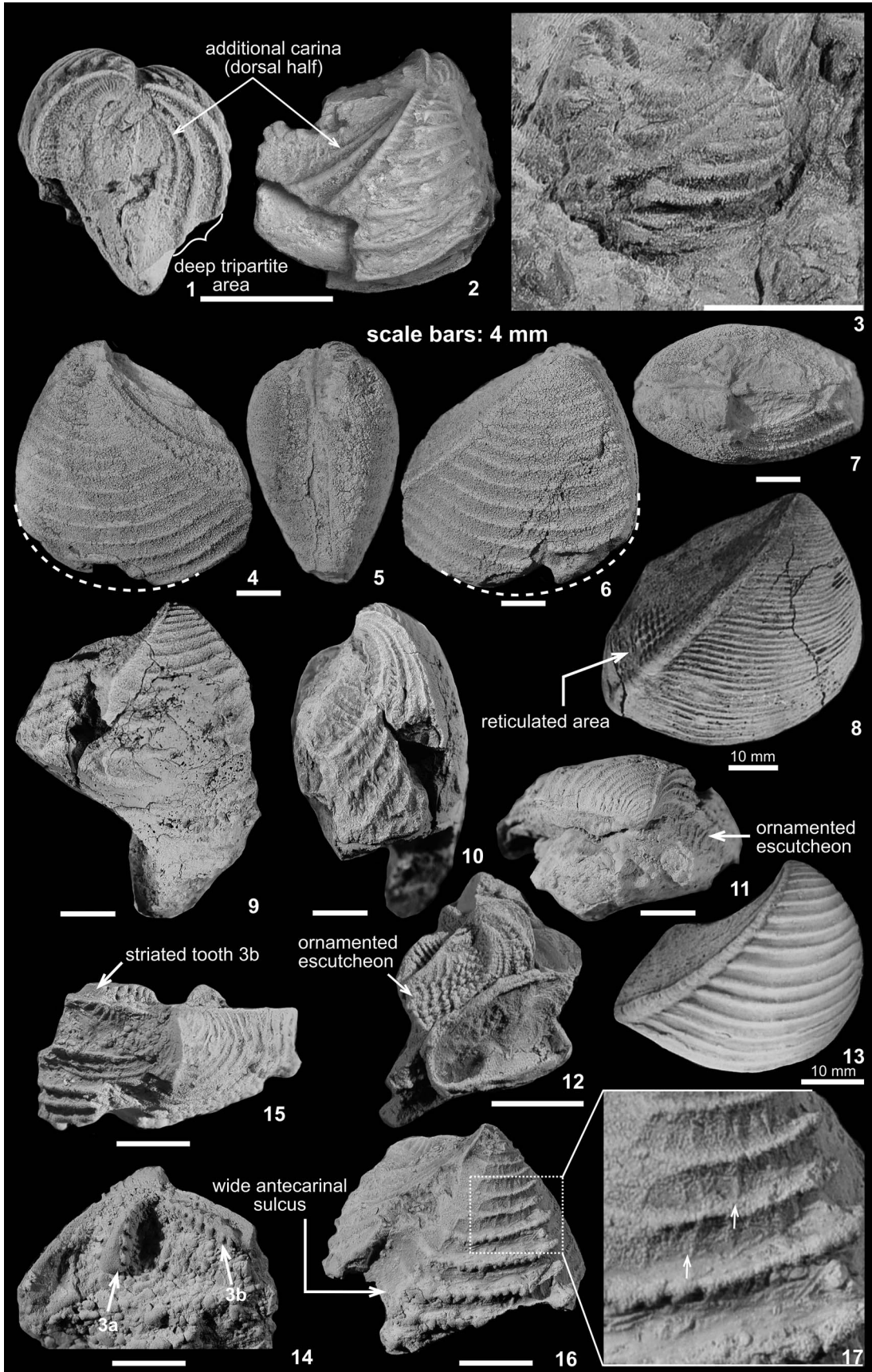


Figure 4. (1, 2) *Magharitrigonia asymmetrica* n. gen. n. sp. from the lower Toarcian Rajabiah Formation, western Bir Maghara, paratype, articulated specimen, BSPG 2014V 317/9; (1) dorsal view showing an additional carina in the dorsal half of the area of right valve, (2) right lateral view. (3) *Magharitrigonia* n. gen. sp. indet. from the lower Kimmeridgian Masajid Formation, western Bir Maghara, right valve, BSPG 2014V 312/23, exterior view showing widely spaced commarginal costae terminating in nodes close to antecarinal sulcus. (4–7) *Cotswoldella* aff. *C. hemisphaerica* (Lycett, 1853) n. gen. n. comb., articulated specimen, BSPG 2014V 316/28, from the lower Kimmeridgian Masajid Formation, western Bir Maghara; (4) left lateral view, showing regular, equally spaced commarginal costae, (5) anterior view, (6) right lateral view showing the small area, (7) dorsal view showing faint radial costellae of area. (8) *Cotswoldella hemisphaerica* (Lycett, 1853) n. gen. n. comb. right valve, BGS GSM 113248, Inferior Oolite, Leckhampton, Gloucestershire, England (figured by Francis, 2000, pl. 8, fig. j). (9–12) *Combrashella pullus* (J. de C. Sowerby, 1826) n. gen. n. comb., from the middle–upper Bathonian Kehailia Formation of Gebel Maghara; (9–11) right valve, BSPG 2014V 325/1, Kehailia Formation, Gebel Mowerib, (9) right lateral view showing the smooth antecarinal sulcus, (10) posterior view showing the wide area with well-developed radial costellae, (11) dorsal view with ornamented escutcheon (arrowed); (12) right valve, BSPG2014V 305/7, Kehailia Formation, Gebel Homayir, posterior view showing ornamented area and escutcheon. (13) *Combrashella pullus* (J. de C. Sowerby, 1826) n. gen. n. comb., right valve, OMU J21371, upper Bajocian, Hook Norton, Oxfordshire, England (figured by Francis, 2000, pl. 4, fig. a). (14–17) *Combrashella* n. gen. sp. indet., right valve, BSPG 2014V 308/54 from the middle–upper Bathonian Kehailia Formation, Gebel Homayir; (14) interior view, (15) dorsal view showing an ornamented area with radial costellae, (16) lateral view showing very wide antecarinal sulcus, (17) close-up showing widely spaced, sharp, sub-straight costae crossed by faint radial riblets (indicated by white arrows), forming a reticulated pattern. Scale bars = 4 mm.

- aff. *1853 *Trigonia hemisphaerica* Lycett, p. 231, pl. 11, fig. 2.
 aff. 1877 *Trigonia hemisphaerica*; Lycett, p. 174, pl. 31, figs. 4–8.
 aff. 1877 *Trigonia hemisphaerica* var. *gregaria* Lycett, p. 174, pl. 33, figs. 4–6.
 aff. 1877 *Trigonia Culleni* Lycett, p. 173, pl. 31, fig. 9.
 aff. 1904 *Trigonia hemisphaerica*; Riche, p. 154, pl. 5, fig. 3a–c.
 aff. 1916 *Trigonia hemisphaerica*, race *Asiatica* Douvillé, p. 29, pl. 4, fig. 9.
 aff. 1932 *Trigonia hemisphaerica*; Fabiani and Ruiz, p. 29, pl. 2, figs. 11, 12a–c.
 aff. 1979 *Trigonia* sp. A aff. *T. hemisphaerica*; Poulton, p. 15, pl. 1, figs. 1, 2.
 aff. 1979 *Trigonia* sp. B aff. *T. hemisphaerica*; Poulton, p. 15, pl. 1, fig. 3.
 aff. 1980 *Trigonia asiatica*; Hirsch, pl. 4, figs. 13, 14.
 aff. 1981 *Trigonia hemisphaerica*; Parnes, p. 35, pl. 4, figs. 36–39.
 aff. 1981 *Trigonia hemisphaerica lunulata* Parnes, p. 35, pl. 4, figs. 34, 35.
 aff. 2000 *Trigonia hemisphaerica*; Francis, p. 81, pl. 8, figs. i, j (with additional synonyms).
 aff. 2003 *Trigonia costulata*; Khalil, p. 308, pl. 1, figs. 3–5.

Occurrence.—Bajocian of England (Lycett, 1877; Francis, 2000), Negev, Israel (Parnes, 1981), upper Sinemurian–Bajocian of California (Poulton, 1979), Bajocian of France (Riche, 1904), Middle Jurassic of south Italy (Fabiani and Ruiz, 1932), and Bajocian–lower Kimmeridgian of Egypt (Douvillé, 1916; Khalil, 2003; present study).

Description.—Shell small, rounded-subquadratic, as long as high, inequilateral, equivalved, moderately inflated (Table 3). Maximum inflation one-third of total shell height from the umbo, gradually fading towards posterior margin. Subvertical anterior margin high, slightly convex, meeting ventral margin in rounded corner. Ventral margin convex, anterodorsal margin slightly

convex. Umbo small, moderately inflated, located one-third of total valve length from anterior end. Beak small, sharp, and slightly opisthogyrate. Marginal carina indistinct, slightly concave dorsally. Area slightly concave, divided by submedian groove into two unequal parts, ventral part narrower than dorsal, and ornamented with ~5 faint radial costellae that dominate the dorsal half (Fig. 4.7). Antecarinal sulcus of left valve very narrow, smooth. Escutcheon carina moderately developed. Escutcheon excavated, small, slightly concave, cordate, smooth. Flank moderately inflated, ornamented with regular, equally spaced commarginal costae, narrower than interspaces, coarsening ventrally and fading anteriorly (Fig. 4.4, 4.6).

Material.—A single specimen, with shell preserved, from the lower part of the Masajid Formation (lower Kimmeridgian), western Bir Maghara (BSPG 2014V 316/28).

Measurements.—See Table 3.

Remarks.—*Cotswoldella* aff. *C. hemisphaerica* n. gen. n. comb. can be easily separated from Jurassic *Trigonia* by its regular commarginal flank costae (Fig. 4.4, 4.6), very small escutcheon, faint marginal carina, and small area. The shape of the shell and the ornamentation of the flank of the present specimen resemble *C. hemisphaerica* (Lycett, 1853) n. gen. n. comb. figured by Lycett (1877) and Francis (2000) from the Middle Jurassic of England, but differs in having a narrower area with far fewer radial costellae that are not reticulated in the ventral part, a finer marginal carina, and flank costae that are narrower than the interspaces. For this reason, the specimen is referred to Lycett's species with qualification. Hirsch (1980) used the "race *Asiatica*" of Douvillé, 1916, as a separate species, *Trigonia asiatica*, on the basis of numerous commarginal flank costae, strong radial costellae of the area, a well-defined marginal carina, and its small size.

Cotswoldella ranvilliana (Bigot, 1893) n. gen. n. comb. (Bigot, 1893, p. 290, pl. 9, fig. 8) from the Bathonian of France resembles *Cotswoldella* aff. *C. hemisphaerica* n. gen. n. comb. in having a narrow area, strongly convex anterior and ventral margins, and relatively widely spaced flank costae, but differs in having a well-developed marginal carina and in being larger and more elongated (higher than long).

Cotswoldella langrunensis (Bigot, 1893) n. gen. n. comb. (Bigot, 1893, p. 287, pl. 1, figs. 10–12, pl. 2, fig. 10) from the upper Bathonian of France resembles *Cotswoldella* aff. *C.*

Table 3. Measurements (in mm) of *Cotswoldella* aff. *C. hemisphaerica* (Lycett, 1853) n. gen. n. comb. See Figure 2 for measurement key.

| Specimen | L | H | I | D | H/L | I/L | D/L |
|-------------------|-------|------|------|-----|------|-------|-------|
| BSPG 2014V 316/28 | ?26.5 | 26.5 | 14.2 | 8.5 | ?1.0 | ?0.54 | ?0.32 |

hemisphaerica n. gen. n. comb. in having a small area and a fine marginal carina, but differs in being larger, more elongated and in having more numerous fine commarginal flank costae.

Cotswoldella parva (Kitchin, 1903) n. gen. n. comb. (Kitchin, 1903, p. 37, pl. 3, figs. 7, 8) from the Jurassic of Kachchh, India, resembles *Cotswoldella* aff. *C. hemisphaerica* n. gen. n. comb. in having regular commarginal costae, and a small, smooth escutcheon, but differs in having an extended posterior area, a concave posterodorsal margin, and in being smaller (L = 11.0–15.0 mm as opposed to L = ?26.5 mm) and much more elongated. Similarly, *C. culleni* (Lycett, 1877) n. gen. n. comb. (Lycett, 1877, p. 173, pl. 31, figs. 9, 9a) from the Jurassic of England is posteriorly produced with a deeply concave posterodorsal margin.

Cotswoldella kidugalloensis (Cox, 1965) n. gen. n. comb. (Cox, 1965, p. 75, pl. 2, fig. 3a–c) from the Bathonian of Kenya differs by its smaller size (L ~17 mm), greater inflation, and in having only 6–7 nodose threads on the area, whereas in adult *C. hemisphaerica* n. gen. n. comb. there are 13–14.

Cotswoldella gadoisi (Cossmann, 1911) n. gen. n. comb. (Cossmann, 1911, p. 8, pl. 1, figs. 6–8) from the Bajocian of France has very fine flank costae.

With respect to general outline and ribbing pattern, *C. elegantissima* (Meek, 1873) n. gen. n. comb. (Meek, 1873, p. 474; Imlay 1964, p. C29, pl. 3, figs. 1–7) from the lower Callovian of Utah, USA, resembles *Cotswoldella* aff. *C. hemisphaerica* n. gen. n. comb., but differs in being smaller (L = 21 mm, H = 14 mm; Imlay, 1964, p. C29, as opposed to L = ? 26.5 mm, H = 26.5 mm) and more elongated (H/L = 0.67).

Cotswoldella densestriata (Behrendsen, 1892) n. gen. n. comb. (Behrendsen, 1892, p. 12, pl. 1, fig. 8; Leanza, 1993, p. 21, pl. 3, figs. 7–9) from the lower Bajocian of Argentina has a poorly defined marginal carina, flat dorsal surface, and numerous fine flank costae.

Genus *Cornbrashella* new genus

Type species.—*Trigonia pullus* J. de C. Sowerby, 1826, p. 10, pl. 508, figs. 2, 3; by original designation herein. Cornbrash Formation (Bajocian–Bathonian) of England.

Other species.—*Cornbrashella distincta* (Kitchin, 1903) n. gen. n. comb. (Kitchin, 1903, p. 25, pl. 2, figs. 6, 7).

Diagnosis.—Small, moderately inflated, trigonally ovate to ovate, with small pointed umbo, opisthogyrate beak, wide, slightly depressed cordate escutcheon with finely crenulated transverse costellae, prominent tuberculate escutcheon and marginal carinae; median carina of left valve evanescent posteriorly, lacking on right valve; area dominated by crenulated radial costellae, lower area with three, upper area with four in the type; antecarinal sulcus narrow; up to 20 commarginal flank costae, narrower than interspaces, not curving downwards posteriorly. Bajocian–Callovian.

Etymology.—From the Cornbrash Formation, in which the type species is common.

Remarks.—*Cornbrashella* n. gen. is easily distinguished from *Trigonia* by its small size, trigonally ovate outline, transverse

costellae to the escutcheon, and non-reticulate area with few radial costellae. The genus *Neuquenitrigonia* Leanza and Garate Zubillaga (1987, p. 209) is very similar, but the type species *Trigonia huenickeni* Leanza and Garate, 1985 (p. 290, fig. 3; pl. 1, figs. 1, 2) from the Bajocian of Argentina differs in being much larger, more inflated, and in having an acute apical angle, well-separated almost straight flank costae, and a larger escutcheon.

Cornbrashella pullus (J. de C. Sowerby, 1826) n. gen. n. comb.
Figure 4.9–4.13

- *1826 *Trigonia Pullus* J. de C. Sowerby, p. 10, pl. 508, figs. 2, 3.
- .1877 *Trigonia pullus*; Lycett, p. 164, pl. 34, figs. 7–9.
- .1886 *Trigonia pullus*; Douvillé, p. 226, pl. 12, figs. 13, 14.
- .1888 *Trigonia pullus*; Greppin, p. 107, pl. 7, fig. 1.
- .1893 *Trigonia pullus*; Bigot, p. 283, pl. 2, figs. 4, 5.
- .1895 *Trigonia pullus*; Newton, p. 82, pl. 3, figs. 6, 7.
- .1903 *Trigonia pullus*; Dainelli, p. 298, pl. 11, figs. 4, 7.
- .1904 *Trigonia pullus*; Riche, p. 153, pl. 5, fig. 2.
- .1916 *Trigonia pullus*; Douvillé, p. 53, pl. 5, fig. 42.
- .1969 *Trigonia pullus*; Fischer, p. 97, pl. 11, figs. 1, 2.
- .1980 *Trigonia* sp. aff. *T. pullus*; Hirsch, p. 136, pl. 4, fig. 26.
- .2000 *Trigonia pulla*; Francis, p. 91, pl. 3, figs. f–h, pl. 4, figs. a, b (with exhaustive synonymy list).
- .2013 *Trigonia pullus*; Néraudeau et al., pl. 25, fig. c.

Lectotype.—BMNH 43133, designated by Cox and Arkell (1948, p. 22) from Ancliff, Wiltshire; figured by J. de C. Sowerby, 1826, p. 10, pl. 508, figs. 2, 3.

Occurrence.—Bajocian–Bathonian of England (J. de C. Sowerby, 1829; Lycett, 1877; Francis, 2000), Bajocian–lower Kimmeridgian of France (Bigot, 1893; Riche, 1904; Fischer, 1969; Néraudeau et al., 2013), Bathonian of Switzerland (Greppin, 1888), Italy (Dainelli, 1903), Ethiopia (Douvillé, 1886), Middle Jurassic of Madagascar (Newton, 1895), and Bathonian–Callovian of Egypt (Douvillé, 1916; Hirsch, 1980; present study).

Description.—Shell very small to small, triangular, inequilateral, slightly higher than long (Table 4), moderately inflated. Anterior and ventral margins convex, meeting in rounded curve. Posterodorsal margin slightly concave, meeting posterior margin at obtuse angle. Posterior margin relatively short. Umbo poorly inflated, triangular, located one-third of total valve length from anterior end. Beak sharply pointed, slightly opisthogyrate. Marginal carina well developed. Antecarinal sulcus smooth, narrow dorsally, widening towards posteroventral corner. Area wide, covered with radial, beaded costellae and crossed by fine commarginal growth lines (Fig. 4.9, 4.10). Escutcheon wide, depressed, cordate in

Table 4. Measurements (in mm) of *Cornbrashella pullus* (J. de C. Sowerby, 1826) n. gen. n. comb. See Figure 2 for measurement key.

| Specimen | L | H | I | D | H/L | I/L | D/L |
|------------------|-------|------|---------|-----|-------|-------|-------|
| BSPG 2014V 325/1 | ?17.2 | 19.2 | 7.5(RV) | 6.1 | ?1.12 | ?0.44 | ?0.35 |
| BSPG 2014V 305/7 | ?9.3 | 9.8 | 3.5(RV) | 3.8 | ?1.05 | ?0.38 | ?0.41 |

outline, and ornamented by transverse costellae (Fig. 4.11, 4.12), bordered by well-developed clavate escutcheon carina. Hinge of right valve with two grooved teeth, running parallel to antero- and posterodorsal margins. Anterior adductor muscle scar subrounded, small, located close to anterodorsal margin. Flank moderately inflated, occupying about two-thirds of shell surface and ornamented with commarginal costae, separated by wide and smooth intercostal spaces (Fig. 4.9, 4.13).

Materials.—Four specimens, fragmented, from the middle-upper Bathonian Kehailia Formation of Gebel Maghara; one from Gebel Mowerib (BSPG 2014V 325/1) and three from Gebel Homayir (BSPG 2014V 305/7–305/9).

Measurements.—See Table 4.

Remarks.—With respect to general outline and ornamentation of the area and flank, the Egyptian material corresponds very well to *Cornbrashella pullus* (J. de C. Sowerby, 1826) n. gen. n. comb. from the Bajocian–Bathonian of southern England. That species can be easily distinguished by its very small shell size and by having a wide area with well-developed radial costellae, a deep, ornamented escutcheon with transverse costellae, a small, smooth antecarinal sulcus, sharp opisthogyrate beaks, and strongly rounded anterior and ventral margins.

Trigonia costata Parkinson, 1811, of Francis (2000, p. 62, pl. 1, figs. a–f; pl. 2, figs. a–f; pl. 3, figs. a–e) from the Middle Jurassic of England and Germany is somewhat similar to *Cornbrashella pullus* n. gen. n. comb. Although *T. costata* is a highly variable species, it differs from the present species in having a subtrigonal valve, an acute umbonal angle, a wide antecarinal sulcus, more numerous flank costae, a raised escutcheon (inset and depressed in *C. pullus* n. gen. n. comb.), and in being larger.

Cornbrashella distincta (Kitchin, 1903) n. gen. n. comb. (Kitchin, 1903, p. 25, pl. 2, figs. 6, 7) from the Middle Jurassic of Kachchh, India, resembles the present species in having an ornamented escutcheon but differs in having an ovate valve, rounded margins, and its radial costellae of the area are fewer and less developed than in *C. pullus* n. gen. n. comb.

Francis (2000, p. 91) regarded *T. langrunensis* Bigot, 1893 (p. 287, pl. 2, fig. 10) from the upper Bathonian of France as a synonym of *C. pullus* n. gen. n. comb. Despite the similarity between the two species, *T. langrunensis* differs in being larger, more elongated (longer than high) and in having numerous fine flank costae. For more details and comparison with other closely related Jurassic taxa, see Francis (2000, p. 95–98).

Cornbrashella n. gen. sp. indet.

Figure 4.14–4.17

Description.—Shell small (L > 16.5 mm), subtriangular, inequilateral, and poorly inflated. Anterodorsal margin slightly convex. Ventral margin missing. Umbo inflated, triangular, located anterior of mid-length of valve. Beak small, sharp, strongly opisthogyrate. Antecarinal sulcus smooth, deep, strongly widening towards posteroventral corner (Fig. 4.16). Area narrow, divided into two unequal parts by median carina and ornamented with radial costellae (Fig. 4.15). Escutcheon

carina distinct, elevated. Escutcheon small with transverse riblets. Hinge of right valve large with two striated cardinal teeth (3a, 3b), separated by a wide triangular socket (Fig. 4.14). Anterior muscle scar small, subrounded, located close to anterodorsal margin. Flank weakly convex and ornamented with widely spaced, sharp, sub-straight costae topped with small tubercles (Fig. 4.16). Costae separated by wide intercostal spaces and crossed by faint radial riblets forming a reticulated pattern (Fig. 4.17).

Materials.—Two incomplete specimens, with shell preservation, from the middle–upper Bathonian Kehailia Formation, Gebel Homayir (BSPG2014V 308/54, 308/55).

Remarks.—The incomplete right valve closely corresponds to similar specimens figured by Cox (1952a, p. 111, pl. 12, figs. 5–9) as *Trigonia kheraensis* Cox, 1952a, from the Middle Jurassic (Bathonian) of India. That species resembles the present material in having a very wide antecarinal sulcus and widely spaced and sub-straight commarginal flank costae, but differs in having a smooth area. The specimens figured by Mongin (1967, pl. 2, figs. 16–19) as *T. kheraensis* from the Bathonian of Morocco have an ornamented area and escutcheon and resemble the Egyptian material more closely than the Indian species.

The general outline and ornamentation of the area is close to *T. interlaevigata* Quenstedt, 1857 (p. 503, pl. 67, figs. 7, 8) from the Middle Jurassic of Germany. That species is, however, larger and has a higher number of commarginal flank costae.

Genus *Trigonia* Bruguière, 1789

Type species.—*Venus sulcata* Hermann, 1781, by subsequent designation (ICZN, 1955).

Diagnosis.—Medium-sized to moderately large, thick-shelled, robust, trigonal to trigonally elongated, strongly inequilateral, moderately inflated, with prominent subterminal umbones, acute umbonal angle and strongly incurved opisthogyrate beaks; anterior margin weakly convex, posteroventral margin with shallow sinus, obliquely truncated respiratory margin, concave posterodorsal margin; escutcheon shallowly sunken with growth rugae and striae; escutcheon carina corded; broad bipartite area with corded median carina and numerous fine radial costellae intersected by strong striae to create a reticulate pattern; prominent marginal carina curved, corded; LV with narrow ante-carinal sulcus, RV with narrow post-carinal groove; flanks with strong, rounded commarginal costellae narrower than interspaces, curving downwards posteriorly.

Trigonia reticulata Agassiz, 1840

Figure 5.1–5.6

- *1840 *Trigonia reticulata* Agassiz, p. 39, pl. 11, fig. 10.
- .1840 *Trigonia papillata* Agassiz, p. 39, 40, pl. 5, figs. 10–14.
- .1840 *Trigonia monilifera* Agassiz, p. 40, pl. 3, figs. 4–6.
- .1840 *Trigonia parvula* Agassiz, p. 41, pl. 11, fig. 8.

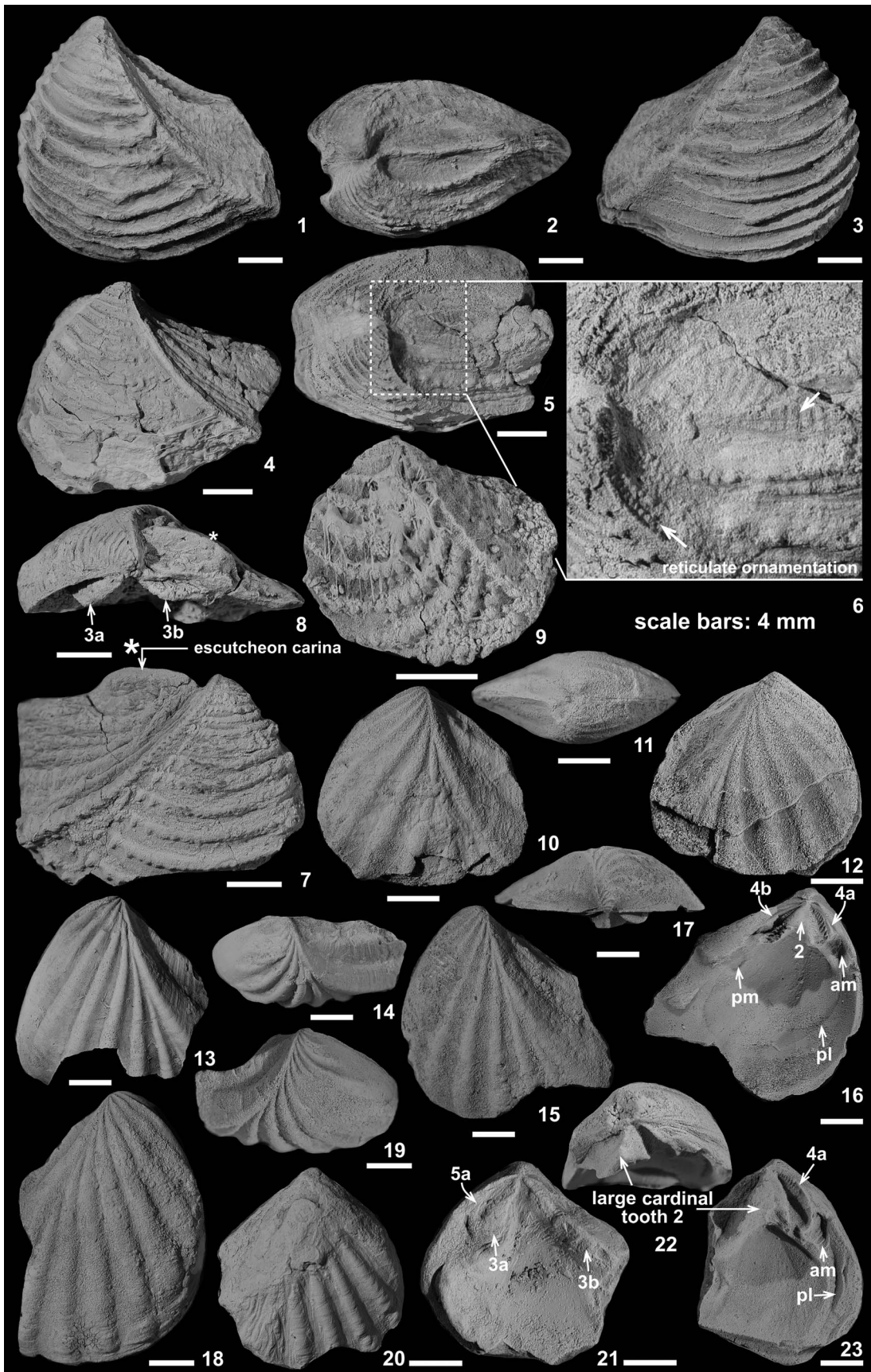


Figure 5. (1–6) *Trigonia reticulata* Agassiz, 1840, from the middle Bathonian–lower Kimmeridgian of Gebel Maghara. (1–3) Articulated specimen, BSPG 2014V 260/1, Kehailia Formation, Gebel Mowerib, (1) left lateral view, (2) dorsal view showing depressed, elongated-cordate escutcheon and tuberculated escutcheon carina, (3) right lateral view with regular, sharp, commarginal costae; (4–6) articulated specimen, BSPG 2014V 432/1, Masajid Formation, western Bir Maghara, (4) left lateral view, (5) dorsal view, (6) close-up showing fine, tuberculated, radial costellae crossed by commarginal costellae, forming a reticulate pattern (arrowed). (7, 8) *Trigonia* cf. *T. castor* d'Orbigny, 1849, right valve, BSPG 2014V 323/4, from the Lower Kimmeridgian Masajid Formation, western Bir Maghara, (7) right lateral view showing large area (45% of total valve surface) and strongly elevated escutcheon carina, marked by asterisk (8) dorsal view with strongly opisthogyrate beak; position of escutcheon carina marked by asterisk. (9) *Myophorella* sp. indet. from the Lower Jurassic (lower Toarcian) Rajabiah Formation, western Bir Maghara, left valve, BSPG 2014V 317/13, left lateral view showing well-developed spinose radial flank costae. (10–23) *Parorthotrigonia lepidomorpha* (Abdallah and Fahmy, 1969) n. gen. n. comb. from the lower Toarcian Rajabiah Formation (marl unit), western Bir Maghara. (10–12) Articulated specimen, BSPG 2014V 317/14, (10) left lateral view, (11) dorsal view, (12) right lateral view, sub-rounded form; (13, 14) left valve, BSPG 2014V 317/15, (13) lateral view showing smooth radial costae, deep and smooth intercostal spaces, and smooth area, (14) dorsal view showing smooth area with distinct median groove; (15–17) left valve, BSPG 2014V 317/16, (15) lateral view, subtriangular form, (16) interior view showing teeth, muscle scars, and entire pallial line, (17) dorsal view showing sharp orthogyrate beak; (18, 19) incomplete right valve, BSPG 2014V 317/17, (18) lateral view, elongated form with smooth, broadly rounded radial costae, (19) dorsal view with distinct median groove of area; (20) right valve, BSPG 2014V 317/18, lateral view, rounded form; (21) right valve, BSPG 2014V 317/19, interior view with two large cardinal teeth (3a, 3b); (22, 23) left valve, BSPG 2014V 317/20, (22) dorsal view showing large cardinal tooth 2, (23) interior view. Scale bars = 4 mm.

- .1840 *Trigonia meriani* Agassiz, p. 41, pl. 11, fig. 9.
 .1930 *Trigonia reticulata*; Arkell, p. 81, pl. 6, figs. 1–4 (with additional synonymies).
 .2000 *Trigonia reticulata*; Francis, p. 116, pl. 6, figs. a–g, pl. 7, figs. a, b (with additional synonymies).
 .2001 *Trigonia (Trigonia)* cf. *T. reticulata*; Delvene, p. 80, pl. 6, fig. 1.
 .2011 *Trigonia reticulata*; Schneider et al., p. 263, pl. 1, figs. F–L.
 v.2015a *Trigonia costata*; Abdelhady and Fürsich, p. 41.
 v.2015c *Trigonia costata*; Abdelhady and Fürsich, p. 267.

Holotype.—*Trigonia reticulata* Agassiz, 1840, p. 39, pl. 11, fig. 10, from Oxfordian–Kimmeridgian strata near Châtelot, W of Montbéliard, Département Doubs, E France; according to Francis (2000, p. 118), housed in the Agassiz Collection, Neuchâtel Museum, Switzerland.

Occurrence.—Upper Oxfordian–lower Kimmeridgian of France (Agassiz, 1840), Spain (Delvene, 2001), central Portugal, and England (Schneider et al., 2011), and middle Bathonian–lower Kimmeridgian of Egypt (first record).

Description.—Shell small, subtriangular, inequilateral, slightly longer than high ($H/L = 0.87$), equivalved, strongly inflated ($I/L = 0.62$; Table 5). Area of maximum inflation around mid-height of valve. Anterior margin strongly convex, meeting ventral margin in continuous rounded curve. Posterior margin oblique, subtruncated; ventral margin regularly convex. Posteroventral corner angulated. Posterodorsal margin slightly concave, sloping, forming obtuse angle with posterior margin. Umbo weakly inflated, triangular, located one-fourth of total valve length from anterior end. Beak sharply pointed, strongly opisthogyrate. Marginal carina prominent, rounded, and crenulated. Area wide, subdivided into two equal parts by well-developed median carina, and ornamented with fine, tuberculated radial costellae, crossed by commarginal costellae, creating reticulate pattern (Fig. 5.6). Escutcheon carina low,

distinct, crenulated. Escutcheon depressed, elongated-cordate in outline, ornamented with faint tuberculated commarginal riblets. Flank strongly inflated and ornamented with prominent, regular, sharp commarginal costae, separated by wide, smooth intercostal spaces (much wider than costae; Fig. 5.3).

Materials.—Two specimens with shell preserved from the middle Bathonian–lower Kimmeridgian of Gebel Maghara; one specimen from the middle–upper Bathonian Kehailia Formation, Gebel Mowerib (BSPG 2014V 260/1) and the second one from the upper part of the Masajid Formation, western Bir Maghara (BSPG 2014V 432/1).

Measurements.—See Table 5.

Remarks.—With respect to shell outline and ornamentation of the area and flank, the present material is very similar to *Trigonia monilifera* Agassiz, 1840 (p. 40, pl. 3, figs. 4–6) from the Upper Jurassic of France. Some authors such as Arkell (1930, p. 81–82) and Schneider et al. (2011, p. 263) regarded that species, together with *T. papillata* Agassiz, *T. parvula* Agassiz, and *T. meriani* Agassiz, as junior synonyms of *T. reticulata* Agassiz. This view is followed here. Schneider et al. (2011, p. 264) noted that *T. reticulata* is a highly variable species, in which the H/L ratio of the shells varies from 0.85 to 0.97, and thus shells are generally slightly longer than high. Although the present specimens are poorly preserved, they exhibit characteristic features of *T. reticulata* Agassiz, such as the strongly rounded anterior and ventral margins and reticulate area, except that they are smaller.

The most closely related species is *T. costata* Parkinson, 1811 (p. 175, pl. 12, fig. 7) figured from the Middle Jurassic of Germany (Quenstedt 1856, p. 335, pl. 45, fig. 15, 1857, p. 440, pl. 60, figs. 10–12), the Aalenian–Bathonian of France (Schneider 1927, p. 71, pl. 5, fig. 3) and from the Bajocian of England (Cox et al., 1962, p. 74, pl. 15, fig. 8). *Trigonia costata* strongly resembles the present species in having the same ornamentation of the flank and area, but differs in having an elevated escutcheon (depressed in *T. reticulata*). In addition, its anterior and anteroventral margins meet at an obtuse angle (rounded curve in *T. reticulata*). According to Schneider et al. (2011, p. 264), the two species are also stratigraphically separated, *T. costata* ranging from the Toarcian to the earliest Callovian, whereas *T. reticulata* is recorded from lower Oxfordian to upper Kimmeridgian.

Table 5. Measurements (in mm) of *Trigonia reticulata* Agassiz, 1840. See Figure 2 for measurement key.

| Specimen | L | H | I | D | H/L | I/L | D/L |
|------------------|------|------|------|-----|------|------|------|
| BSPG 2014V 260/1 | 23.3 | 20.2 | 14.5 | 6.1 | 0.87 | 0.62 | 0.26 |
| BSPG 2014V 432/1 | 24.7 | 21.5 | 15.2 | 6.5 | 0.87 | 0.61 | 0.25 |

Trigonia infracostata Lycett, 1881 (p. 3, text-figs. 3, 4) differs from *T. reticulata* in being more elongated and the radial costellae of its area are spinose.

Trigonia elongata J. de C. Sowerby, 1823, of Bigot (1893, p. 291, pl. 10, fig. 7) from the Callovian–Oxfordian of France has a reticulated area as in *T. reticulata* but differs in being much more elongated.

Trigonia cf. *T. castor* d’Orbigny, 1849
Figure 5.7, 5.8

cf.*1849 *Trigonia castor* d’Orbigny, no. 321.

cf.1893 *Trigonia castor*; Bigot, p. 285, pl. 9, figs. 6–7, pl. 11, fig. 7.

cf.1913 *Trigonia castor*; Thevenin, p. 146 (74), pl. 27, fig. 19.

Holotype.—*Trigonia castor* d’Orbigny, 1849, no. 321 from Bathonian strata of northern France, figured in the “Types du Prodrome” by Thevenin, 1913 (p. 146 [74], pl. 27, fig. 19; No. 321, Coll-no. 2798).

Occurrence.—Bathonian of France (d’Orbigny, 1849; Bigot, 1893; Thevenin, 1913) and probably from the lower Kimmeridgian of Egypt (present study, first record).

Description.—Shell small (L > 22.0 mm), thick-shelled, subtriangular, inequilateral, moderately inflated. Maximum inflation slightly below umbo. Anterodorsal margin short, slightly convex. Posterodorsal margin long, straight. Ventral margin missing. Umbo narrow, inflated, located anteriorly. Beak small, sharply pointed, strongly opisthogyrate (Fig. 5.8). Marginal carina rounded, strongly tuberculated. Antecarinal sulcus distinct, narrow dorsally, and very widened posteriorly. Escutcheon carina very prominent, strongly elevated (Fig. 5.7). Escutcheon well defined, smooth, deeply excavated. Area well defined, occupying ~45% of total valve surface, bordered by marginal and escutcheon carinae, and ornamented by tuberculated, fine radial costellae running subparallel to marginal carina. Flank moderately inflated and ornamented with strong, tuberculated commarginal costae, separated by wide, deep, smooth intercostal spaces (Fig. 5.7).

Materials.—An incomplete specimen, with shell preservation, from the lower Kimmeridgian Masajid Formation, western Bir Maghara (BSPG 2014V 323/4).

Remarks.—*Trigonia castor* d’Orbigny, 1849, can be easily distinguished from other Jurassic *Trigonia* species by its thick shell, large area, regular flank costae, and thick tuberculated marginal carina. The present specimen is incomplete and is, therefore, placed with reservation in *T. castor*, a species with similar shell outline and ornamentation of the area and flank.

The most closely related species are *T. carinata aliexpandita* Leanza and Garate Zubillaga, 1987 (pl. 5, figs. 1–3; pl. 6, fig. 1; Leanza, 1993, p. 24, pl. 10, figs. 3, 4) and *T. stelzneri* Gottsche, 1878 (p. 24, pl. 6, fig. 1a–d; Weaver, 1931, p. 240, pl. 20, figs. 103, 104) from the Lower–Middle Jurassic of Argentina. These species have a strongly protruding escutcheon, but

differ in being much larger than the present material (e.g., L = 78.0 mm [Leanza, 1993, p. 24] as opposed to L > 22.0 mm [present study]) and their flank costae appear to be non-tuberculated.

Trigonia wiedmanni Leanza and Garate Zubillaga, 1987 (p. 209, pl. 6, figs. 3–5; Leanza, 1993, p. 24, pl. 17, figs. 7–10) from the Lower Jurassic of Argentina has fewer flank costae and wider intercostal spaces.

Trigonia similis Agassiz, 1840 (p. 36, pl. 2, figs. 18–21, pl. 3, fig. 7, 7’) from the Lower Jurassic of France and *T. patchamensis* Fürsich and Heinze, 1998 (p. 155, pl. 2, figs. 6–10) from the Middle Jurassic of Kachchh, India, have a smaller area than *T. castor*.

Another similar species is *T. bella* Lycett, 1877 (p. 162, pl. 32, figs. 6, 7, 8, 8a) from the Bajocian of England. That species resembles *T. castor* in having a large, ornamented area, a blunt, tuberculated marginal carina, and a protruding escutcheon, but differs in having a narrow antecarinal sulcus, less-tuberculated flank costae, and in being larger.

Trigonia americana Meek, 1873 (p. 472; Imlay, 1964, p. C28, pl. 3, figs. 8–13) from the Bajocian–Callovian of Utah, USA, resembles *T. castor* in having a wide ornamented area, but differs in lacking an antecarinal sulcus and in having an area with regular, smooth, radial costellae.

Superfamily Myophorelloidea T. Kobayashi, 1954
Epifamily Myophorelloidea T. Kobayashi, 1954
Family Myophorellidae T. Kobayashi, 1954
Subfamily Myophorellinae T. Kobayashi, 1954
Tribe Myophorellini T. Kobayashi, 1954
Genus *Myophorella* Bayle, 1878

Type species.—*Myophorella nodulosa* Bayle, 1878, by subsequent designation (Crickmay, 1932), Oxfordian of France.

Diagnosis.—See Duff (1978, p. 85).

Myophorella sp. indet.
Figure 5.9

Description.—Shell small, subtriangular, distinct inequilateral, moderately inflated, length nearly equaling height (H/L = ?0.96; Table 6). Maximum inflation slightly below umbo. Anterodorsal margin slightly convex, higher than posterodorsal one. Anterior margin regularly curved, strongly convex. Ventral margin incomplete. Posterodorsal margin slightly concave, oblique. Umbo triangular, convex, located one-third of total valve length from anterior end. Beak sharply pointed, slightly opisthogyrate. Marginal carina inconspicuous, becoming tuberculated close to posteroventral corner. Escutcheon carina tuberculated, separating ornamented area from moderately wide, steeply inclined, slightly concave, smooth escutcheon. Area wide, slightly concave, and ornamented with fine, transversely and radially

Table 6. Measurements (in mm) of *Myophorella* sp. indet. See Figure 2 for measurement key.

| Specimen | L | H | I | D | H/L | I/L | D/L |
|-------------------|------|-------|---------|-----|-------|------|------|
| BSPG 2014V 317/13 | 11.5 | ?11.0 | 3.3(LV) | 4.3 | ?0.96 | 0.29 | 0.37 |

aligned spines. Flanks covered with well-developed spinose oblique costae (14), straight, oblique from marginal carina to mid-flank, strongly curved anteriorly, and separated by wide and smooth intercostal spaces (Fig. 5.9).

Materials.—A single incomplete left valve, with shell preserved, from the Lower Jurassic (lower Toarcian) Rajabiah Formation, western Bir Maghara (BSPG 2014V 317/13), Gebel Maghara.

Measurements.—See Table 6.

Remarks.—The poor preservation of the incomplete left valve precludes identification at the species level, and the specimen is, therefore, kept in open nomenclature. With respect to ornamentation of the flank, *Myophorella* sp. indet. resembles *Myophorella* (*Promyophorella*) *spinulosa* (Yong and Bird, 1828) figured by Francis (2000, p. 134, pl. 10, figs. a–g) from the Middle Jurassic (Bajocian) of England, but the latter differs in having a trapezoidal shell (rounded in the present specimen) and in being larger (L = 40 mm as opposed to 11.5 mm) and more elongated.

Genus *Parorthotrigonia* new genus
(= *Awadia* Abdallah and Fahmy, 1969)

Type species.—*Trigonia* (*Awadia*) *lepidomorpha* Abdallah and Fahmy, 1969 (p. 149, figs. 1, 2), from the Middle Jurassic (Bathonian) of Khashm El Galala, Eastern Desert, Egypt.

Other species.—*Trigonia* sp. of Shuwen (1999, pl. 1, fig. 9) and *Trigonia* (s.l.) sp. of Yin and Grant-Mackie (2005, p. 567, fig. 6.16) from the Middle–Upper Jurassic rocks of Tibet, China.

Diagnosis.—Triangularly ovate trigoniid, higher than long, inequilateral, equivalved with sharply pointed orthogyrate beak, an area with distinct median groove, a generally sharp, but occasionally blunt escutcheon carina, an elevated smooth escutcheon, smooth area except for growth lines, 9–13 smooth, rounded sub-radial flank costae meeting the marginal carinae in acute angles, separated by deep and smooth intercostal spaces widening ventrally, and with 3–5 V-shaped early growth costae.

Occurrence.—Middle Jurassic (Bathonian) of Khashm El Galala, Eastern Desert, Egypt (Abdallah and Fahmy, 1969), Lower Jurassic (Toarcian) of the Sinai Peninsula, Egypt (Hirsch, 1980; present study), and Middle–Upper Jurassic of Tibet, China (Shuwen, 1999; Yin and Grant-Mackie, 2005).

Etymology.—Combination of Para (Greek) = next to, and the genus *Orthotrigonia* Cox, 1952b.

Remarks.—Abdallah and Fahmy (1969, p. 149, pl. 1, figs. 1, 2) erected the subgenus *Awadia* (erroneously labeled as *Galalea* on their plate 1) to describe *Trigonia* (*Awadia*) *lepidomorpha* from the Middle Jurassic (Bathonian) of Khashm El Galala, Eastern Desert, Egypt, on the basis of rounded sub-radial flank costae, smooth intercostal spaces, and a terminal beak. Abbass

(1962), however, had used the same name to describe his new species *Nemocardium* (*Awadia*) *magharensis* (Abbass, 1962, p. 128, pl. 21, figs. 7, 10, 12) from the Lower Cretaceous (lower Aptian) of Gebel Maghara. Cox et al. (1969, p. N589) regarded *Nemocardium* (*Awadia*) of Abbass (1962) as a junior synonym of the genus *Nemocardium* Meek, 1876. According to the International Commission on Zoological Nomenclature (e.g., Richter 1948, Article 34; ICZN 1999, Article 59.2), the subgenus of Abdallah and Fahmy (1969) is a junior homonym and, therefore, an unavailable name. For this reason, *Parorthotrigonia* n. gen. is erected to describe *T.* (*A.*) *lepidomorpha* from the Middle Jurassic of the Eastern Desert (Abdallah and Fahmy, 1969) and Lower Jurassic of Sinai (Hirsch, 1980; Abdelhady, 2014; Abdelhady and Fürsich, 2015c). *Orthotrigonia* Cox, 1952b (type species: *Trigonia duplicata* J. de C. Sowerby, 1819) resembles *Parorthotrigonia* n. gen. in general outline, smooth area, and V-shaped costae in early growth, but differs in being larger, more elongated, and its flank costae are sharper, and occasionally bifurcate ventrally. The early commarginal costae and the V-shaped costae that extend across the mid and late growth stages easily distinguish *Vaugonia* Crickmay, 1930, from *Parorthotrigonia* n. gen.

Parorthotrigonia lepidomorpha (Abdallah and Fahmy, 1969)
n. gen. n. comb.

Figures 5.10–5.23, 6.1–6.4, 7

- *1969 *Trigonia* (*Awadia*) *lepidomorpha* Abdallah and Fahmy, p. 149, figs. 1, 2.
- .1980 *Awadia lepidomorpha*; Hirsch, p. 136, pl. 4, figs. 15–19.
- v.2014 *Awadia lepidomorpha*; Abdelhady, p. 68, table 5.1.
- v.2015c *Awadia lepidomorpha*; Abdelhady and Fürsich, p. 265.

Holotype.—*Trigonia* (*Awadia*) *lepidomorpha* Abdallah and Fahmy, 1969 (p. 149, figs. 1, 2), from the upper Bathonian of Khashm El Galala, Eastern Desert, Egypt. The holotype is housed in the Geological Museum, Cairo, Egypt (G.M.C.L).

Occurrence.—Middle Jurassic (Bathonian) of the Eastern Desert (Abdallah and Fahmy, 1969; Abdel-Gawad and Salama, 2015), Lower–Middle Jurassic (Toarcian–lower Bajocian) of Gebel Maghara, Sinai (Hirsch, 1980; Abdelhady, 2014; Abdelhady and Fürsich, 2015c; present study).

Description.—Specimens small to medium-sized, variable in outline, subrounded to subtriangular, occasionally elongated-ovate, distinctly inequilateral, equivalved, slightly higher than long, and little inflated (I/L = 0.39 on average). Anterior margin strongly rounded, meeting convex ventral margin in rounded curve. Posterior margin short, less convex, slightly extended posteriorly, meeting posterodorsal margin in an obtuse angle (~125°). Posterodorsal margin faintly concave. Anterodorsal margin slightly convex. Umbo moderately inflated, located slightly more than one-third of total valve length from anterior end (D/L = 0.38 on average; Table 7).

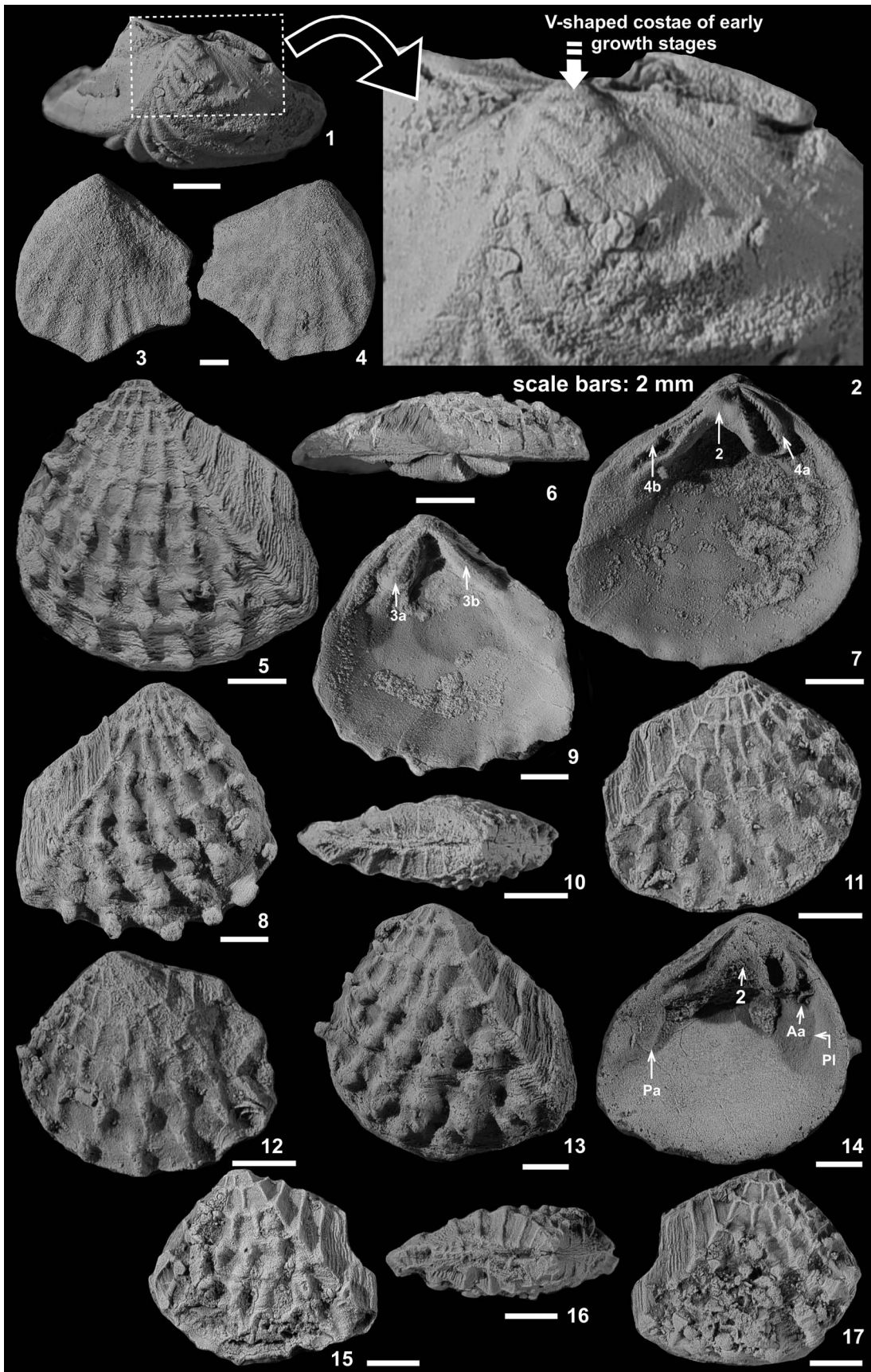


Figure 6. (1–4) *Parorthotrigonia lepidomorpha* (Abdallah and Fahmy, 1969) n. gen. n. comb. from the lower Toarcian Rajabiah Formation (marl unit), western Bir Maghara. (1, 2) Right valve, BSPG2014V 317/21, (1) dorsal view, (2) close-up showing V-shaped early growth costae; (3, 4) incomplete composite mold of articulated specimen, BSPG2014V 317/22, (3) left lateral view, (4) right lateral view. (5–17) Variation in outline of *Retetrigonia imbricata* (J. de C. Sowerby, 1826) n. gen. n. comb. from the middle–upper Bathonian and lower Kimmeridgian of Gebel Maghara. (5–7) Left valve, BSPG2014V 305/10, middle–upper Bathonian Kehailia Formation, Gebel Homayir, (5) lateral view showing flank with radial costae crossed by commarginal costae forming a reticulate pattern with large spines at their intersections, (6) dorsal view with very narrow, smooth escutcheon, (7) interior view showing teeth (2, 4a, 4b); (8, 9) right valve, BSPG2014V 305/11, (8) lateral view showing reticulate ornamentation with large spines, (9) interior view with two cardinal teeth (3a, 3b); (10–12) articulated specimen, BSPG2014V 316/29, lower Kimmeridgian Masajid Formation, western Bir Maghara, (10) dorsal view showing the absence of median and escutcheon carinae, (11) right lateral view showing widely spaced commarginal area costellae with numerous fine growth lines in between, (12) left lateral view; (13, 14) left valve, BSPG2014V 305/12, Kehailia Formation, Gebel Homayir, (13) lateral view, subrounded form, (14) interior view showing teeth, muscle scars, and pallial line (arrowed); (15–17) articulated specimen, BSPG2014V 305/13, (15) left lateral view, (16) dorsal view, (17) right lateral view. Scale bars = 2 mm.

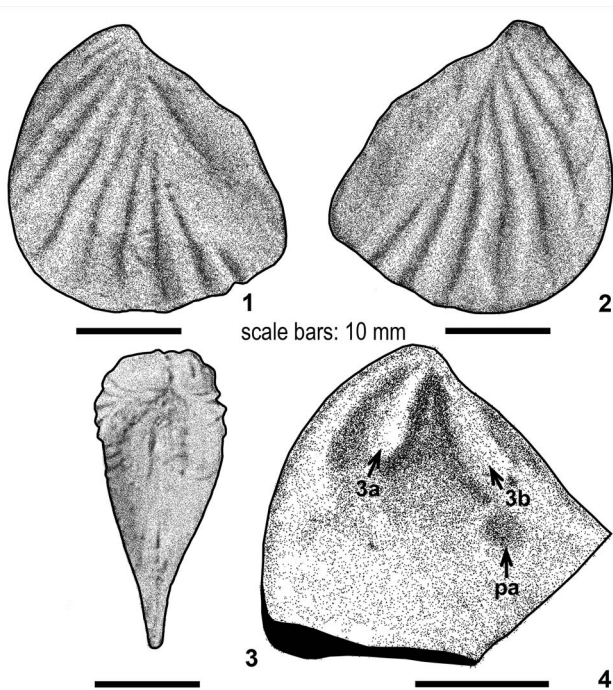


Figure 7. Sketches of *Awadia lepidomorpha* Abdallah and Fahmy, 1969 (= *Parorthotrigonia lepidomorpha* [Abdallah and Fahmy, 1969] n. gen. n. comb.) from the Toarcian–early Bajocian of Gebel Maghara. (1–3) Rajabiah Formation, Wadi Mashabba, Gebel Maghara, (1) left valve with distinct median groove, (2) right valve showing smooth, rounded radial costae of flank (subrounded form), (3) dorsal view; (4) Shusha Formation, Wadi Mashabba, Gebel Maghara, interior view of right valve showing two cardinal teeth (3a, 3b) and small rounded posterior adductor muscle scar. Scale bars = 10 mm.

Table 7. Measurements (in mm) of *Parorthotrigonia lepidomorpha* (Abdallah and Fahmy, 1969) n. gen. n. comb. See Figure 2 for measurement key.

| Specimen | L | H | I | D | H/L | I/L | D/L |
|-------------------|-------|-------|-----|------|-------|------|-------|
| BSPG 2014V 317/14 | 15.0 | 14.3 | 6.3 | 5.7 | 0.95 | 0.42 | 0.38 |
| BSPG 2014V 317/15 | 16.5 | 16.8 | 6.2 | 6.2 | 1.02 | 0.38 | 0.37 |
| BSPG 2014V 317/16 | 21.5 | ?22.0 | — | 7.5 | ?1.02 | — | 0.35 |
| BSPG 2014V 317/17 | 21.7 | ?22.2 | 8.5 | 7.8 | ?1.02 | 0.39 | 0.36 |
| BSPG 2014V 317/18 | ?24.5 | 25.0 | — | 10.5 | ?1.02 | — | ?0.43 |

Beak sharply pointed, small, orthogyrate to slightly opisthogyrate. Flank subtriangular, separated from area by a distinct, blunt marginal carina. Area wide, smooth, slightly concave, strongly inclined towards the flank, and subdivided into two equal halves by a median groove (Fig. 5.13, 5.14). Marginal carina well defined, sharp dorsally, becoming blunt

towards posteroventral corner. Escutcheon narrow, lanceolate, smooth except for growth lines, delimited by distinct escutcheon carina. Left valve with very large triangular cardinal tooth (2), separated from narrow anterior and posterior teeth (4a, 4b) by anterior and posterior sockets, respectively (Fig. 5.16, 5.22, 5.23). Right valve with large cardinal socket and two narrow, striated anterior and posterior teeth (3a, 3b) (Fig. 5.21). Anterior adductor muscle scar small, subrounded, deep, located close to posterior tooth. Posterior adductor muscle scar subrounded, shallow, and larger than anterior one. Pallial line entire (Fig. 5.16). Flank with 9–13 rounded sub-radial costae, meeting marginal carina at acute angle. Early growth costae (3–5) are fine, spinose, and V-shaped (Fig. 6.1, 6.2), followed by sub-radial costae, separated by wide smooth intercostal spaces centrally and ventrally, rapidly narrowing towards dorsal margin (Fig. 5.13).

Materials.—Fourteen specimens, incomplete and disarticulated; few of them are composite molds, from the lower Toarcian Rajabiah Formation (marl unit), western Bir Maghara (BSPG 2014V 317/14–317/27).

Measurements.—See Table 7.

Remarks.—*Parorthotrigonia lepidomorpha* (Abdallah and Fahmy, 1969) n. gen. n. comb. Differs distinctly from other Jurassic myophorellid species. It can be easily distinguished by its smooth radial costae (folded in cross-section) with V-shaped early growth costae (3–5), a smooth area, an orthogyrate to slightly opisthogyrate sharp beak, and slightly elevated escutcheon.

Shuwen (1999, pl. 1, fig. 9) and Yin and Grant-Mackie (2005, p. 567, fig. 6.16) described *Trigonia* sp. and *Trigonia* (s.l.) sp., respectively, from the Middle–Upper Jurassic rocks of Tibet, China. Their material strongly resembles *P. lepidomorpha* n. gen. n. comb. in size (e.g., L = 18.0 mm, Shuwen, 1999, fig. 9, as opposed to L = 19.8 mm on average, present study, Table 7), in having subtriangular valves, rounded flank costae, and a smooth area. Because only lateral views of incomplete left valves are available, it is difficult to regard their specimens as belonging to *P. lepidomorpha* n. gen. n. comb.

Another similar species is *Trigonia baylei* Philippi, 1899 (p. 86, pl. 36, fig. 9) from the Upper Jurassic (Tithonian) of Chile. Although it also has smooth radial costae, it differs from the present species in being much more elongated (L > H) and in having wider intercostal spaces, a blunt marginal carina, and flank costae meeting the marginal carina almost at right angles (acute angles in the present species).

“*Trigonia*” *catenifera* Hupé, 1854 (Philippi 1899, p. 85, pl. 36, fig. 5) from the Upper Jurassic of the same area has, in contrast to *P. lepidomorpha* n. gen. n. comb., costae that bifurcate towards the anteroventral margin and carry small tubercles on their crests (see Echevarría et al., 2021, fig. 18.3).

Genus *Retetrigonia* new genus

Type species.—*Trigonia imbricata* J. de C. Sowerby, 1826.

Other species.—*Retetrigonia parcinoda* (Lycett, 1872) n. gen. n. comb. from the Middle Jurassic of England.

Diagnosis.—Very small myophorellid, outline pentagonal to subrounded, little inflated, inequilateral, with strongly rounded anterior and ventral margins, broad obliquely subtruncated posterior margin, straight posterodorsal margin, and a convex anterodorsal margin. Beaks very small, orthogyrate to slightly prosogyrate, area wide with widely spaced commarginal costellae passing over marginal carina onto flank. Median and escutcheon carinae absent; escutcheon very narrow and smooth; marginal carina distinct, sharp, and tuberculated; flank with radial costae crossed by commarginal costae forming a reticulate pattern with large spines at their intersections.

Occurrence.—Middle–upper Bathonian (ammonite *Clydomphalites clydocromphalus* Zone) to lower Kimmeridgian of Gebel Maghara, Sinai, Egypt.

Etymology.—Combination of Rete (Latin) = net, and the genus *Trigonia*.

Remarks.—*Retetrigonia* n. gen. can be easily distinguished from other Jurassic genera by its reticulate flank ornamentation, wide area, lack of median and escutcheon carinae, a very narrow, smooth escutcheon, a subtruncated posterior margin, and small orthogyrate to slightly prosogyrate beaks.

With respect to shell outline and size, *Retetrigonia* n. gen. is somewhat similar to *Ibotrigonia* Kobayashi in Kobayashi and Tamura 1957, but that genus has a median carina and its flank is covered by widely spaced, tuberculated commarginal costae.

The wide antecarinal sulcus of the genus *Frenguelliella* Leanza, 1942 (type species: *Trigonia inexpectata* Jaworski, 1915, from the Pliensbachian of Argentina) distinguishes it from *Retetrigonia*. In addition, the flank and area of *Frenguelliella* is differently ornamented.

Retetrigonia imbricata (J. de C. Sowerby, 1826) n. gen. n. comb.
Figures 6.5–6.17, 8.1–8.3

*1826 *Trigonia imbricata* J. de C. Sowerby, p. 8, pl. 507, figs. 2, 3.

.1853 *Trigonia imbricata*; Morris and Lycett, p. 63, pl. 6, figs. 8, 8a.

?1872 *Trigonia imbricata*; Lycett, p. 33, pl. 6, fig. 5a, b.

?1879 *Trigonia imbricata*; Lycett, p. 209, pl. 36, figs. 9, 10, pl. 41, figs. 10–12.

.1916 *Trigonia imbricata*; Douvillé, p. 54, pl. 5, figs. 43, 44.

.1936 *Trigonia imbricata*; Marzloff et al., p. 97, pl. 11, figs. 10–12.

?1980 *Ibotrigonia* sp. cf. *I. imbricata*; Hirsch, pl. 4, fig. 23.

Holotype.—*Trigonia imbricata* J. de C. Sowerby, 1826, pl. 507, figs. 2, 3, from the Bajocian of England (Natural History Museum, London).

Occurrence.—Upper Jurassic (Bajocian–Bathonian) of England (J. de C. Sowerby, 1829; Morris and Lycett, 1853; Lycett, 1872, 1879), Bajocian of France (Marzloff et al., 1936), Upper Bajocian–Lower Kimmeridgian of Gebel Maghara, Sinai (Douvillé, 1916; Hirsch, 1980; present study).

Description.—Shell very small, outline variable, ranging from subrounded to subtriangular, from oval to subpentagonal (Fig. 6.5–6.17), inequilateral, equivalved, slightly longer than high (H/L = 0.84–0.97; Table 8), and weakly inflated. Anterior and ventral margins strongly rounded. Posterior margin broad, obliquely sub-truncated, almost perpendicular to ventral margin. Posterodorsal margin straight, steeply oblique posteriorly, forming an obtuse angle with posterior margin. Anterodorsal margin shorter than posterodorsal one and slightly convex. Umbo weakly inflated, located slightly anterior of mid-length of valve. Beak small, orthogyrate to slightly prosogyrate. Marginal carina narrow, sharp, smooth in early growth, tuberculated in later growth. Area steeply inclined towards flank, wide, covered by widely spaced commarginal costellae with numerous fine growth lines in between. Costellae extending across the marginal carina onto the flank, crossing the radial costae of flank to form a reticulate pattern (Fig. 8.1). No median or escutcheon carina (Fig. 6.10, 6.16). Escutcheon narrow, deep, smooth (Fig. 8.2). Hinge of left valve with a large triangular cardinal tooth (2), a narrow subvertical anterior (4a) one, and very narrow posterior tooth (4b) running parallel to posterodorsal margin (Fig. 6.7). Hinge of right valve with two cardinal teeth (3a, 3b), separated by a deep triangular socket, with narrow anterior tooth (5a) (Fig. 6.9). Pallial line entire. Flank weakly inflated, carrying widely spaced commarginal costae crossed by radial costae and forming a grid-like pattern with spines at intersection points (Figs. 6.5, 6.8, 8.1).

Materials.—Thirteen specimens with shell preserved, mostly disarticulated, from the middle–upper Bathonian and lower Kimmeridgian of Gebel Maghara: ten specimens from the middle–upper Bathonian Kehailia Formation, Gebel Homayir (BSPG 2014V 305/10–305/19); a single specimen from the same formation of Gebel Arousiah (BSPG 2014V 320/5); one specimen from Gebel Mowerib (BSPG 2014V 319/5); and a single specimen from the lower marl beds of the lower Kimmeridgian Masajid Formation, western Bir Maghara (BSPG 2014V 316/29).

Measurements.—See Table 8.

Remarks.—Characteristic features of *Retetrigonia imbricata* (J. de C. Sowerby, 1826) n. gen. n. comb. are its very small size, weak inflation, well-developed reticulate pattern of flank

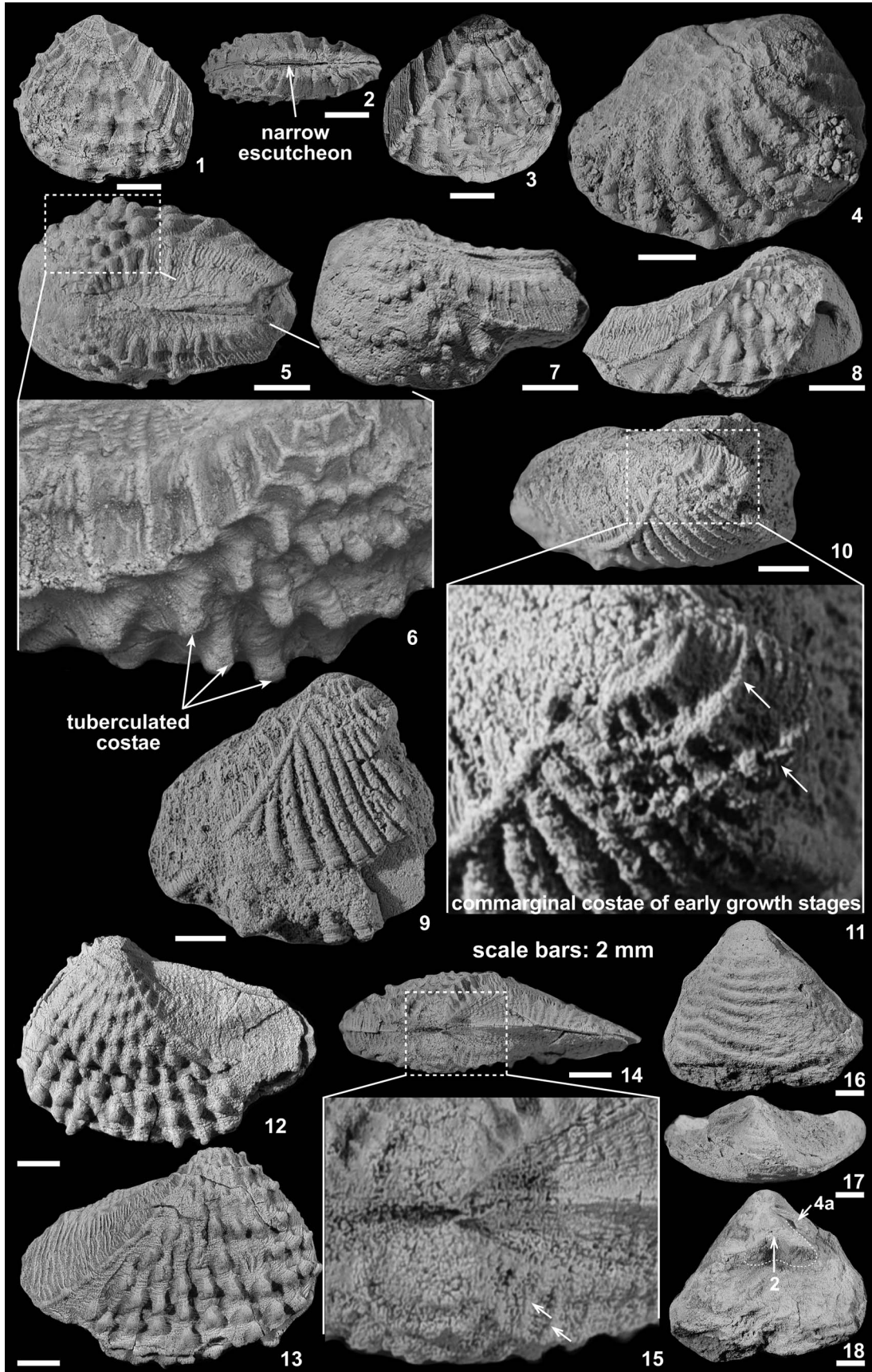


Figure 8. (1–3) *Retetrigonia imbricata* (J. de C. Sowerby, 1826) n. gen. n. comb. from the middle–upper Bathonian Kehailia Formation, Gebel Arousiah, (1) articulated specimen, BSPG 2014V 320/5, left lateral view showing reticulate flank ornamentation, (2) dorsal view with very narrow, smooth escutcheon, (3) right lateral view showing wide area with widely spaced commarginal costellae and absence of median and escutcheon carinae. (4–8) *Promyophorella tuberculata* (Agassiz, 1840) n. comb. from the Lower Jurassic Toarcian Shusha Formation, western Bir Maghara; (4) right valve, BSPG2014V 314/15, lateral view; (5–8) articulated specimen, BSPG2014V 317/28, (5) dorsal view, (6) close-up showing thick flank costae, which is coarser close to ventral margin, and carrying well-developed nodes (arrowed), (7) left lateral view showing very widely spaced tuberculated flank costae, (8) right lateral view. (9–11) *Orthotrigonia exortiva* (Kitchin, 1903) n. comb. from the lower Kimmeridgian Masajid Formation, western Bir Maghara, right valve, BSPG2014V 313/19; (9) lateral view showing tuberculated, oblique radial flank costae, (10) dorsal view, (11) close-up showing arcuate commarginal costae of early growth stages. (12–15) *Orthotrigonia gracilis* (Kitchin, 1903) n. comb. from the Lower Toarcian Rajabiah Formation, western Bir Maghara, articulated specimen, BSPG2014V 317/29; (12) left lateral view showing tuberculated radial costae, (13) right lateral view, (14) dorsal view, (15) close-up showing the arcuate flank costae of early growth stages extending across the marginal carina to cover the dorsal part of the area (arrowed). (16–18) Trigoniid gen. et sp. indet. from the middle–late Bathonian Kehailia Formation, Gebel Arousiah, left valve, BSPG2014V 258/1; (16) left lateral view showing slightly undulated flank costae, meeting anterior margin at right angle, (17) dorsal view, (18) interior view showing large cardinal tooth 2 and anterior tooth 4a. Scale bars = 2 mm.

costellae with short spines at their intersections, wide and ornamented area, and the lack of median and escutcheon carinae.

The figured specimen of *R. parcinoda* (Lycett, 1872) n. gen. n. comb. (Lycett, 1872, p. 46, with text-fig.) from the Middle Jurassic of England strongly resembles the present species with respect to shell outline, size, and lack of median and escutcheon carina. Therefore, it probably falls in the variation of *R. imbricata* n. gen. n. comb. Although *R. parcinoda* n. gen. n. comb. Also has a reticulate flank ornamentation, it differs by its tiny spines at the intersections of radial and commarginal costae.

Myophorella (Haidaia) pulex Tamura, 1959 (p. 25, pl. 5, figs. 15–18) from the Jurassic of Japan differs from *R. imbricata* n. gen. n. comb. in having eight or more crenulated flank costae (steep on dorsal area), an ornamented escutcheon, a wide antecarinal sulcus (Tamura, 1959, text-fig. 2.1–2.4), and in being smaller.

Myophorella (H.) gracilentia Kobayashi, 1956 (p. 4, pl. 1, fig. 8; see also Tamura, 1984, p. 25, pl. 2, figs. 3–13, text-fig. 2.1–2.4) from the Upper Jurassic of China agrees with the present material with respect to shell outline and size, but differs in having a median groove, wide and ornamented escutcheon, and an indistinct marginal carina.

Genus *Promyophorella* Kobayashi and Tamura, 1955

Type species.—*Myophorella (Promyophorella) sigmoidalis* Kobayashi and Tamura, 1955, from the Bajocian of Japan.

Remarks.—Kobayashi and Tamura (1955) erected the subgenus *Promyophorella* based on sharp costae carrying numerous small tubercles. They considered *Promyophorella* as ancestral to *Myophorella* s.s., but included it in that genus because they recognized numerous intermediate forms. Echevarría et al.

(2021, p. 31) modified the diagnostic features listed by Kobayashi and Tamura (1955) to include a clearly opisthogyrate shell, crescentic outline, well-defined prominent tuberculate marginal carina in early growth becoming conspicuous angular tubercles later, an ornamented area with commarginal costellae that occasionally fade at late growth stages, with median groove; narrow oblique, diverging flank costae carrying numerous small regularly aligned tubercles, a smooth antecarinal space, and an escutcheon that is smooth or covered with transverse pustulose costellae. *Myophorella* Bayle (1878) differs from *Promyophorella* in having a triangular valve, a slightly orthogyrate to opisthogyrate beak, a conspicuously nodate median carina, strongly tuberculate flank costae, and by its large size.

Moerickella Echevarría, Damborenea, and Manceñido, 2021 (p. 26, fig. 13) can be easily distinguished by its flank ornamentation. It carries oblique costae, subparallel, anteroventrally sloping, and orthogonal to the antecarinal space, which bear well-developed elongated tubercles on their posterior segments.

Fleming (1964, 1987) and Kelly (1995) considered *Promyophorella* as a junior synonym of *Scaphogonia* Crickmay, 1930. According to Francis (2000, p. 133), although *Scaphogonia* and *Promyophorella* are closely related, the subgenus *Promyophorella* should be used to describe those species of *Myophorella* that have a continuous set of highly aligned tuberculated costae across the flank. Echevarría et al. (2021) regarded *Scaphogonia* as a separate genus, related to *Promyophorella*, but differing by its flank ornamentation.

Orthotrigonia has V-shaped or L-shaped flank costae in early growth stages and steep, straight costae bifurcating anteriorly at later growth stages. For more details about the generic history of *Promyophorella* and comparison with other closely related genera, see Francis (2000, p. 133) and Echevarría et al. (2021, p. 31).

Based on the diagnostic features mentioned above, the present material can be assigned to *Promyophorella* with certainty. That genus is recorded here from the Lower Jurassic (Toarcian) rocks of Gebel Maghara, Egypt, for the first time.

Promyophorella tuberculata (Agassiz, 1840) new combination
Figure 8.4–8.8

*1840 *Trigonia tuberculata* Agassiz, p. 20, pl. 2, fig. 17, pl. 9, figs. 6–8.

.1905 *Trigonia tuberculata*; Benecke, p. 197, pl. 14, figs. 11, 11a.

Table 8. Measurements (in mm) of *Retetrigonia imbricata* (J. de C. Sowerby, 1826) n. gen. n. comb.; *inflation of single valve; see Figure 2 for measurement key.

| Specimen | L | H | I | D | H/L | I/L | D/L |
|-------------------|------|------|---------|-----|------|-------|------|
| BSPG 2014V 305/10 | 9.0 | 7.6 | 3.2 | 3.6 | 0.84 | 0.35 | 0.40 |
| BSPG 2014V 305/11 | 8.0 | 7.8 | 3.2 | 3.5 | 0.95 | 0.40 | 0.44 |
| BSPG 2014V 305/12 | 11.3 | 11.0 | 2.6(RV) | 4.3 | 0.97 | *0.23 | 0.38 |
| BSPG 2014V 305/13 | 10.5 | 10 | 2.4(LV) | 4.2 | 0.95 | *0.23 | 0.40 |
| BSPG 2014V 316/29 | 7.2 | 6.7 | 2.8 | 3.0 | 0.93 | 0.38 | 0.42 |
| BSPG 2014V 319/5 | 10.1 | 9.0 | 2.5(RV) | 3.8 | 0.89 | *0.24 | 0.38 |
| BSPG 2014V 320/5 | 9.7 | 9.0 | 3.6 | 3.7 | 0.93 | 0.37 | 0.38 |

.1927 *Trigonia tuberculata*; Schneider, p. 73, pl. 5, figs. 6, 7.
 ?1993 *Myophorella* (*Myophorella*) cf. *M. tuberculata*; Leanza, p. 29, pl. 1, fig. 9.

Holotype.—*Trigonia tuberculata* Agassiz, 1840, pl. 2, fig. 17 from the Lower Jurassic of Gundershofen, Swabian Alb, housed in the Agassiz Collection, Neuchâtel Museum, Switzerland.

Occurrences.—Lower–lower Middle Jurassic of the Swabian Alb, South Germany (Agassiz, 1840; Benecke, 1905), lower Middle Jurassic (Aalenian) of France (Schneider, 1927), and upper Lower Jurassic (Toarcian) of Egypt (present study, first record).

Description.—Shell very small, crescentic, longer than high (H/L = ?0.63–0.79; Table 9), strongly inequilateral, equivalved, and strongly inflated. Maximum inflation at mid-height of valve. Posterodorsal margin long, slightly concave. Anterodorsal margin short, slightly convex, meeting anterior margin in rounded curve. Anterior margin convex, ventral margin broken off. Umbo inflated, located one-third of total valve length from anterior end. Beak small, sharply pointed, opisthogyrate. Area widening considerably towards posterior end, divided into two unequal parts by sub-median groove, and ornamented with fine commarginal costellae that fade in later growth (Fig. 8.5). Marginal carina well defined, narrow, slightly curved posterodorsally, with small tubercles, coarsening towards posteroventral corner. Antecarinal sulcus narrow, smooth, widening posteriorly. Escutcheon carina distinct, tuberculated. Escutcheon lanceolate, very shallow, ornamented with short irregular transverse costellae. Flank moderately convex with thick costae, coarser close to ventral margin, carrying well-developed nodes, separated by wide and smooth intercostal spaces (1.5–2.1 mm; Fig. 8.6).

Materials.—Two incomplete specimens, with shell preservation, from the Lower Jurassic (Toarcian) Rajabiah and Shusha formations, western Bir Maghara (BSPG 2014V 314/15; 317/28).

Measurements.—See Table 9.

Remarks.—*Promyophorella tuberculata* (Agassiz, 1840) n. comb. can be easily distinguished by its small size, elongated and inflated valves, very widely spaced tuberculated flank costae, smooth intercostal spaces, and a tuberculated escutcheon carina. Francis (2000, p. 140) mentioned that Agassiz (1840) erected *Trigonia tuberculata* based on small and broken specimens from the Lower Jurassic of France. Therefore, he regarded *T. tuberculata* as a junior synonym of *Myophorella* (*Promyophorella*) *spinulosa* (Young and Bird, 1828) from the Middle Jurassic (Bajocian) of England (Francis, 2000, p. 134, pl. 10, figs. a–g). However, *T.*

tuberculata differs from *Myophorella* (*Promyophorella*) *spinulosa* in being smaller, more elongated, and in having a crescentic valve, a tuberculated escutcheon carina, a well-developed marginal carina with small tubercles (coarsening towards the posteroventral corner), and aligned well-developed nodes, separated by wide and smooth intercostal spaces.

Promyophorella tuberculata n. comb. closely matches specimens described and illustrated as *Trigonia hispida* Kitchin, 1903 (p. 90, pl. 9, figs. 4, 5) from the Bathonian of India, *T. aspera* Lamarck, 1819, of Hébert (1861, p. 183, pl. 7, fig. 3) from the Oxfordian of France, and *Myophorella* (*M.*) *bolitoensis* Pérez and Reyes in Pérez et al., 2008 (p. 84, pl. 13, figs. 2, 3, 5, 6) from the lower Middle Jurassic (lower Aalenian) of Chile in shell outline and ornamentation of the area and flank. Compared with these species, *Promyophorella tuberculata* n. comb. differs only in being smaller (L = 11.6–12.2 mm, present material, as opposed to 42.0 mm in Kitchin, 1903; L = 65.0 mm in Pérez et al., 2008).

Trigonia formosa Lycett, 1872 (p. 35, pl. 5, figs. 4–6) from the Middle Jurassic of England (see also Benecke, 1898, p. 28, pl. 5, fig. 1; 1905, p. 193, pl. 14, figs. 7, 8; Bigot, 1893, p. 313, pl. 13, fig. 2, from the Lower and Middle Jurassic rocks of France) resembles the present material in having widely spaced tuberculated flank costae, but differs in being less elongated and larger, and in having convex posterodorsal margins and smooth areas.

Trigonia clavellata J. Sowerby, 1826, of Agassiz (1840, p. 17, pl. 5, figs. 16–18) from the Oxfordian of France is much larger and has tuberculate median and escutcheon carina.

Family Vaugoniidae T. Kobayashi, 1954
 Subfamily Vaugoniinae T. Kobayashi, 1954
 Tribe Vaugoniini T. Kobayashi, 1954
 Genus *Orthotrigonia* Cox, 1952

Type species.—*Trigonia duplicata* J. Sowerby, 1819, Middle Jurassic (Bathonian–Callovian) rocks of India.

Remarks.—Cox (1952b, p. 56) erected *Orthotrigonia* as a subgenus of *Myophorella* with the type species *Myophorella* (*Orthotrigonia*) *duplicata* (J. Sowerby, 1819) from the Middle Jurassic (Bathonian–Callovian) strata of England. The subgenus was characterized by relatively straight and steep flank costae, a narrow, prominent umbo, and an ornamented escutcheon (Fürsich and Heinze, 1998). Some authors placed *Orthotrigonia* Cox, 1952b, as a subgenus of *Myophorella* Bayle, 1878, in the family Vaugoniidae (e.g., Agrawal, 1956, p. 100; Fischer, 1969, p. 99). Other authors placed it as a genus of the *Vaugonia–Myophorella* group or as a subgenus of *Vaugonia* Crickmay, 1930, in the family Trigoniidae (e.g., Poulton, 1979; Fleming, 1987; Kelly, 1995; Fürsich and Heinze, 1998; Fürsich et al., 2019). Kobayashi (in Kobayashi and Mori, 1955) proposed the new subgenus *Hijitrigonia* from the Jurassic of Japan within *Vaugonia*. Cox et al. (1969, p. N488) considered *V. (Hijitrigonia)* as a junior synonym of *V. (Vaugonia)* and assigned a Jurassic range to the genus, including two subgenera: *V. (Vaugonia)* and *V. (Orthotrigonia)*. *Orthotrigonia* resembles *Promyophorella* in

Table 9. Measurements (in mm) of *Promyophorella tuberculata* (Agassiz, 1840) n. comb. See Figure 2 for measurement key.

| Specimen | L | H | I | D | H/L | I/L | D/L |
|-------------------|------|------|---------|-----|-------|----------|------|
| BSPG 2014V 314/15 | 12.2 | ?9.7 | 3.5(RV) | 4.1 | ?0.79 | 0.29(RV) | 0.33 |
| BSPG 2014V 317/28 | 11.6 | ?7.3 | 7.2 | 3.8 | ?0.63 | 0.62 | 0.33 |

having an ornamented area (commarginal costellae), a median groove, and tuberculate marginal carina, but differs in flank ornamentation. According to Echevarría et al. (2021, p. 32), the flank of *Orthotrigonia* is ornamented with V-shaped or L-shaped costae at early growth stages and steep, straight costae bifurcating anteriorly at late growth stages. In contrast, *Vaugonia* has V-shaped tuberculated costae, which cover the entire flank. For more details and comparison with other closely related genera, see Echevarría et al. (2021, p. 31–32).

Orthotrigonia exortiva (Kitchin, 1903) new combination
Figure 8.9–8.11

- *1903 *Trigonia exortiva* Kitchin, p. 88, pl. 9, figs. 2, 3.
- .1952a *Trigonia (Scaphotrigonia) exortiva*; Cox, p. 117.
- .1998 *Vaugonia (Orthotrigonia) exortiva*; Fürsich and Heinze, p. 166, pl. 4, figs. 8, 9.
- .2013 *Vaugonia (Orthotrigonia) exortiva*; Fürsich et al., fig. 38c.

Holotype.—*Trigonia exortiva* Kitchin, 1903 (p. 88, pl. 9, figs. 2, 2a, 2b) from the lower part of the Jumara Formation (“Chari Group”), Kachchh, western India (collections of the Geological Survey of India, Kolkatta).

Occurrence.—Middle Jurassic of India (Kitchin, 1903; Fürsich and Heinze, 1998; Fürsich et al., 2013) and Upper Jurassic (lower Kimmeridgian) of Gebel Maghara (present study, first record).

Description.—Shell small, triangular, inequilateral, longer than high (H/L = ?0.87; Table 10), moderately inflated. Posterior margin subtruncated, forming angle with ventral margin. Posterodorsal margin faintly concave. Anterior and anterodorsal margins broken off. Umbo inflated, located anteriorly of mid-length of valve. Beak sharply pointed and opisthogyrate. Flank subtriangular, weakly inflated, separated from area by blunt marginal carina. Area wide, slightly concave, and covered by widely spaced commarginal costellae. Escutcheon carina distinct, slightly incurved, tuberculated. Escutcheon not well preserved. The flank ornament consists of five arcuate costae with numerous radially arranged riblets that extend from the crest of the costae (Fig. 8.11), followed ventrally by ~13 subradial costae, meeting marginal carina at acute angle and carrying small tubercles. Costae separated by narrow, deep, smooth intercostal spaces (Fig. 8.9).

Materials.—An incomplete right valve, with shell preserved, from the upper part of the lower Kimmeridgian Masajid Formation, western Bir Maghara (BSPG 2014V 313/19).

Measurements.—See Table 10.

Table 10. Measurements (in mm) of *Orthotrigonia exortiva* (Kitchin, 1903) n. comb. See Figure 2 for measurement key.

| Specimen | L | H | I | D | H/L | I/L | D/L |
|-------------------|-------|------|----------|-----|-------|-------|------|
| BSPG 2014V 313/19 | ?13.0 | 10.2 | 3.7 (RV) | 4.5 | ?0.78 | ?0.28 | 0.35 |

Remarks.—According to Fürsich and Heinze (1998, p. 166), *Orthotrigonia exortiva* (Kitchin, 1903) n. comb. can be easily distinguished from other Jurassic species of the genus by having a weakly inflated valve, 13–14 fairly dense, tuberculated, oblique radial costae, an area with widely spaced commarginal costellae, and by its much smaller size. With respect to general shape, outline, and ornamentation, the present material strongly corresponds to the figures given by Kitchin (1903), Fürsich and Heinze (1998), and Fürsich et al. (2013) from the Middle–Upper Jurassic of India, but differs in being smaller (L = ?13.0 mm).

Orthotrigonia duplicata (J. Sowerby, 1819) (Lycett, 1872, p. 14, pl. 1, figs. 8–10) from the Bajocian of England differs from the present species in having bifurcating flank costae close to the anteroventral corner and in being larger and much more inflated than *O. exortiva* n. comb.

Orthotrigonia gracilis (Kitchin, 1903) n. comb. can be easily distinguished by having seven arcuate costae in early growth stages, which pass over the marginal carina to cover the dorsal part of the area (Fig. 8.12).

Orthotrigonia hispida (Kitchin, 1903, p. 93, pl. 9, fig. 6) from the Jurassic rocks of Kachchh, India (see also Fürsich et al., 2019, p. 170, pl. 7, figs. 4, 5, from the Upper Jurassic of Madagascar) is more inflated and has a shorter escutcheon and fewer subvertical radial flank ribs.

Orthotrigonia kutchensis (Kitchin, 1903) n. comb. (p. 84, pl. 8, figs 7–9) from the Upper Jurassic of Kachchh, India, differs from *Orthotrigonia exortiva* n. comb. in being larger and in having fewer flank costae (Kitchin, 1903, p. 85).

Orthotrigonia gracilis (Kitchin, 1903) n. comb.
Figure 8.12–8.15

- *1903 *Trigonia gracilis* Kitchin, p. 95, pl. 9, fig. 7, 7a.
- .1952a *Trigonia (Scaphotrigonia) gracilis*; Cox, p. 117.
- .1998 *Vaugonia (Orthotrigonia) gracilis*; Fürsich and Heinze, p. 164, pl. 3, fig. 10, pl. 4, figs. 1–3.
- .2017 *Vaugonia (Orthotrigonia) gracilis*; Jaitly, p. 49, appendix B.

Holotype.—*Trigonia gracilis* Kitchin, 1903 (p. 95, pl. 9, fig. 7, 7a) from the lower part of the Jumara Formation (“Chari Group”) of Keera Dome, Kachchh, western India (collections of the Geological Survey of India, Kolkatta).

Occurrence.—Middle Jurassic of India (Kitchin, 1903; Fürsich and Heinze, 1998; Jaitly, 2017) and Lower Jurassic (Toarcian) of Gebel Maghara (present study, first record).

Description.—Shell small, crescentic, distinctly inequilateral, equivalved, longer than high, weakly inflated (Table 11). Anterior and ventral margins strongly convex, meeting in continuous curve. Posterior margin narrowly rounded, meeting

Table 11. Measurements (in mm) of *Orthotrigonia gracilis* (Kitchin, 1903) n. comb. See Figure 2 for measurement key.

| Specimen | L | H | I | D | H/L | I/L | D/L |
|-------------------|------|------|------|-----|------|-------|------|
| BSPG 2014V 317/29 | 15.7 | 10.8 | ?5.2 | 3.7 | 0.69 | ?0.33 | 0.24 |

ventral margin in rounded angle. Posterodorsal margin long, straight. Anterodorsal margin slightly convex. Umbo inflated, located approximately one-fourth of total valve length from anterior end. Beak small, inconspicuous, slightly opisthogyrate. Flank weakly inflated, separated from wide area by distinct, slightly curved and tuberculated marginal carina. Area wide, flat, divided into two equal parts by median groove, and ornamented by irregular commarginal costellae (Fig. 8.13). Escutcheon excavated, moderately wide, ornamented with small, rounded tubercles, forming transverse costellae. Ornamentation of flank consisting dorsally of seven arcuate costae with numerous fine, radially arranged riblets extending from their crests, where they form short spines. Arcuate costae cross over the marginal carina to cover dorsal part of area (Fig. 8.12, 8.15). Ventrally, flank costae extend radially to ventral margin and carry radially elongated tubercles. Costae separated by wide and smooth intercostal spaces.

Materials.—A single articulated specimen, with shell preserved, from the upper part of the lower Toarcian Rajabiah Formation (marl unit), western Bir Maghara (BSPG 2014V 317/29).

Measurements.—See Table 11.

Remarks.—The present specimen closely corresponds in outline and ornamentation of area and flank to the figures of *Trigonia gracilis* Kitchin (1903, pl. 9, fig. 7, 7a) from the Middle Jurassic (Callovian) of Kachchh, India. According to Fürsich and Heinze (1998, p. 164), the flank ornamentation of *Orthotrigonia gracilis* (Kitchin, 1903) n. comb. varies and they regarded these variations to be the result of intraspecific variation. The most diagnostic feature of the species appears to be that the arcuate flank costae of the early growth stages extend across the marginal carina to cover the dorsal part of the area (Fig. 8.12, 8.15). Other characteristic features are the low inflation ($I/L = 0.33$) and small size ($H = 10.8$ mm). The most closely related species is *O. jumarensis* (Kitchin, 1903) n. comb. (Kitchin, 1903, p. 93, pl. 9, fig. 6) from the Middle Jurassic of Kachchh, India. Fürsich and Heinze (1998, p. 167) noted that the most diagnostic features of that species are the strongly tuberculated flank and a flat area covered with strong, but somewhat irregular commarginal growth rugae. Based on the description of Kitchin (1903, p. 95), the ornamentation of the flank of *O. jumarensis* n. comb. and *O. gracilis* n. comb. is very similar. Therefore, they are possibly synonymous.

Orthotrigonia hispida (Kitchin, 1903) (p. 90, pl. 9, figs. 4, 5; see also Fürsich and Heinze, 1998, p. 166, pl. 4, fig. 6) from the Middle Jurassic of Kachchh resembles the present species in having strongly rounded shell margins and in the ornamentation of its flank, but is larger ($L = 45.0$ mm, Fürsich and Heinze, 1998, as opposed to $L = 15.7$ mm), more inflated (e.g., Kitchin, 1903, pl. 9, fig. 4a), and has a rounded escutcheon carina. Similarly, *O. kutchensis* (Kitchin, 1903) n. comb. (Kitchin, 1903, p. 84, pl. 8, figs. 7–9) from the Middle Jurassic of Kachchh differs by being larger and has strong radial flank costae that carry large, rounded tubercles.

Trigoniid gen. et sp. indet.
Figures 8.16–8.18, 9

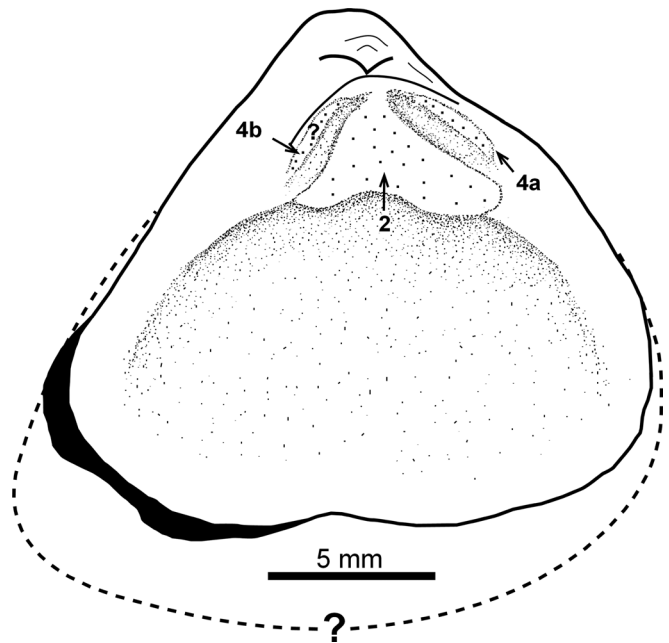


Figure 9. Drawing of hinge of left valve of Trigoniid gen. et sp. indet. from the middle–late Bathonian Kehailia Formation, Gebel Arousiah, BSPG2014V 258/1.

Description.—Shell small, triangular, inequilateral, longer than high (Table 12), and moderately inflated. Maximum inflation just below umbo. Ventral and posterior margins broken off. Umbo triangular, moderately inflated, located near mid-length of valve. Beak sharply pointed, slightly opisthogyrate. Antecarinal sulcus narrow, smooth. Hinge of left valve wide, with triangular cardinal tooth (2) and well-developed anterior tooth (4a; Figs. 8.18, 9). Anterior tooth (4a) striated, running parallel to anterodorsal margin. Flank weakly inflated, triangular, ornamented with commarginal costae separated by narrow and deep intercostal spaces, flexing slightly downwards anteriorly (Fig. 8.16).

Materials.—An incomplete left valve, with shell preserved, from the middle–late Bathonian Kehailia Formation, Gebel Arousiah (BSPG 2014V 258/1).

Measurements.—See Table 12.

Remarks.—Due to the missing area, generic identification is not possible. With respect to shell size, outline, and flank ornamentation, the present specimen is somewhat similar to *Trigonia mirandaensis* Lambert, 1944 (p. 371, pl. 1, fig. 9) from the Upper Jurassic of Argentina, but the latter differs in having a well-developed marginal carina and a wide and smooth antecarinal sulcus. *Trigonia densestriata* Behrendsen, 1892 (Leanza and Garate-Zubillaga 1987, p. 207, pl. 1, fig. 4;

Table 12. Measurements (in mm) of Trigoniid gen. et sp. indet. See Figure 2 for measurement key.

| Specimen | L | H | I | D | H/L | I/L | D/L |
|------------------|-------|------|---------|-----|------|------|------|
| BSPG 2014V 258/1 | ?17.5 | 15.3 | 6.5(LV) | 7.3 | 0.87 | 0.37 | 0.42 |

Leanza, 1993, p. 21, pl. 3, figs. 7–9) from the early Bajocian of the same area has a more elongated valve with a higher number of commarginal flank costae.

Size of trigoniids from Gebel Maghara

In general, trigoniids were very minor elements of Jurassic macrobenthic communities with some notable exceptions such as the Oxfordian “*Trigonia clavellata* Beds” of Dorset, southern England (Fürsich, 1977) and the Kimmeridgian strata of Portugal where *Myophorella lusitanica* (Sharpe, 1850) and related species are quite common (e.g., Choffat, 1885–1888; personal observation, F.T.F.). Trigoniids are also comparatively rare in the Jurassic succession of Gebel Maghara, (Abdelhady, 2014).

Nearly all of the taxa from Gebel Maghara are of very small to small size, most specimens not exceeding 1–2 cm in height. This is quite unusual for the group, in which the average size of most taxa is several times larger. There are several potential explanations for the small size. (1) The individuals could be juveniles, stunted, or could represent small species, but there is no indication that the trigoniids are juveniles. In the Kimmeridgian part of the succession, they occur associated with normal-sized brachiopods and other bivalves and there is no indication of size sorting (the fine-grained sediment pointing to low energy conditions). Moreover, the absence of any large adult specimens is difficult to explain. (2) Stunting, which cannot be ruled out with certainty, would imply adverse environmental conditions. However, normal-sized associated faunal elements and the moderate species diversity do not support such conditions. Stunting is, however, commonly known to affect benthic macrofauna in argillaceous substrates that experienced a certain deficiency of oxygen (e.g., Urlichs, 2011). Many of the infaunal trigoniids are found in silty marl and other infaunal bivalves, such as nuculids and the astartid *Nicaniella*, are commonly also smaller than elsewhere (personal observation, F.T.F.), therefore such substrates might not have been fully oxygenated. (3) With the present evidence we cannot exclude that the trigoniid fauna consists of small-sized taxa. In fact, some trigoniids do exhibit crowding of growth lines towards the ventral margin suggesting that they are adults, but other specimens are not well enough preserved to study this feature in detail. Regardless, whether these trigoniids are stunted to a certain degree or represent small species, their morphology does not just reflect juvenile but also adult features, and thus they should be described as taxa in their own right.

Conclusions

Based on newly collected material from the Jurassic strata of Gebel Maghara, Sinai, 14 species belonging to nine genera and two families of the bivalve order Trigoniida are systematically described, including the five new genera *Magharitrigonia*, *Cotswoldella*, *Cornbrashella*, *Parorthotrigonia*, *Retetrigonia*, and the new species *Magharitrigonia asymmetrica*.

Five species, *Trigonia reticulata* Agassiz, 1840, *T. cf. T. castor* d’Orbigny, 1849, *Promyophorella tuberculata* (Agassiz, 1840), *Orthotrigonia exortiva* (Kitchin, 1903), and *O. gracilis* (Kitchin, 1903) have been recorded from the Jurassic rocks of the studied area for the first time.

Acknowledgments

A.A. Abdelhady gratefully acknowledges the German Academic Exchange Service (DAAD) and the Egyptian Ministry of Higher Education and Scientific Research “GERLS” Programme for their financial support. We thank the editor S. Schneider and the reviewers T. Poulton and J. Echevarría for their careful and constructive criticism of the manuscript.

Declaration

The material for this study has been 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

- Abbass, H.L., 1962, A monograph on the Egyptian Cretaceous pelecypods: Geological Survey and Mineral Research Department, Palaeontological Series, Monograph, v. 1, p. 1–224.
- Abdallah, A.M., and Fahmy, N., 1969, A new pelecypod subgenus and species from Middle Jurassic of Khashm El Galala, Gulf of Suez: Journal of Geology of the United Arab Republic, v. 13, p. 145–152.
- Abdel-Gawad, G.I., and Salama, Y.F., 2015, Middle Jurassic *Trigonia* from Khashm El-Galala, western side of Gulf of Suez, Egypt: The 2nd Symposium of International Geoscience Programme Project 632, Shenyang, 12–13 September 2015.
- Abdelhady, A.A., 2014, Palaeoenvironments and palaeoecology of the Middle and Upper Jurassic succession of Gebel Maghara (Sinai) [Ph.D. dissertation]: Friedrich-Alexander-Universität Erlangen–Nürnberg, 125 p.
- Abdelhady, A.A., and Fürsich, F.T., 2014, Macroinvertebrate palaeo-communities from the Jurassic succession of Gebel Maghara (Sinai, Egypt): Journal of African Earth Sciences, v. 97, p. 173–193.
- Abdelhady, A.A., and Fürsich, F.T., 2015a, Quantitative biostratigraphy of the Middle to Upper Jurassic strata of Gebel Maghara (Sinai, Egypt): Newsletters on Stratigraphy, v. 48, p. 23–46.
- Abdelhady, A.A., and Fürsich, F.T., 2015b, Sequence architecture of a Jurassic ramp succession from Gebel Maghara (North Sinai, Egypt): implications for eustasy: Journal of Palaeogeography, v. 4, p. 305–330.
- Abdelhady, A.A., and Fürsich, F.T., 2015c, Palaeobiogeography of the Bajocian–Oxfordian macrofauna of Gebel Maghara (North Sinai, Egypt): implications for eustasy and basin topography: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 417, p. 261–273.
- 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.
- Abd El-Motaal, E., and Kusky, T.M., 2003, Tectonic evolution of the intraplate s-shaped Syrian Arc Fold-Thrust Belt of the Middle East region in the context of plate tectonics: The Third International Conference on the Geology of Africa, v. 2, p. 139–157.
- Agassiz, L., 1840, Études Critiques sur les Mollusques Fossils: Mémoire sur les Trigoniens, Neuchâtel, Imprimerie de Petitpierre, 58 p.
- Agrawal, S.K., 1956, Contribution à l’étude stratigraphique et paléontologique du Jurassique du Kutch (Inde): Annales du Centre d’Études et de Documentation Paléontologiques, v. 19, p. 1–188.
- 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.
- Arkell, W.J., 1930, A monograph of British Corallian Lamellibranchia: Part 2: Monographs of the Palaeontographical Society, v. 82, p. 73–104.
- 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.

- Ayoub-Hannaa, W.S., Fürsich, F.T., and Abdelhady, A.W., 2023, Revision of Jurassic protobranch bivalves from Gebel Maghara, northern Sinai, Egypt: *Journal of Paleontology*, v. 97, Memoir 93, p. 1–45.
- Bayle, E., 1878, Explication de la Carte Géologique de la France; Atlas, Première Partie. Fossiles Principaux des Terrains, 4: Paris, Imprimerie Nationale, 158 p.
- Behrendsen, O., 1892, Zur Geologie des Ostabhanges der Argentinischen Cordillere. II. Theil: *Zeitschrift der Deutschen Geologischen Gesellschaft*, v. 44, p. 1–42.
- Benecke, E.W., 1898, Beiträge zur Kenntnis des Jura in Deutsch-Lothringen: *Abhandlungen zur Geologischen Specialkarte von Elsass-Lothringen, Neue Folge*, v. 1, p. 1–97.
- Benecke, E.W., 1905, Die Versteinerungen der Eisenerzformation von Deutsch-Lothringen und Luxemburg: *Abhandlungen zur Geologischen Specialkarte von Elsass-Lothringen, Neue Folge*, v. 6, p. 1–598.
- Bengtson, P., 1988, Open nomenclature: *Palaeontology*, v. 31, p. 223–227.
- Bigot, A., 1893, Contributions à l'Étude de la Faune Jurassique de Normandie; Premier Mémoire sur les Trigonies: *Mémoires de la Société Linnéenne de Normandie*, v. 17, p. 261–345.
- Bruguère, J.G., 1789, *Encyclopédie Méthodique*: Paris, Panckoucke, v. 1, pt. 1, p. 1–344.
- Carter, J.G., Altaba, C.R., Anderson, L.C., Araujo, R., Biakov, 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., et al., 2012, Chapter 31: Illustrated Glossary of the Bivalvia: *Treatise on Invertebrate Paleontology, Part N, Revised, Volume 1*, Kansas University Paleontological Institute, Lawrence, v. 48, p. 1–209.
- Choffat, P., 1885–1888, Description de la faune Jurassique du Portugal. Mollusques Lamellibranches. 2e ordre. Asiphonida: *Mémoires de la Direction des Travaux géologiques du Portugal*, p. 1–115.
- Cossmann, M., 1911, Description de quelques pélecypodes Jurassiques recueillis en France: *Comptes Rendus de l'Association Française pour l'Avancement des Sciences (Congress Dijon)*, Paris, p. 1–48.
- Cox, L.R., 1952a, The Jurassic lamellibranch fauna of Cutch (Kachh). No. 3, Families Pectinidae, Amusidae, Plicatulidae, Limidae, Ostreidae and Trigonidae (supplement): *Memoirs of the Geological Survey of India: Palaeontologica Indica*, series 9, v. 3, no. 4, p. 1–128.
- Cox, L.R., 1952b, Notes on the Trigonidae with outlines of a classification of the family: *Proceedings of the Malacological Society*, v. 29, 45–70.
- Cox, L.R., ed., 1962 [= Cox, L.R., Castell, C.P. and Muir-Wood, H.M., 1962], *British Mesozoic Fossils*: London, British Museum, Natural History, 205 p.
- Cox, L.R., 1965, Jurassic Bivalvia and Gastropoda from Tanganyika and Kenya: *Bulletin of the British Museum of Natural History (Geology)*, Supplement, v. 1, p. 1–213.
- Cox, L.R., and Arkell, W.J., 1948–1950, A survey of the Mollusca from the British Great Oolite Series: primarily a nomenclatorial revision of monographs by Morris & Lycett (1851–55), Lycett (1863) and Blake (1905–07): *Monographs of the Palaeontographical Society*, v. 102, p. 1–48; v. 103, p. 49–105.
- Cox, L.R., Newell, N.D., Branson, C.C., Casey, R., Chavan, A., et al., 1969, Systematic descriptions, in Moore, R.C., and Teichert, C., eds., *Treatise on Invertebrate Paleontology, Part N, Mollusca 6, Bivalvia, Volume 1*: Lawrence, Kansas, Geological Society of America and the University of Kansas Press, p. N225–N590.
- Crickmay, C.H., 1930, The Jurassic rocks of Ashcroft, British Columbia. University of California Publications: *Bulletin of the Department of Geological Sciences*, v. 19, p. 23–74.
- Crickmay, C.H., 1932, Contribution towards a monograph of the Trigonidae, 1. *American Journal of Science*, v. 24, p. 443–464.
- Dainelli, G., 1903, Fossili batoniani della Sardegna: *Bollettino della Società Geologica Italiana*, v. 22, p. 253–347.
- 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 and Arts*, v. 38, no. 228, p. 445–462.
- Delvene, G., 2001, Middle and Upper Jurassic bivalves from the Iberian Range (Spain): *Beringeria*, v. 28, p. 43–104.
- 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, 394 p., v. 2, 428 p., v. 3, 387 p.
- Douvillé, H., 1886, Examen des fossiles rapportés du Choa par M. Aubry: *Bulletin de la Société Géologique de France*, v. 14, p. 223–241.
- 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*, v. 132, p. 1–137.
- Echevarría, J., Damborenea, S.E., and Manceñido, M.O., 2021, Early Jurassic Trigonidae (Bivalvia) from Argentina: *Journal of Paleontology*, v. 95, supplement 85, p. 1–55.
- Fabiani, R., and Ruiz, C., 1932, Giacitura e fauna dei tuffi vulcanici giuresi di Roccapalumba (Palermo): *Memorie della Società Geologica Italiana*, v. 1, p. 1–52.
- Fischer, J.-C., 1969, Géologie, paléontologie et paléocécologie du Bathonien au sud-ouest du Massif Ardennois: *Mémoires du Muséum National d'Histoire Naturelle, nouvelle série, série C, Sciences de la Terre*, v. 20, p. 1–319.
- Fleming, C.A., 1964, History of the bivalve family Trigonidae in the southwest Pacific: *The Australian Journal of Science*, v. 26, p. 96–204.
- Fleming, C.A., 1987, New Zealand Mesozoic bivalves of the superfamily Trigonacea: *New Zealand Geological Survey Paleontological Bulletin*, v. 53, p. 1–104.
- Francis, A.O., 2000, *The palaeobiology of the European Jurassic Trigonidae* [Ph.D. thesis]: Birmingham, UK, University of Birmingham, 359 p.
- Francis, A.O., and Hallam, A., 2003, Ecology and evolution of Jurassic trigonid bivalves in Europe: *Lethaia*, v. 36, p. 287–304.
- Fürsich, F.T., 1977, Corallian (Upper Jurassic) marine benthic associations from England and Normandy: *Palaeontology*, v. 20, p. 337–385.
- Fürsich, F.T., and Heinze, M., 1998, Contributions of the Jurassic of Kachchh, Western India. VI. The bivalve fauna. Part III. Subclass Palaeoheterodonta (Order Trigonoida): *Beringeria*, v. 21, p. 151–168.
- Fürsich, F.T., Alberti, M., and Pandey, D.K., 2013, Stratigraphy and palaeoenvironments of the Jurassic rocks of Kachchh - Field Guide, 9th International Congress on the Jurassic System, Jaipur, India, 2014: *Beringeria, Special Issue 7*, p. 1–174.
- Fürsich, F.T., Heinze, M., and Ayoub-Hannaa, W.S., 2019, Middle to Upper Jurassic bivalves of the southwestern Morondava Basin (Madagascar): *Zitteliana*, v. 93, p. 143–203.
- Ghandour, I.M., and Fürsich, F., 2022, Allogenic and autogenic controls on facies and stratigraphic architecture of the Lower Jurassic Mashabba Formation, Gebel Al-Maghara, North Sinai, Egypt: *Proceedings of the Geologists' Association*, v. 133, p. 67–86.
- Goldfuss, F.A., 1834–1840, *Petrefacta Germaniae tam ea, quae in Museo Universitatis Regiae Borussicae Fridericiae Wilhelmae Rhenanae Servantur quam alia Quaecunquae in Museis Hoenighusiano Muensteriano Aliisque Extant. Iconibus et Descriptionibus Illustrata. Abbildungen und Beschreibungen der Petrefacten Deutschlands und der angränzender Länder unter Mitwirkung des Herrn Grafen Georg zu Münster. Zweiter Theil [Bivalvia]: p. 1–68 [1834]; p. 69–140 [1835]; p. 141–224 [1837]; p. 225–312 [1840]*: Düsseldorf, Arz & Co.
- Gottsche, C., 1878, Beiträge zur Geologie und Palaeontologie der Argentinischen Republik. II. Palaeontologischer Theil. III Abth. Ueber jurassische Versteinerungen aus der argentinischen Cordillere: *Palaeontographica*, Supplement, v. 3, no. 2, p. 1–50.
- Gray, J.E., 1854, A revision of the arrangement of the families of bivalve shells (Conchifera): *The Annals and Magazine of Natural History*, v. 13, p. 408–418.
- Greppin, E., 1888, Description des fossiles de la Grande Oolithe des environs de Bâle: *Mémoires de la Société Paléontologique Suisse*, v. 15, p. 1–155.
- Haq, B.U., Hardenbol, J., and Vail, P.R., 1987, Chronology of fluctuating sea levels since the Triassic: *Science*, v. 235, p. 1156–1167.
- Hayami, I., 1972, Lower Jurassic Bivalvia from the environs of Saigon: *Geology and Palaeontology of Southeast Asia*, v. 10, p. 179–223.
- Hébert, E., 1861, Sur les trigonies clavellées de l'Oxford-Clay et du coral-rag: *Journal de Conchyliologie*, 3ème série, v. 1, p. 178–187.
- Hermann, J., 1781, Brief über einige Petrefacten: *Der Naturforscher*, v. 15, p. 115–134.
- Hertwig, R., 1895, *Lehrbuch der Zoologie*, 3rd edition: Jena, Gustav Fischer, 599 p.
- Hirsch, F., 1980, Jurassic bivalves and gastropods from northern Sinai and southern Israel: *Israel Journal of Earth-Sciences*, v. 28, p. 128–163.
- Hupé, L.H., 1854, Fauna Chilena. Molluscos, in Gray, C., 1854, ed., *Historia Física y Política de Chile según documentos adquiridos en esta Republica durante doce años de residencia en ella y publicada bajo los auspicios del Supremo Gobierno*. *Zoología*, 8, p. 1–407, Paris, Maulde & Rénaud; Atlas II, Paris, E. Thunot.
- ICZN, 1955, Opinion 327: designation, under the plenary powers, of a type species for the nominal genus *Trigonia* Bruguère, 1789, in harmony with accustomed nomenclatorial usage: *Opinions and Declarations Rendered by the International Commission on Zoological Nomenclature*, v. 9, p. 283–298.
- ICZN, 1999, *International Code of Zoological Nomenclature online*, 4th ed.: International Trust for Zoological Nomenclature, available from: <http://www.nhm.ac.uk/hosted-sites/iczn/code/>.
- Imlay, R.W., 1964, Marine Jurassic pelecypods from central and southern Utah: *United States Geological Survey, Professional Papers*, v. 483-C, p. C1–C42.

- 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.
- Jaworski, E., 1915, Beiträge zur Kenntnis des Jura in Süd Amerika. Teil II. Spezieller, paläontologischer Teil: Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, v. 40, p. 364–456.
- 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., 1995, New trigonoid bivalves from the Early Jurassic to earliest Cretaceous of the Antarctic Peninsula region: systematics and Austral paleobiogeography: *Journal of Paleontology*, v. 69, p. 66–84.
- 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.
- Kitchin, G.L., 1903, The Jurassic fauna of Cutch. The Lamellibranchiata. Genus *Trigonia*: *Memoirs of the Geological Survey of India, Palaeontologic Indica*; ser. 9, v. 3, no. 2, p. 1–122.
- Kobayashi, T., 1954, Studies on the Jurassic trigonians in Japan. Part 1, preliminary notes: *Japanese Journal of Geology and Geography*, v. 25, p. 61–80.
- Kobayashi, T., 1956, Some Jurassic trigonians from central and west Japan. *Studies on Jurassic trigonians in Japan*, Part 5: *Japanese Journal of Geology and Geography*, v. 27, p. 1–8.
- Kobayashi, T., and Kaseno, Y., 1947, A new Liassic species of *Trigonia* s. str. (i.e. *Lyriodon*) from the Kitakami Mountains, Nippon: *Japanese Journal of Geology and Geography*, v. 20, no. 2–4, p. 41–44.
- Kobayashi, T., and Mori, K., 1954, Studies on Jurassic trigonians in Japan. Part II. *Prosogyrotrigonia* and the Trigoniinae: *Japanese Journal of Geology and Geography*, v. 25, p. 155–175.
- Kobayashi, T., and Mori, K., 1955, On the Jurassic Trigoniinae in Japan. Part III. The Vaugoniinae from the Kitakami Mountains in North Japan: *Japanese Journal of Geology and Geography*, v. 26, p. 73–88.
- Kobayashi, T., and Tamura, M., 1955, The Myophorellinae from North Japan. *Studies on the Jurassic Trigoniinae in Japan*, part 4: *Japanese Journal of Geology and Geography*, v. 26, p. 89–103.
- Kobayashi, T., and Tamura, M., 1957, Additional new genera and species of trigonians from the Jurassic of Soma, North Japan: *Japanese Journal of Geology and Geography*, v. 28, p. 35–41.
- Lamarck, J.B. de, 1819, *Histoire Naturelle des Animaux sans Vertèbres*, 1st edition: v. 6, 232 p., Déterville, Paris.
- Lambert, L.R., 1944, Algunas trigonias del Neuquén: *Revista del Museo de La Plata, nueva ser., Paleontología*, v. 2, p. 357–397.
- Leanza, A.F., 1942, Los pelecípodos del Lias de Piedra Pintada en el Neuquén: *Revista del Museo de La Plata (n.s.) Paleontología*, v. 2, p. 143–206.
- Leanza, H.A., 1993, Jurassic and Cretaceous trigoniid bivalves from west-central Argentina: *Bulletins of American Paleontology*, v. 105, p. 1–95.
- Leanza, H.A., and Garate, J.L., 1985, Una nueva especie de *Trigonia* Bruguière (Bivalvia) del Jurásico Medio del Neuquén, Argentina: *Boletín de la Academia Nacional de Ciencias*, v. 56, p. 287–292.
- Leanza, H.A., and Garate Zubillaga, J.L., 1987, Faunas de Trigonias (Bivalvia) del Jurásico y Cretácico Inferior de la Provincia del Neuquen, Argentina, conservadas en el Museo Juan Olsches de Zapata: *Bioestratigrafía de los Sistemas regionales del Jurásico y Cretácico de América del Sur*, v. 1, p. 201–255.
- Lycett, J., 1853, On some new species of *Trigonia* from the Inferior Oolite of the Cotteswolds, with preliminary remarks upon that genus: *The Annals and Magazine of Natural History, Zoology, Botany and Geology*, ser. 2, v. 12, p. 225–240.
- Lycett, J., 1872–1879, 1881–1883, A monograph of the British fossil *Trigoniinae*: *Monographs of the Palaeontographical Society*, v. 26 (no. 120), part 1, p. 1–52, 1872; v. 28 (no. 129), part 2, p. 53–92, 1874; v. 29 (no. 132), part 3, p. 93–148, 1875; v. 32 (no. 138), part 4, p. 149–204, 1877; v. 33 (no. 153), part 6, p. 205–245, 1879; Supplement No. 1, p. 1–4, 1881; Supplement No. 2, p. 5–19, 1883.
- Marzloff, D., Daresté de la Chavanne, J., and Moret, L., 1936, Étude sur la faune du Bajocien supérieur du Mont d'Or Lyonnais (Cret). Deuxième partie. Gasteropodes, Lamellibranches, Brachiopodes, Echinodermes, Anthozoaires, Spongiaires: *Travaux du Laboratoire de Géologie de la Faculté des Sciences de Lyon*, v. 28, no. 9, p. 56–147.
- Mathews, S.C., 1973, Notes on open nomenclature and on synonymy lists: *Palaeontology*, v. 16, p. 713–719.
- Meek, F.B., 1873, Preliminary paleontological report, consisting of lists and descriptions of fossils, with remarks on the ages of the rocks in which they were found, etc.: *United States Geological and Geographical Survey of the Territories, Annual Report 6*, p. 431–541.
- Meek, F.B., 1876, A report on the invertebrate Cretaceous and Tertiary fossils of the upper Missouri country: *Report of the United States Geological Survey of the Territories (Hayden)*, v. 9, p. 1–629.
- Mongin, D., 1967, Les mollusques du Bathonien saumâtre du Moyen Atlas: *Notes et Mémoires, Service Géologique du Maroc*, v. 200, p. 37–94.
- Morris, J.F., and Lycett, J., 1853–1854, A monograph of the Mollusca from the Great Oolite, chiefly from Minchinhampton and the coast of Yorkshire. Part II. Bivalves: *Monographs of the Palaeontographical Society*, v. 7 (1853), p. 8 (1854), p. 1–148.
- Néraudeau, D., Vullo, R., and Mazan, P., 2013, Fossiles de la Préhistoire Charontaine: *Éditions Le Croît Vif*, 288 p.
- Newton, R.B., 1895, On a collection of fossils from Madagascar obtained by the Rev. R. Baron: *Quarterly Journal of the Geological Society*, v. 51, p. 72–91.
- Parkinson, J., 1811, Organic Remains of a Former World. An examination of mineralized remains of the vegetables and animals of the antediluvian world, generally termed extraneous fossils. Containing of the fossil starfish, echini, shells, insects, amphibia, mammalia, & c.: London, Sherwood, Neely & Jones, 479 p.
- 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.
- Pérez, E., Aberhan, M., Reyes, R., and Hillebrandt, A. von, 2008, Early Jurassic Bivalvia of northern Chile. Part III. Order Trigonioida: *Beringeria*, v. 39, p. 51–102.
- Philippi, R.A., 1899, Los Fósiles Secundarios de Chile; Primera Parte: Santiago, Gobierno de Chile, 104 p.
- Poulton, T.P., 1979, Jurassic trigoniid bivalves from Canada and western United States of America: *Geological Survey of Canada Bulletin*, v. 282, p. 1–82.
- Pugaczewska, H., 1976, Trigoniidae of the Dogger of Łęczycza (central Poland): *Acta Palaeontologica Polonica*, v. 21, p. 79–96.
- Quenstedt, F.A., 1856–1857, Der Jura: Tübingen, Germany, Laupp and Siebeck, p. 1–368 [1856]; p. 369–842 [1857].
- Riche, A., 1904, Étude stratigraphique et paléontologique sur la zone à *Lioceras concavum* du Mont d'Or Lyonnais: *Annales de l'Université de Lyon (NS, I, Science)*, v. 14, p. 1–221.
- Richter, R., 1948, Einführung in die Zoologische Nomenklatur durch Erläuterung der Internationalen Regeln: Frankfurt, Senckenberg Gesellschaft für Naturforschung, Frankfurt am Main (Kramer), 252 p.
- Schneider, N., 1927, Étude stratigraphique et paléontologique de l'Aalénien de Gundershoffen (Bas-Rhin): *Mémoires du Service de la Carte Géologique d'Alsace et de la Lorraine*, v. 3, p. 1–132.
- Schneider, S., Fürsich, F.T., and Werner, W., 2011, Biometric methods for species recognition in *Trigonia* Bruguière (Bivalvia; Trigoniidae): a case study from the Upper Jurassic of Western Europe: *Paläontologische Zeitschrift*, v. 85, p. 257–267.
- Sharpe, D., 1850, On the secondary district of Portugal, which lies on the north of the Tagus: *Quarterly Journal of the Geological Society London*, v. 6, p. 135–201.
- Shuwen, P., 1999, Early and Middle Jurassic bivalve fauna in volcanic rocks of Tibetan Lhasa Block and its paleobiogeography: *Geoscience*, v. 13, p. 291–297.
- Sowerby, J. de C., 1812–1846, The Mineral Conchology of Great Britain: London, Meredith, v. 1, p. 9–32, pls 1–9 [1812]; p. 33–96, pls 10–44 [1813]; p. 97–178, pls 45–78 [1814]; p. 179–236, pls 79–102 [1815]; v. 2, p. 1–28, pls 103–114 [1815]; p. 29–116, pls 115–150 [1816]; p. 117–194, pls 151–186 [1817]; p. 195–239, pls 187–203 [1818]; v. 3; p. 1–40, pls. 204–221 [1818], p. 41–98, pls. 222–253 [1819]; v. 4, p. 105–114, pls. 384–407 [1822]; p. 115–151, pls. 384–407 [1823]; v. 5, p. 1–64, pls. 408–443 [1823]; p. 65–138, pls. 444–485 [1824]; 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 Systematic Index to the six volumes, p. 239–250 [1835]; Alphabet Index to volumes 1–6, p. 1–11 [1840]; 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].
- Stanley, S.M., 1977, Coadaptation in the Trigoniidae, a remarkable family of burrowing bivalves: *Palaeontology*, v. 20, p. 869–899.
- Tamura, M., 1959, Trigoniidae, Ostreidae, Bakevelliidae, Pteriidae, Cardiidae and Astartidae from the Upper Jurassic Sakamoto Formation in Central Kyushu, Japan: *Transactions and Proceedings of the Palaeontological Society of Japan*, n. ser., v. 33, p. 23–32.
- Tamura, M., 1984, Upper Jurassic bivalve fauna from the Ebirase Formation, Middle Kyushu, with a note on the *Haidaia* species (trigoniid) in the Torinosu fauna: *Memoirs of the Faculty of Education, Kumamoto University*, v. 33, p. 23–33.
- Thevenin, A., 1913, Types du Prodrome de Paléontologie stratigraphique universelle d'Alcide d'Orbigny. Tome 1. Silurien–Bathonien: *Annales de Paléontologie*, v. 8, p. 145–176 (73–104).
- Ulrichs, M., 2011, Stunting in invertebrates from the type area of the Cassian Formation (early Carnian) of the Dolomites (Italy): *GeoAlp*, v. 8, p. 164–169.

- Wandel, G., 1936, Beiträge zur Kenntnis der Jurassischen Molluskenfauna von Misol, Ost-Celebes, Buton, Seran und Jamdena: *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*, v. 75, p. 447–526.
- Weaver, C.E., 1931, Paleontology of the Jurassic and Cretaceous of west central Argentina: *Memoirs of the University of Washington*, v. 1, p. 1–595.
- Yin, J., and Grant-Mackie, J.A., 2005, Late Jurassic-Cretaceous bivalves from volcanic sediments of the Lhasa Block, Tibet: *New Zealand Journal of Geology and Geophysics*, v. 48, p. 555–577.
- Young, G., and Bird, J., 1828, A Geological Survey of the Yorkshire Coast: describing the strata and fossils occurring between the Humber and the Tees, from the German Ocean to the plain of York: 2nd edition, Whitby, England, R. Kirby, 235 p.

Accepted: 11 October 2023