
A Jurassic (Bathonian-Callovian) *Daghanirhynchia* brachiopod fauna from Jordan

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| ABSTRACT |

A Jurassic (Bathonian-Callovian) brachiopod fauna from Jordan consists of seven rhynchonellid species all belonging to the genus *Daghanirhynchia* of which two are new: *Daghanirhynchia rawyaensis* and *D. jordanica*. Emended diagnoses are given for *Daghanirhynchia daghaniensis* and *D. macfadyeni*. Additional taxa described include *Daghanirhynchia angulocostata*, *D. susanae* and *D. triangulata*. Three-dimensional reconstructions illustrate the internal morphology of the articulated shells for the first time in this genus. The material studied herein was collected from Wadi Zarqa in northwestern Jordan, almost due north of the Dead Sea, and to the east of the Rift Valley. Most species seem to be geographically restricted within the Jurassic Ethiopian Province, however specimens from Somalia and Ethiopia are larger in size than in other parts of the Province and shell size increases in stratigraphically younger specimens. The occurrence of *Daghanirhynchia* in India is the only appearance of the genus outside the Ethiopian Province.

KEYWORDS | Brachiopoda. Systematics. Wadi Zarqa. Ethiopian Province. Middle Jurassic.

INTRODUCTION

According to Kiessling *et al.* (2011) the Jurassic Ethiopian Province includes Tunisia, the Levant, Arabia and much of East Africa, but excludes Tanzania and India. They consider that the special status of India and Tanzania is possibly due to latitudinal gradients in faunal composition. In this paper we believe that the Ethiopian Province consists of today's Arabian Peninsula, Jordan, the Sinai Peninsula and other neighboring basins, the Horn of Africa, parts of the eastern Mediterranean coast, and northeastern Africa. During the Middle Jurassic it was part of the southern Tethys with a characteristic faunal content. Strata of the Ethiopian Province were studied intensely during petroleum exploration after the First World War; however, primary attention was paid to structural geology and sedimentology. Italian and British geologists made large fossil collections that were described piecemeal by paleontologists (*e.g.* Weir 1925, 1929; Hudson, 1958; Jaboli, 1959; Ficarelli, 1968). Special attention was paid to the ammonite and foraminiferal faunas because of their stratigraphical value. Referring to the brachiopod faunal assemblages, Weir (1925, 1929) and Muir-Wood (1935, 1936) described the brachiopod fauna from Somalia; Weir (1929) from Kenya, Cooper (1983, 1989) from Saudi Arabia, and Feldman (1986, 1987), Feldman *et al.* (1991, 2012a), and Hegab (1989, 1992) from Sinai; Feldman *et al.* (2001) and Krawczynski and Wilson (2011) from Israel, and Feldman *et al.* (2012b) from Jordan. A more detailed stratigraphical summary of the Jurassic strata in Somalia (formerly British Somaliland) can be found in Weir (1929) and Muir-Wood (1935). Cooper (1989) described brachiopods from Saudi Arabia that were collected from 1125.6m of Jurassic strata. These strata are comprised of seven formations, for a more detailed description of these formations see Cooper (1989) and Sharief (*et al.*, 1991). Overall correlation of the faunas among these regions on a larger scale is, with few exceptions, still lacking. This paper is one of a series dealing with fossil finds from Jordan and their correlation with various regions within the Ethiopian Province.

The genus *Daghanirhynchia* was first established by Muir-Wood (1935). However, its first species were described by Weir (1925) and subsequently Cooper (1989) described additional species. Cooper (1989) and Shi and Grant (1993) discussed the inclusion of taxa assigned to other genera into *Daghanirhynchia*. In a preliminary work, Feldman *et al.* (2012b, figs. 1-3) identified a new species in the Arda section of Jordan. Two new species of *Daghanirhynchia* are described herein and the paleobiogeographical relationship between the *Daghanirhynchia* faunas from the Ethiopian Province is noted. The genus occurs in the Sinai Peninsula at Gebel Engabashi (Feldman, *et al.*, 2012a) and Saudi Arabia (Cooper, 1989) however this distribution is a

bit puzzling since it is apparently missing from correlative strata in the Negev. This paper presents new data that will add to our knowledge of the distribution of the genus within the Jurassic Ethiopian Province, enhance the genus as a biostratigraphical tool and increase our knowledge of the genus within the Tethyan Faunal Realm as a whole, except for the comparison with specimens from Asia which were omitted due to lack of material.

GEOLOGICAL SETTING

The material studied herein include two stratigraphic sections, the Arda section and the Tel el Dhahab section, both from Wadi Zarqa (Figs. 1; 2) in northwestern Jordan almost due north of the Dead Sea. Wadi Zarqa was first recognized by Wetzstein (1859) and further discussed by Libbey and Hoskins (1905). The base of the Jurassic in northwestern Jordan lies on Triassic siliciclastic sediments (Bender, 1974). The Jurassic in northwestern Jordan is subdivided into seven formations: Hihi, Nimr, Silal, Dhahab, Ramla, Hamam, and Mughanniyya (Khalil and Muneizel, 1992). Brachiopod-bearing levels are found in the Hamam Formation (Bathonian) and Mughanniyya Formation (Callovian) (Fig. 3). The ages of the formations under study are based mainly on bivalves, gastropods and corals since ammonites are relatively scarce in the region (Ahmad, 2002).

The mixed carbonate and siliciclastic Hamam Formation was defined by Khalil and Muneizel (1992) from its type area along Wadi Hamam. It consists of friable sandstones, marls, and clayey silts. Its base is marked by the first appearance of fossiliferous limestone beds, whereas the top is marked by the overlying Mughanniyya Formation.

The Mughanniyya Formation is composed of alternating claystones, siltstones, and marly limestone beds with minor dolomite, dolomitic limestone, and coquinas; it represents the upper part of the Jurassic sequence in Jordan cropping out consistently below the overlying Kurnub Sandstone Group.

STRATIGRAPHY AND CORRELATION

The genus *Daghanirhynchia* is easy to recognize due to its external morphology and rib structure. It is subtriangular to subpentagonal, subglobose, dorsibiconvex, and often with large and curved ventral beak. The shell is uniplicate with a distinct dorsal fold. The costae are coarse and angular and do not bifurcate. There are fine radial striae on the slopes of the costae. Its taxa are very useful index fossils for Middle Jurassic strata from the Ethiopian Province; however, most species seem to be

geographically restricted. In general, it can be said that specimens from Somalia and Ethiopia are larger in size than in other parts of the Ethiopian Province and shell size increases in stratigraphically younger specimens. Figure 4 shows an overview of the stratigraphical and geographical distribution of *Daghanirhynchia* species in the Ethiopian Province. Our data are taken from Weir (1925, 1929), Muir-Wood (1935), Hudson (1958), Jaboli (1959), Dubar (1967), Cooper (1989), Shi and Grant (1993), Howarth and Morris (1998), Ahmad (1998, 2000, 2002, 2003), Feldman *et al.* (2001, 2012b), the PBDB (Paleobiology Database; <http://www.paleodb.org>), and our own observations. According to Kiessling *et al.* (2011), India, Tanzania, and China are not included in the Ethiopian Province. However, it must be noted that Muir-Wood (1937) reported *Daghanirhynchia* from India. We believe in the accuracy of her assignment since she had erected the genus. At present, the occurrence of *Daghanirhynchia* in India is the only appearance of the genus outside the Ethiopian Province. During the Jurassic India was still attached to Africa (Gondwana) and was part

of the Ethiopian Province; it began drifting toward Asia only in the Cretaceous.

MATERIAL AND METHODS

All 213 specimens studied are preserved as articulated shells. To study the internal morphology we used serial sections and computer tomographical (CT) scans of nine specimens. The latter was only suitable for the type species, *Daghanirhynchia daghaniensis*, from Ethiopia because the shells were silicified and the composition of shell and sediment matrix allowed sufficient contrast for adequate images. Computer tomographical data were taken with a Phoenix / X-Ray with a 180kV high-power nanofocus tube and a tungsten target using a scanning distance between 10 and 35 μ m. Serial sections were prepared using a Struers Discoplan-TS grinding machine with slice-spacing of 50 or 100 μ m starting from apex in an anterior direction perpendicular to

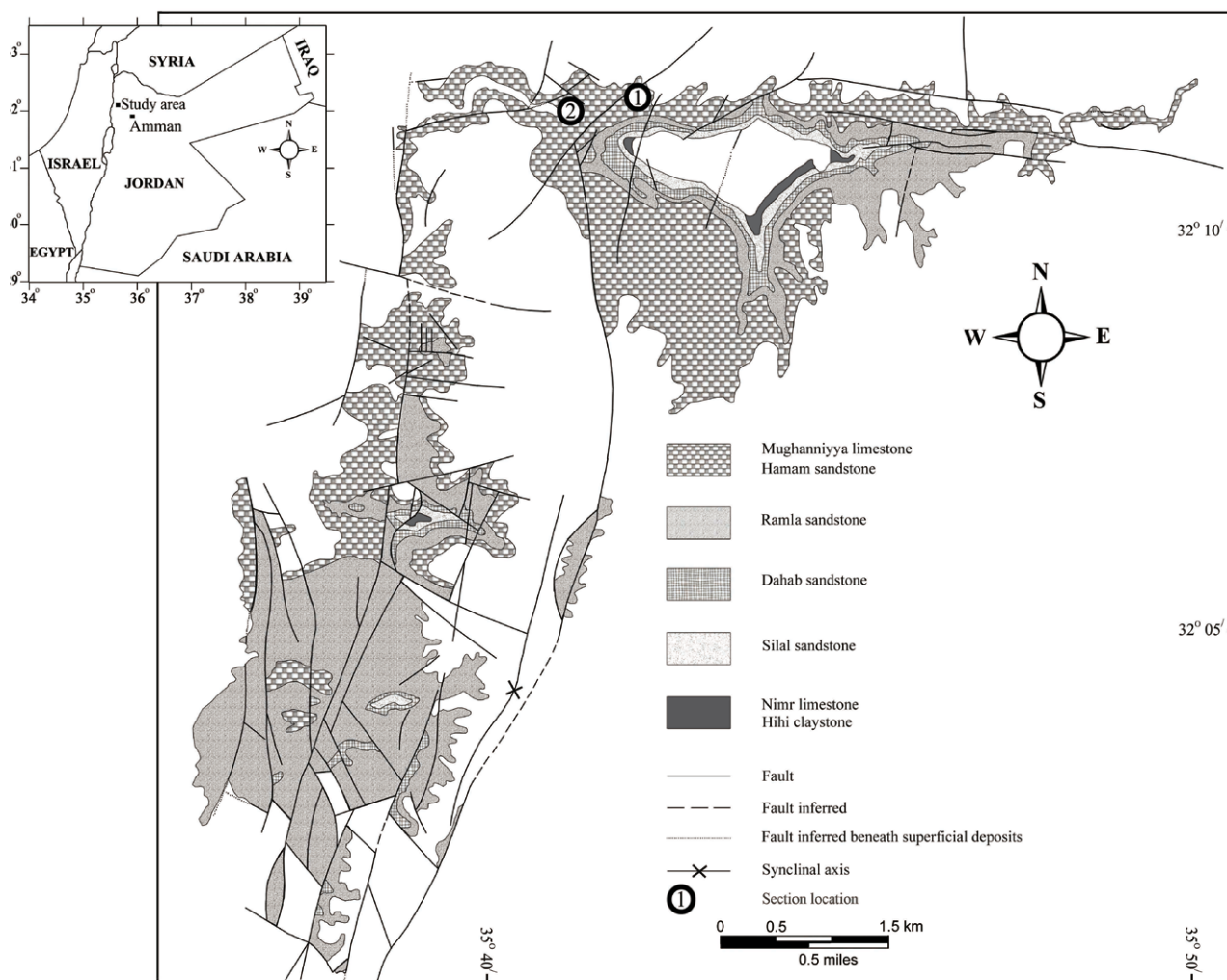


FIGURE 1. Geographical map of the study area, Wadi Zarqa, with collecting localities indicated.

commissural plane. Grinding surfaces were subsequently digitized using a digital camera (Canon 300D). Three-dimensional reconstruction methods are those of Sutton *et al.* (2001, 2005), using the custom SPIERS software suite for registration, virtual preparation, and interactive visualization. The photos of the grinding surfaces were subsequently manually aligned with SPIERSalign. In a second step, photos and CT (Computed Tomography) images were edited using different masks in SPIERSedit. The obtained 3D images were copied out of SPIERSview. Drawings of the peels were made with the help of a camera lucida. Measurements were taken with a digital caliper and rounded to 0.1mm or using free ImageJ 1.43 μ software. Specimens were coated with ammonium chloride or magnesium oxide prior to photographing. The systematics follows the revised *Treatise on Invertebrate Palaeontology* (Part H, no. 4); taxonomic assignments follow (Manceñido *et al.*, 2002). Specimens are in repository at the American Museum of Natural History, New York, the Geological Survey of Israel, Jerusalem, the Natural History Museum, London, The Museum für Naturkunde, Berlin, and the United States National Museum of Natural History/Smithsonian Institution, Washington.

Institutional abbreviations

AMNH: American Museum of Natural History, New York, USA;
 MB.B.: Museum für Naturkunde Berlin, Germany;
 GSI: Geological Survey of Israel, Jerusalem, Israel;
 NHM: Natural History Museum, London, UK;
 USNM: United States National Museum of Natural History/Smithsonian Institution, Washington DC, USA.

Systematic paleontology

Phylum BRACHIOPODA Duméril, 1806
 Subphylum RHYNCHONELLIFORMEA Williams *et al.* 1996
 Class RHYNCHONELLATA Williams *et al.* 1996
 Order RHYNCHONELLIDA Kuhn, 1949
 Superfamily HEMITHYRIDOIDEA Rzhonsnitskaya, 1956
 Family TETRARHYNCHIIDAE Ager, 1965
 Subfamily TETRARHYNCHIIDAE Ager, 1965
 Genus *Daghanirhynchia* Muir-Wood, 1935
 1935 *Daghanirhynchia* –Muir-Wood, p. 82-83.
 1989 *Daghanirhynchia*. – Cooper, p. 26.
 1993 *Daghanirhynchia*. – Shi and Grant, p. 73.

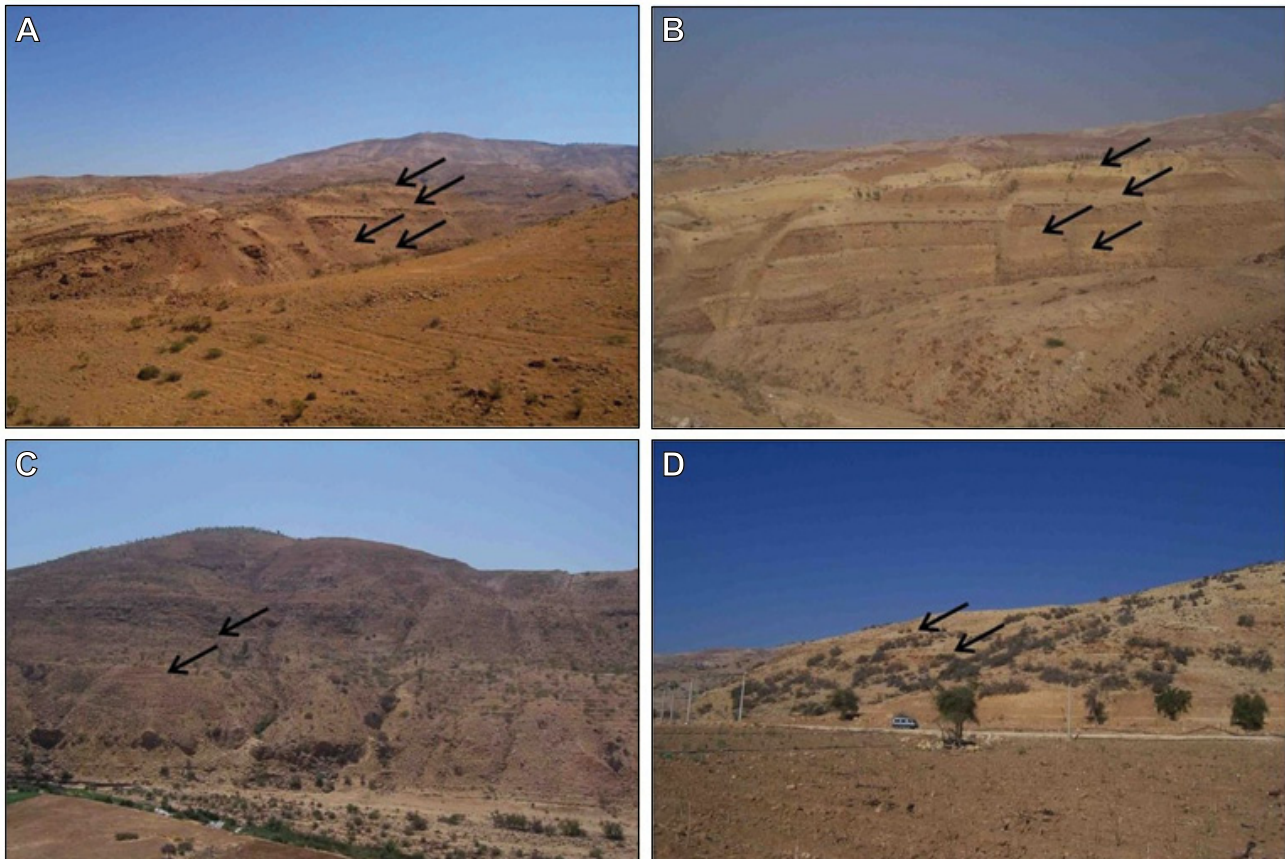


FIGURE 2. Studied sections at Wadi Zarqa with *Daghanirhynchia*-yielding beds indicated by arrows. A-B) Arda section. C-D) Tel el Dhahab section.

Type species. *Daghanirhynchia daghaniensis* Muir-Wood, 1935: 82; by original designation.

Emended diagnosis (from Muir-Wood, 1935). Shells medium-sized, subtriangular to subpentagonal, subglobose, dorsibiconvex, and often with large and curved ventral beak. Uniplicate and with distinct dorsal fold. Lateral commissure straight. Three to 6 costae on fold. Sulcus tongue high and trapezoidal. Beak acute, erect to incurved. Foramen large, circular to elongate elliptical. Deltidial lamellae lacking. Dental plates strong. Dorsal median septum weak, persistent. Hinge plate divided. Septalium usually pendant. Crura nearly horizontal, raduliform, and slightly to strongly incurved ventrally. Slightly modified after Manceñido et al. (2002, 1347).

Stratigraphical and geographical occurrence. Bathonian to Oxfordian (Middle to Upper Jurassic) (Manceñido et al., 2002, 1347); Somalia, Kenya, Ethiopia, Jordan, Egypt (Sinai), Arabia, Israel, Syria, India; questionable Morocco, Tunisia.

Species included

- Daghanirhynchia daghaniensis* Muir-Wood, 1935;
- ?*Rhynchonella hadramautensis* Stefanini, 1925;
- Somalirhynchia subversabilis* Weir, 1925;
- Daghanirhynchia daghaniensis* var. *elongata* Muir-Wood, 1935;
- Daghanirhynchia daghaniensis* var. *platilobata* Muir-Wood, 1935;
- Daghanirhynchia farquarsoni* Muir-Wood, 1935;
- Daghanirhynchia kabeitensis* Muir-Wood, 1935;
- Daghanirhynchia macfadyeni* Muir-Wood, 1935;
- Rhynchonella* (*Daghanirhynchia*) n. sp. ind. sensu Jaboli, 1959;
- ?*Burmhirhynchia termierae preathiensis* Rouselle, 1965;
- ?*Burmhirhynchia termierae atheniensis* Rouselle, 1965;
- ?*Rhynchonella tazerdunensis* Dubar, 1967;
- ?*Rhynchonella dieffarae* Dubar, 1967;
- Daghanirhynchia angulocostata* Cooper, 1989;
- Daghanirhynchia sulcata* Cooper, 1989;

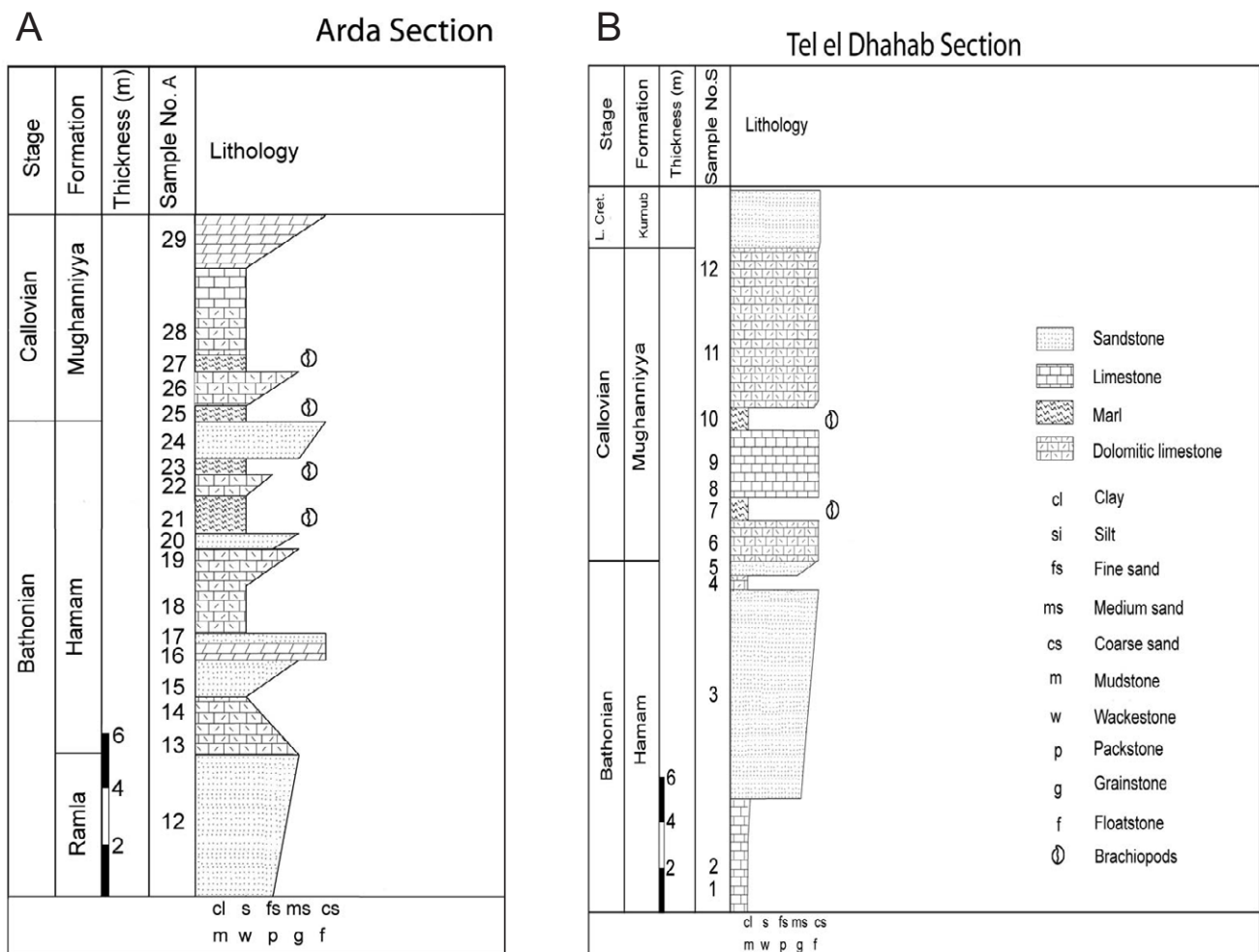


FIGURE 3. Stratigraphical columns of the sections sampled showing lithology and *Daghanirhynchia*-yielding beds. A) Arda section. B) Tel el Dhahab section.

Bajocian	Bathonian	Callovian	Oxfordian	<i>Daghanirhynchia</i> species	Country
				sp. A <i>subversabilis</i> <i>daghaniensis</i> <i>angulocostata</i> <i>triangulata</i> <i>susanae</i> <i>rawyaensis</i> <i>jordanica</i> <i>macfadeyni</i>	Jordan
				<i>daghaniensis</i> <i>macfadeyni</i> <i>elongata</i> <i>subversabilis</i> <i>platilobata</i> <i>farquarsoni</i> <i>kabeitensis</i>	Somalia
				<i>triangulata</i> <i>subversabilis</i> <i>sulcata</i> <i>angulocostata</i> <i>daghaniensis</i> <i>hadramautensis</i>	Saudi Ar.
				n. sp. ind. <i>subversabilis</i> <i>daghaniensis</i>	Eth.
				<i>daghaniensis</i> <i>macfadeyni</i> <i>sulcata</i>	Yem.
				<i>daghaniensis</i> sp.	Is.
				<i>subversabilis</i>	K.
				? <i>macfadeyni</i> <i>tazerdunensis</i> <i>dieffarae</i>	Mor.
				<i>termierae praeathiensis</i> <i>termierae athiensis</i>	Tun.

FIGURE 4. Stratigraphical and geographical distribution of *Daghanirhynchia* taxa from the Ethiopian Province (Cooper, 1989; Dubar, 1967; Feldman *et al.* 2001, 2012a, 2012b; Muir-Wood, 1935; Rousselle, 1965; Stefanini, 1925; Weir, 1925, 1929). Eth.: Ethiopia, Is.: Israel, K.: Kenya, Mor.: Morocco, Saudi Ar.: Saudi Arabia, Tun.: Tunisia, Yem.: Yemen.

?Daghanirhynchia triangulata Cooper, 1989
Daghanirhynchia susanae Feldman *et al.* 2012b;
Daghanirhynchia rawyaensis [described herein];
Daghanirhynchia jordanica [described herein].

Discussion. Species of *Daghanirhynchia* are mostly defined based on external morphology rather than on internal features. Serial sections of *D. daghaniensis* and *D. angulocostata* are given in Muir-Wood (1935) and Cooper (1989). In an earlier work (Feldman *et al.*, 2012b) we showed serial sections of *D. susanae* which are re-figured herein. Serial sections of *D. macfadeyni* from the Muir-Wood collection housed in the NHM were taken and a CT scan of *D. daghaniensis* from Ethiopia was prepared. Owing to strong homoeomorphy we recommend the erection of new taxa based on internal and external shell morphology. For comparison the diagnoses, stratigraphical

and geographical distribution of all *Daghanirhynchia* species are given, but further description is omitted due to lack of (internal) information. We could not study the specimens from Jaboli (1959), Rousselle (1965), and Dubar (1967), therefore, species assignment to *Daghanirhynchia* is noted with a question mark; these were noted by Cooper (1989) and Shi and Grant (1993).

***Daghanirhynchia rawyaensis* n. sp.**

Figs. 5C; 6B; 7; 8

Derivatio nominis. After Rawya Fayeze, wife of F. Ahmad, for her assistance in the field.

Holotype. Articulated shell stored at the AMNH under the repository number AMNH FI-86469; length 24.6mm, width 29.2mm, and thickness 25.4mm.

Type horizon and type locality. Wadi Zarqa, Arda Section, Bed S-7, Mughanniyya Formation, Callovian (upper Middle Jurassic), Jordan.

Material. 18 articulated shells. Age: Callovian (upper Middle Jurassic). Locality: beds Arda 21b, Arda 23, Arda 25, Arda 27, S-7, S-10. Locality: Wadi Zarqa. AMNH 86469 (holotype), 86485-86494.

Diagnosis. *Daghanirhynchia* with 11 to 15 costae on each shell, 3 to 4 in the sulcus and 4 to 5 on the fold, thick and divergent dental plates, a long and thick dorsal median septum, raduliform crura, wedge-like dental plates.

Description. Shells medium-sized subpentagonal, dorsibiconvex with maximum width at midlength. Apical angle is 99 degrees. Eleven to 15 costae on each valve, of which 3 to 4 are in the sulcus and 4 to 5 on the fold. Costae simple and angular in cross-section. Fold and sulcus originating at midlength of shell. Sulcus tongue high, reaching maximum curvature of dorsal valve, and with rounded to rarely straight anterior margin. Beak erect and incurved in adult specimens. Dorsal interarea concealed.

Interior of ventral valve. Moderate development of secondary shell material in the apical region slightly filling the umbonal cavities (see Fig. 5C). Dental plates thick, divergent, and wedge-like posteriorly leading into massive teeth that are oriented in a dorsal direction. Denticular cavities rounded in cross-section (Figs. 5C; 7).

Interior of dorsal valve. Moderate development of secondary shell material. Dorsal median septum long, pronounced, and thick. Septalium lacking or imbedded into secondary shell material. Dental sockets rounded in cross-section, inner socket ridges straight. Hinge plates

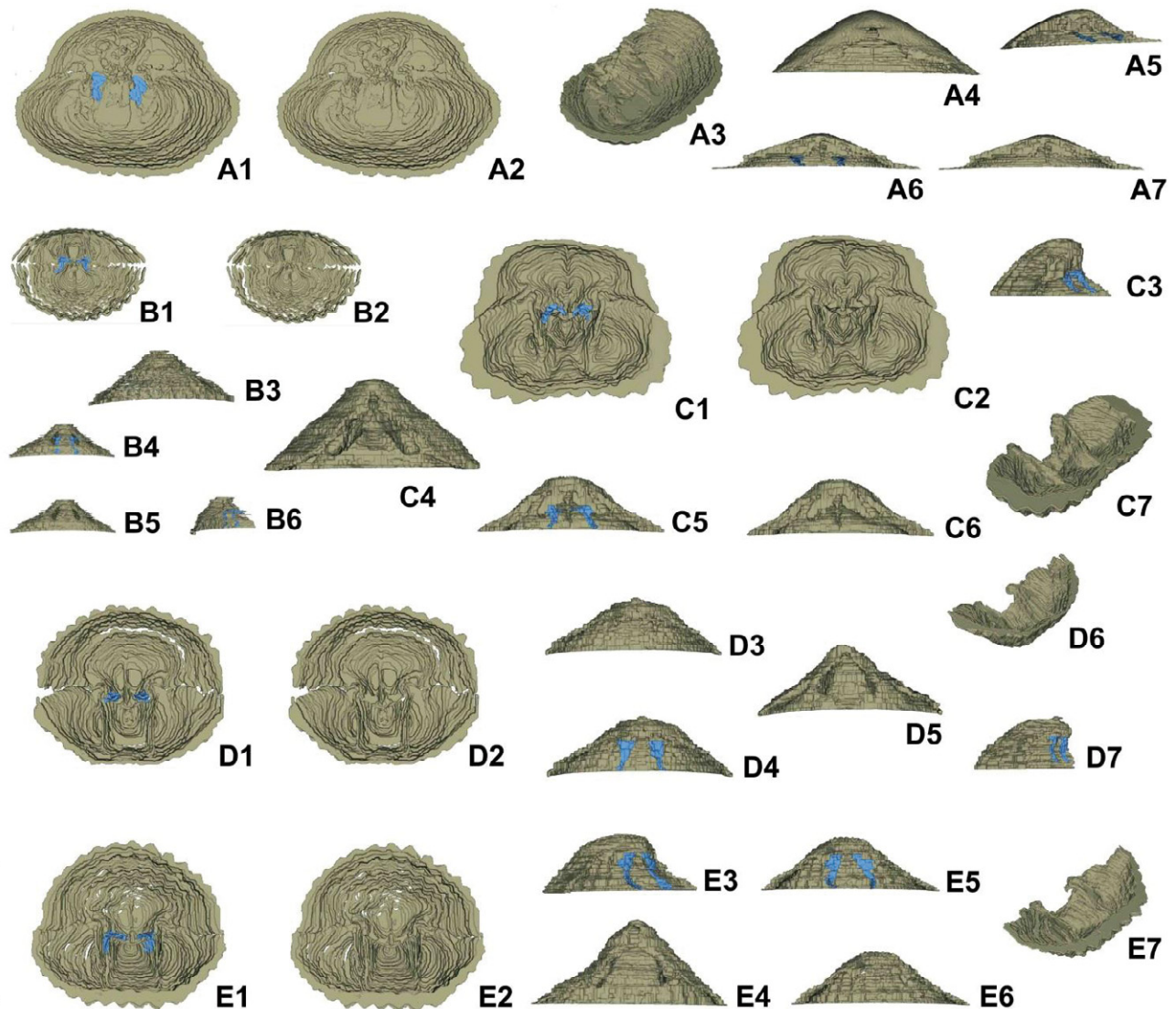


FIGURE 5. Three-dimensional reconstructions of *Daghanirhynchia* species after A) CT images and B-E) serial sections of articulated shells. All figures magnified (x2.0); scale bar 10mm. A) *Daghanirhynchia daghaniensis* Muir-Wood, 1935 (MB.B. 3358) from the Antalo. Limestone, Callovian/Oxfordian boundary interval from Geyedamo River, Mekele Outlier, Ethiopia. Anterior view of internal apical region of articulated shells A1) with and A2) without crura of internal dorsal shell. A3) Oblique posterolateral and A4) dorsal views of internal ventral shell. A5) Oblique venterolateral and ventral views A6) with and A7) without crura of internal dorsal shell. B) *Daghanirhynchia susanae* Feldman et al. (2012b) (AMNH FI-72410) from Bed S-7, Mughanniyya Formation, Callovian, Arda section, Jordan. Anterior view of internal apical region of articulated shells B1) with and B2) without crura. B3) Dorsal view of internal ventral shell. Ventral views B4) with and B5) without crura and B6) oblique venterolateral and of internal dorsal shell. C) *Daghanirhynchia rawyaensis* n. sp. (AMNH FI-86479) Bed S-7, Mughanniyya Formation, Callovian, Arda section, Jordan. Anterior view of internal apical region of articulated shells C1) with and C2) without crura. C3) Oblique venterolateral view of dorsal internal shell. C4) Dorsal view of internal ventral shell. Ventral views C5) with and C6) without crura of internal dorsal shell. C7) Oblique posterolateral view of internal ventral shell. D) *Daghanirhynchia jordanica* n. sp. (AMNH FI-86480) from Bed S-7, Mughanniyya Formation, Callovian, Arda section, Jordan. Anterior view of internal apical region of articulated shells D1) with and D2) without crura. Ventral view D3) with and D4) without crura of internal dorsal shell. D5) Dorsal and D6) oblique posterolateral views of internal ventral shell. D7) Oblique venterolateral view of dorsal internal shell. E) *Daghanirhynchia macfadyeni* Muir-Wood, 1935 (NHM B. 85416) from Dhurma Formation, Bathonian/Callovian boundary interval from Al Haddar near Riyadh, Saudi Arabia. Anterior view of internal apical region of articulated shells E1) with and E2) without crura. E3) Oblique venterolateral view of dorsal internal shell. E4) Dorsal view of ventral internal shell. Ventral view E5) with and E6) without crura of internal dorsal shell. E7) Oblique posterolateral views of internal ventral shell.

arched leading into short raduliform crura that are slightly curved ventrally.

Stratigraphical and geographical occurrence. Wadi Zarqa, Arda Section, Beds S-7, S-10, 21b, 23, 25, 27,

Mughanniyya Formation, Callovian (upper Middle Jurassic), Jordan.

Discussion. *Daghanirhynchia rawyaensis* differs from *D. jordanica* in 1 to 2 costae less on fold and sulcus, gently

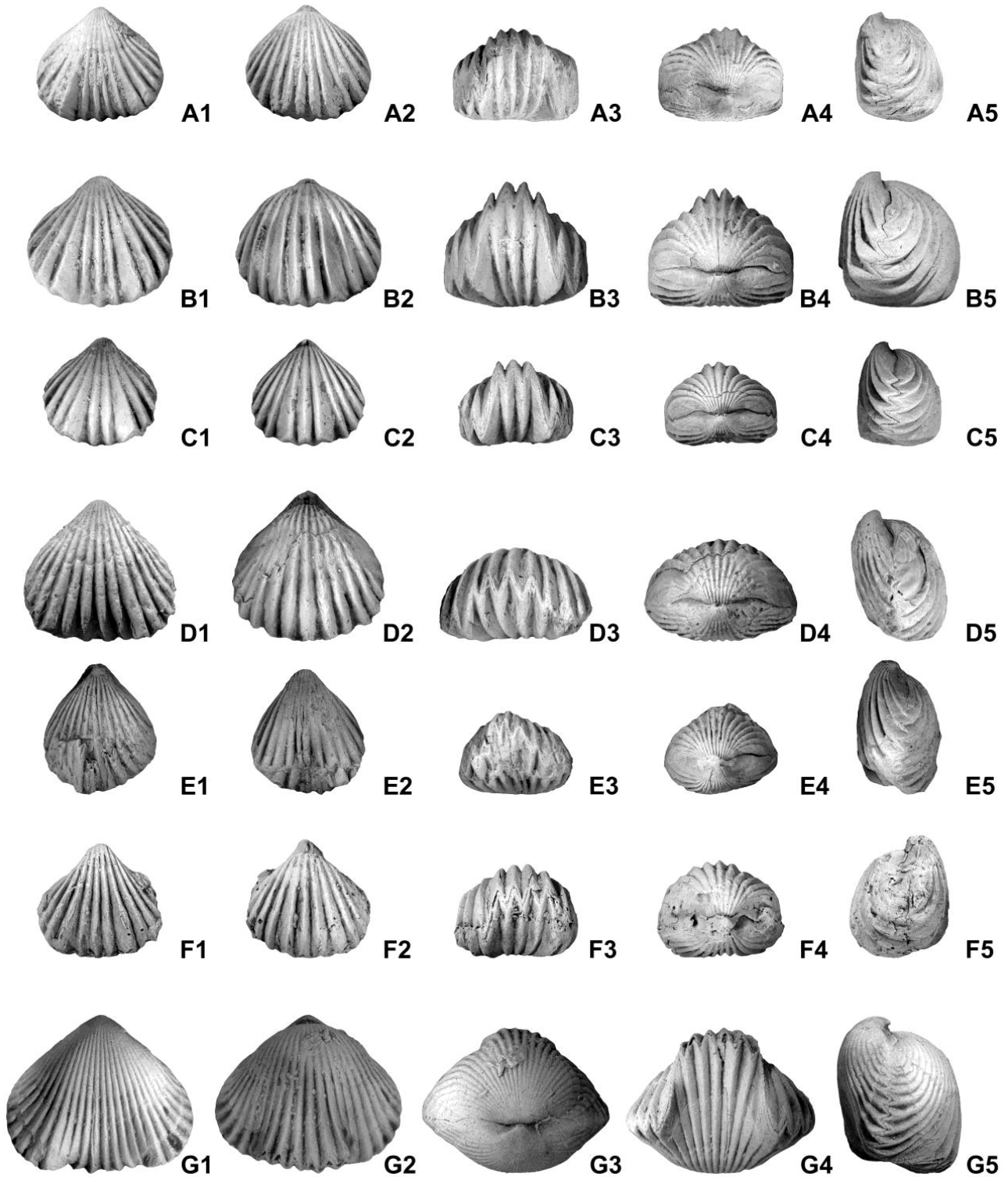


FIGURE 6. A) *Daghanirhynchia jordanica* n. sp. (AMNH FI-86481 from Wadi Zarqa, Arda Section, Bed S-7. B) *Daghanirhynchia rawyaensis* n. sp. (AMNH FI-86482) from Wadi Zarqa, Arda Section, Bed S-7, Mughanniyya Formation, Callovian (upper Middle Jurassic), Jordan. C) *Daghanirhynchia susanae* Feldman et al. (2012b) (AMNH FI-72380) from Bed 7, Mughanniyya Formation, Callovian, Arda section, Jordan. D) *Daghanirhynchia angulocostata* Cooper, 1989 (AMNH FI-72395) from Bed S-7, Mughanniyya Formation, Callovian, Tel el Dhahab section, Jordan. E) ?*Daghanirhynchia triangulata* Cooper, 1989 (AMNH FI-72398) from Bed 21a, Hamam Formation, Bathonian, Arda section, Jordan. F) *Daghanirhynchia macfadyeni* Muir- Wood, 1935 (NHM B 85416) from Dhurma Formation, Bathonian/Callovian boundary interval, Al Haddar near Riyadh, Saudi Arabia. G) *Daghanirhynchia daghaniensis* Muir-Wood, 1935 (MB.B. 3358) from Antalo Limestone, Callovian/Oxfordian boundary interval, Geyedamo River, Mekel Outlier, Ethiopia. 1) Ventral, 2) dorsal, 3) anterior, 4) posterior, and 5) lateral views of articulated shells. All figures of original size (x1.0).

more development of secondary shell material, thick and divergent dental plates, and a longer and thick dorsal median septum.

Daghanirhynchia rawyaensis n. sp. has 6 costae less on each valve than *D. daghaniensis*; the sulcus shows 1 rib less and the fold 1 to 2 costae less than in the type species. *Daghanirhynchia daghaniensis* has a short and fine dorsal median septum, whereas *D. rawyaensis* has a long and thick dorsal median septum. The crura of the type species extends further in a ventral direction than the crura of *D. rawyaensis*.

Daghanirhynchia macfadyeni differs from *D. rawyaensis* n. sp. By having 3 to 7 more costae on each shell, but the amount of costae in sulcus and fold is the same, less secondary shell material, a subtriangular outline, thin and parallel dental plates, and a shorter dorsal median septum.

The shells of *Daghanirhynchia susanae* are smaller and have less secondary shell material, 1 to 2 costae less on fold and sulcus, thin dental plates, a short dorsal median septum, and longer crura than *D. rawyaensis*.

?*Daghanirhynchia triangulata* has a subtriangular outline compared to *D. rawyaensis*. *Daghanirhynchia angulocostata* differs from *D. rawyaensis* in that there are 1 to 3 more costae on each shell and a thin dorsal median septum is present.

***Daghanirhynchia jordanica* n. sp.**

Figs. 5D; 6A; 9; 10

Derivatio nominis. After the country Jordan in which the type locality is located; *jordanica* (= latinization, adj. of Jordan).

Holotype. Articulated shell housed at the AMNH under the repository number AMNH FI-86469; length 24.6mm, width 25.6mm, and thickness 21.4mm.

Type horizon and type locality. Wadi Zarqa, Arda Section, Bed S-7, Mughanniyya Formation, Callovian (upper Middle Jurassic), Jordan.

Material. 16 specimens. Age: Callovian (upper Middle Jurassic). Locality: beds Arda 21a, b, S-7, S-10. Locality: Wadi Zarqa. AMNH FI-86495 (holotype), FI-86496, FI-86497 (5 pcs), FI-86498, FI-85499, FI-86500 (3 pcs), FI-86501 (3 pcs), FI-86502.

Diagnosis. *Daghanirhynchia* with 14 to 16 costae on each shell, 4 to 5 in sulcus and 5 on fold. Hardly any development of secondary shell material, thin and parallel dental plates, and a high and blade-like dorsal median septum. Septalial plates are narrow and parallel to one another.

Description. Shells medium-sized, subpentagonal, gently dorsibiconvex with maximum width at midlength of shell or anterior to it. Apical angle is 98 degrees. Shells covered by 14 to 16 simple and rounded to angular costae, of which are 4 to 5 in the sulcus and 5 on the fold. Sulcus and fold originating at midlength of shell. Sulcal tongue almost reaching maximum curvature of ventral valve and with rounded anterior margin. Ventral umbo moderately long and suberect. Dorsal interarea concealed.

Interior of ventral valve. Hardly any development of secondary shell material. Umbonal cavities free, ventral median septum lacking. Dental plates short, thin, and parallel to each other, leading into short and knob-like teeth that project dorsally.

Interior of dorsal valve. No development of secondary shell material. Dorsal median septum short and blade-like. Septalium weakly developed, hardly recognizable. Septalial plates narrow and parallel to one another. Dental sockets rounded in cross-section. Inner socket ridges show tendency to curve over dental sockets. Hinge plate arched leading into raduliform, slightly curved ventrally crura.

Stratigraphical and geographical occurrence. Wadi Zarqa, Arda Section, Beds S-7, S-10, 21a, Mughanniyya Formation, Callovian (upper Middle Jurassic), Jordan.

Discussion. *Daghanirhynchia jordanica* n. sp. has 3 to 5 costae less than the type species *D. daghaniensis*, but the amount of costae on fold and sulcus is the same. Furthermore, *D. jordanica* has hardly any development of secondary shell material, parallel and thin dental plates, a higher dorsal median septum, narrow and parallel septalial plates, and gently ventrally curved crura. *Daghanirhynchia daghaniensis* shows stronger development of secondary shell material, divergent dental plates, a lower dorsal median septum and septalial plates that are oriented almost parallel to each other. *Daghanirhynchia jordanica* has 2 to 4 less costae on each shell than *D. macfadyeni*, a subpentagonal outline, a higher dorsal median septum, and parallel septalial plates. *Daghanirhynchia jordanica* differs from *D. susanae* (see Fig. 11) in that it possesses 1 to 2 more costae, less secondary shell material, parallel dental plates, a higher dorsal median septum, and shorter crura. *Daghanirhynchia angulocostata* has 1 less costa on the sulcus and 1 more costa on the fold than *D. jordanica*. ?*Daghanirhynchia triangulata* shows a subtriangular outline and 1 to 2 costae less on fold and sulcus than *D. jordanica*.

***Daghanirhynchia daghaniensis* Muir-Wood, 1935**

Figs. 5A; 6G

1935 *Daghanirhynchia daghaniensis* Muir-Wood, p. 83-85, figs. 4-6, pl. 8 figs. 5a-c.

1959 *Rhynchonella* (*Daghanirhynchia*) *daghaniensis*. – Jaboli, p. 23-24, pl. 3 fig. 4a-d. v 1993 *Daghanirhynchia* *daghaniensis*. – Shi and Grant, p. 73-74, pl. 10 fig. 7, 44.

2011 *Daghanirhynchia* sp. – Kiessling *et al.* fig. 11P-T

Holotype. Articulated shell housed in the NHM under the repository number B.85408; length 26.1mm, width 28.2mm, and thickness 19.4mm.

Type horizon and type locality. Bed ϕ .227, Daghani section, Somalia (detailed description is given in Muir-Wood, 1935, table 2).

Material. One silicified articulated shell (MB.B. 3358). Stratum: Antalo Limestone, Callovian/Oxfordian boundary interval. Locality: Geyedamo River, Mekele Outlier, Ethiopia.

Diagnosis. Dorsibiconvex *Daghanirhynchia* with subtriangular to subpentagonal outline and with moderate

development of secondary shell material in the apical region of both valves. Costae coarse and subangular, 17 to 21 on each valve, with 3 to 6 on fold and 2 to 5 in the sulcus. Dental plates slightly divergent and dorsal median septum short. Septalium lacking or imbedded into secondary shell material.

Description. Shells medium-sized, subtrigonal to subpentagonal, and dorsibiconvex. Ventral valve posteriorly convex with maximum convexity at midvalve to anterior. Apical angle is 95 degrees. Numerous rounded costae, 17 to 21 on each valve, 3 to 6 on fold, 2 to 5 in sulcus. Sulcus well developed, broad, steep, with flattened bottom and beginning at posterior 1/3 to 1/2 part of shell. Sulcus tongue high, trapezoidal. Fold raised significantly over flanks, broad, pronounced, rounded at top, and starting at posterior 1/3 to 1/2 part of shell.

Exterior. Ventral beak long, massive, and suberect. Foramen large, subcircular to elongate elliptical, hypothryid with or without deltidial lamellae. Interareas small but distinct and gently curved.

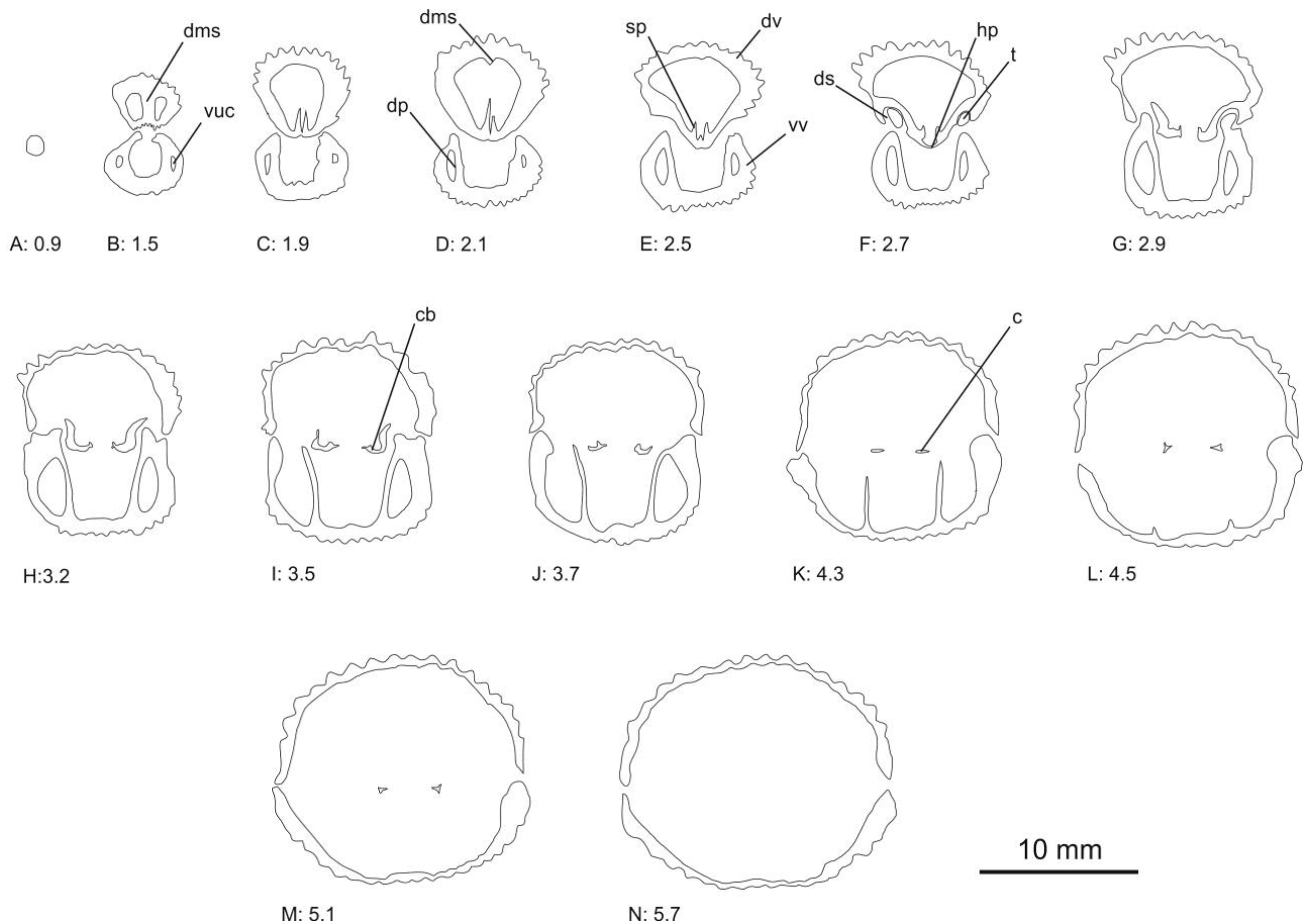


FIGURE 7. Drawings of grinding surfaces of serial sections perpendicular to commissural plane of articulated shell of *Daghanirhynchia rawyaensis* n. sp. 11 *Daghanirhynchia* sp. 1, (AMNH FI-86483). Numbers show section distance from apex in mm. All figures magnified (x2.0). c: crus, cb: crural base, dms: dorsal median septum, dp: dental plate, ds: dental socket, dv: dorsal valve, t: tooth, vuc: ventral umbonal cavity, vv: ventral valve.

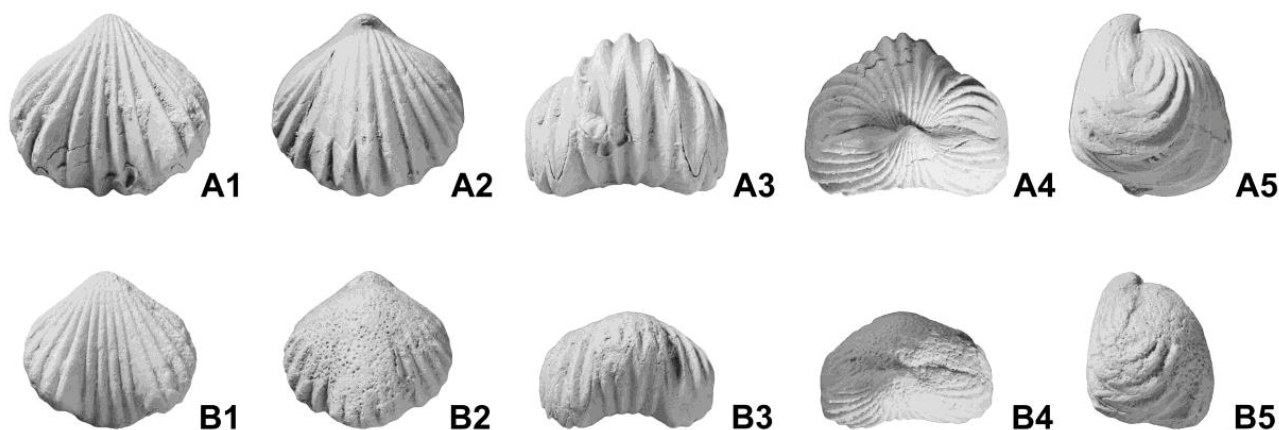


FIGURE 8. A. *Daghanirhynchia rawyaensis* n. sp. from Bed S-7, Mughanniyya Formation, Callovian, Tel el Dhahab section, Jordan. A) AMNH FI-86469 Holotype. B) AMNH FI-86470. 1) Ventral, 2) dorsal, 3) anterior, 4) posterior, and 5) lateral views of articulated shells. All figures of original size (x1.0).

Interior of ventral valve. Hardly any development of secondary shell material in the apical region. Ventral umbonal cavities small and narrow. Dental plates slightly divergent toward ventral valve floor, splitting away from floor just at hinge line, and leading into short, massive teeth rectangular in cross-section. Crenulation was not observed.

Interior of dorsal valve. Hardly any development of secondary shell material in the apical region. Dorsal median septum short and supporting hinge plates only at very posterior of apical cavity; it is preserved as a reduced ridge extending for about 1/4 of valve length in an anterior direction. Septalium lacking, septalial plates very short. Hinge plates broad, clearly separated, slightly inclined or arched ventrally and tapering anteriorly. Inner socket ridges low, well demarcated from hinge plates. Crural bases not well formed, leading into raduliform crura that extend about 1/5 of dorsal valve length almost protruding along commissural plane and only slightly incurved ventrally at distal ends. Crura arise from prolongations of hinge plate, relatively wide and somewhat similar to ciliform at preliminary parts in cross-section.

Stratigraphical and geographical occurrence. Bathonian to ?Oxfordian (Middle to ?lower Upper Jurassic); Yemen, Jordan, Saudi Arabia, Somalia, Ethiopia.

Discussion. *Daghanirhynchia daghaniensis* Muir-Wood, 1935 differs from all *Daghanirhynchia* taxa from Jordan in its larger shells and more numerous costae.

Daghanirhynchia susanae Feldman *et al.* (2012b) differs from *D. daghaniensis* in smaller shells, 5 ribs less on each valve, only 2 to 3 costae on fold and sulcus, less secondary shell material, parallel septalial plates, and long crura that are slightly curved ventrally.

Daghanirhynchia macfadyeni Muir-Wood, 1935 has almost the same number of costae, but less secondary shell material, a subtriangular outline, thin dental plates, a small and short septalium, and crura extending less distance in a ventral direction than in *D. daghaniensis*.

?*Daghanirhynchia triangulata* Cooper, 1989 has 1 to 3 less costae on each shell, less secondary shell material in the apical region, and a subtriangular outline. *Daghanirhynchia angulocostata* Cooper, 1989 has 3 to 5 less costae on each shell, a longer dorsal median septum and a small septalium.

A morphological comparison of *Daghanirhynchia* taxa from Jordan and the type species is given in Table 1.

***Daghanirhynchia macfadyeni* Muir-Wood, 1935**

Figs. 5E; 6F; 12

1935 *Daghanirhynchia macfadyeni* Muir-Wood, p. 88-89, pl. 8 figs. 7a-c.

2012b *Daghanirhynchia macfadyeni* – Feldman *et al.*, p. 199.

Holotype. Articulated shell housed in the NHM under the repository number NHM B85416; length 26.5mm, width 25.7mm, and thickness 21.4mm.

Type horizon and type locality. Bed 226, Daghani section, near Bihendula, Somalia (detailed description is given in Muir-Wood, 1935, table 2).

Material. 1 articulated shell (NHM B. 85416). Age: Callovian (upper Middle Jurassic). Locality: Daghani section, Somalia. 120 articulated shells. Age: Callovian (upper Middle Jurassic), beds Arda 21a, b, 23, 27, S-7, S-10.

Locality: Wadi Zarqa: AMNH FI-86503-86526, Strata: Callovian (upper Middle Jurassic), beds unknown. Locality: Wadi Zarqa: GSI M734, GSI M2974, GSI M4506 (2pcs.), GSI M4552 (2pcs), GSI M4557 (4pcs), GSI M4558.

Emended diagnosis. *Daghanirhynchia* with subtriangular shell outline, strongly dorsibiconvex with low median fold and broad shallow sulcus, ornamentation consists of 18 strong and angular costae, with 4 to 5 on fold and 3 to 4 in sulcus, and anterior commissure significantly thickened in adult specimens. After Muir-Wood (1935, 88).

Description. Shells medium to large, subtriangular and strongly dorsibiconvex. Ventral valve convex posteriorly, medially flattened. Slightly longer than wide with maximum

width at midlength. Apical angle is 94 degrees. Fold low, sulcus broad and shallow at anterior margin. Eighteen costae on each valve, 4 to 5 in fold, 3 to 4 on sulcus. Costae coarse, prominent angular and curved on flanks. Sulcus tongue broad and rectangular. Ventral umbo long and strongly incurved in adult specimens. Interareas narrow, flattened, and smooth. Anterior commissure deflected toward dorsal valve, whereas the lateral commissure is slightly curved. Beak ridges rounded.

Interior of ventral valve. Hardly any development of secondary shell material in the apical region. Umbonal cavities free. Ventral median septum lacking. Dental plates thin and parallel to each other, leading into coarse and knob-like teeth that are pointing in a dorsal direction. Denticular cavities rounded in cross-section.

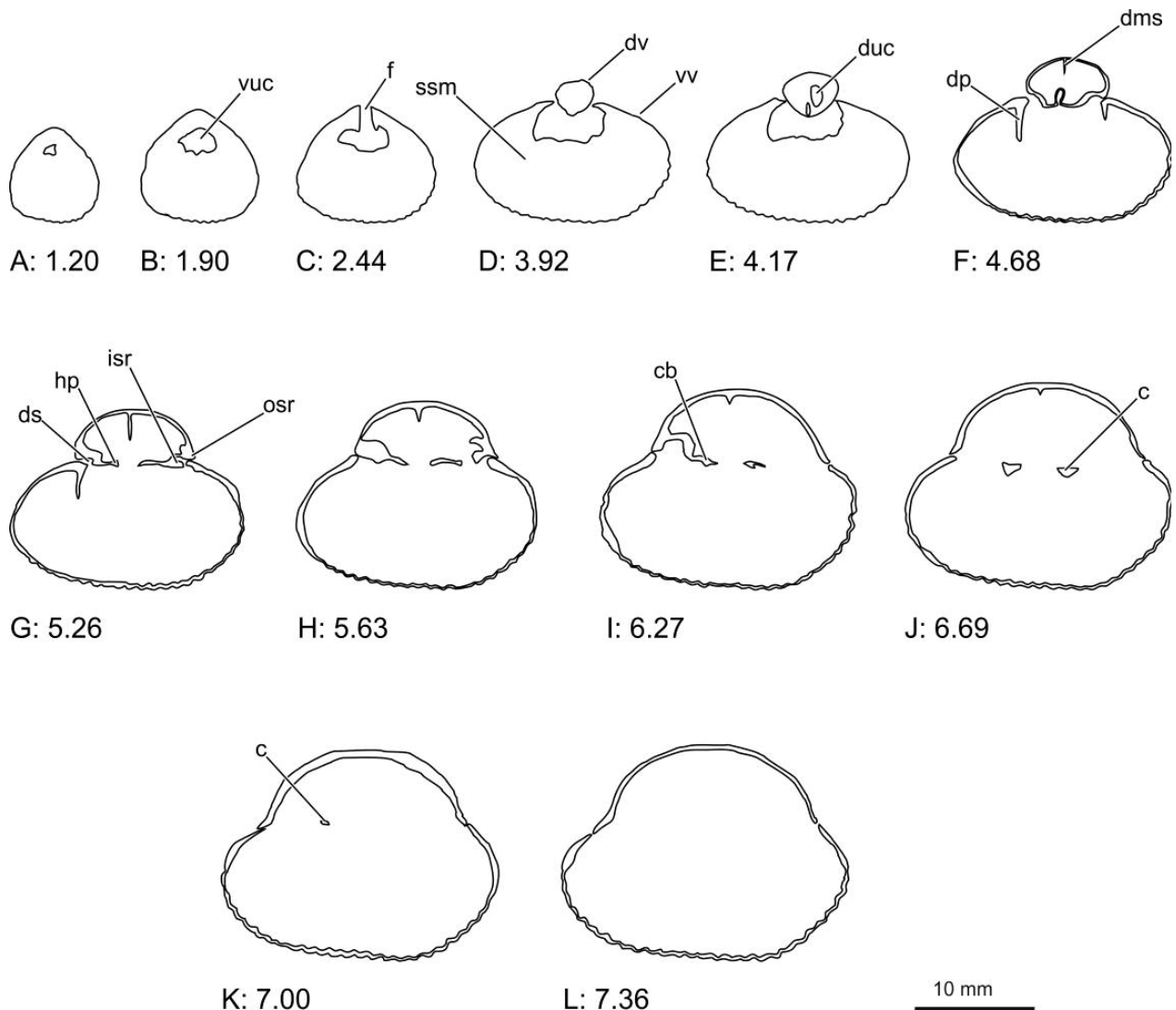


FIGURE 9. Drawings of grinding surfaces of serial sections perpendicular to commissural plane of articulated shell of *Daghanirhynchia jordanica* n. sp. [16*Daghanirhynchia* 5 costae] (AMNH FI-86484). Numbers show section distance from apex in mm. All figures magnified (x2.0). c: crus, cb: crural base, dms: dorsal median septum, dp: dental plate, ds: dental socket, dv: dorsal valve, hp: hinge plate, sp: septalial plate, t: tooth, vuc: ventral umbonal cavity, vv: ventral valve.

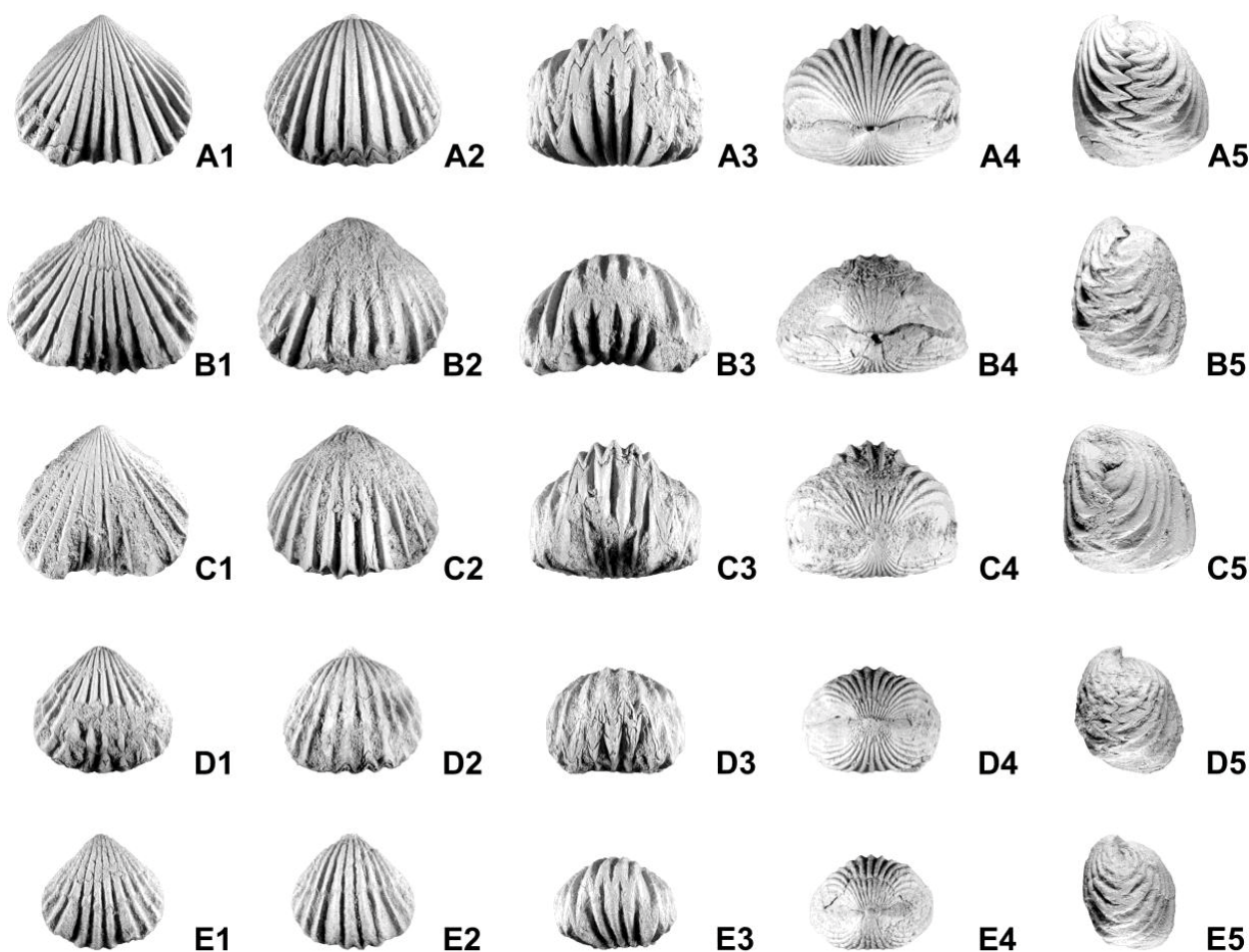


FIGURE 10. *Daghanirhynchia jordanica* n. sp. from Wadi Zarqa, Arda Section, Bed S-7, Mughanniyya Formation, Callovian (upper Middle Jurassic), Jordan. A) AMNH FI86469 (holotype). B) AMNH FI-86475. C) AMNH FI-86476. D) AMNH FI-86477. E) AMNH FI-86478. 1) Ventral, 2) dorsal, 3) anterior, 4) posterior, and 5) lateral views of articulated shells. All figures of original size (x1.0).

Interior of dorsal valve. Hardly any development of secondary shell material. Dorsal median septum short and thin. Septalium small and short, only developed in the posterior part of the shell with septalial plates that are oriented almost parallel to each other. Dental sockets rounded in cross-section. Inner socket ridges straight. Hinge plate very short, divided, and leading into short raduliform crura that do not extend far ventrally.

Stratigraphical and geographical occurrence. Callovian to Oxfordian (upper Middle to lower Upper Jurassic); Yemen, Jordan, Somalia.

Discussion. *Daghanirhynchia susanae* differs from *D. macfadyeni* in its smaller size, slightly greater development of secondary shell material, a subpentagonal outline, divergent dental plates, parallel septalial plates, and longer crura that are extending further in an anterior direction.

?*Daghanirhynchia triangulata* has 1 to 2 costae less on shells and on fold and sulcus and a narrower triangular outline than *D. macfadyeni*.

Daghanirhynchia angulocostata has two less costae than *D. macfadyeni*, a subpentagonal outline, and a longer dorsal median septum.

***Daghanirhynchia angulocostata* Cooper, 1989**

Fig. 6D

1989 *Daghanirhynchia angulocostata* Cooper, p. 26-27, figs. 13, 14, pl. 6 figs. 1-19, pl. 7 figs. 44-53, pl. 11 figs. 16-21.

Holotype. Articulated specimens housed in the USNM under the repository number USNM 380201a; length 25.0mm, width 29.9mm, and thickness 19.6mm.

Type horizon and type locality. S1145, Hisyan Member, Upper Dhurma Formation, Callovian; Jebel Balaidiyah, in outlier at Khashm Balaidiyah, Saudi Arabia (detailed description is given in Cooper, 1989, appendix 2).

Material. 6 specimens. USNM 380201a, USNM 380201b, USNM 380404a, USNM 380441, USNM 380498a, USNM 380520.

Diagnosis. As in Cooper (1989, 26).

Description. Shells large, wide, and subpentagonal in outline with maximum width shifted toward the anterior margin. Anterior margin broadly rounded, uniplicate. Apical angle is 99 degrees. Fourteen to 16 costae on each shell, 3 to 5 on sulcus and 4 to 6 on fold. Sulcus starts slightly posterior to midvalve and widens rapidly. Sulcal tongue moderately long. Flanks bounding the sulcus narrow and become flat to slightly convex. Dorsal valve fairly strongly convex, median region swollen. Fold starting slightly posterior of midvalve elevating moderately, slowly widening at the anterior margin. Ventral beak narrow and suberect. Foramen large and elliptically elongated. Deltoidal plates disjunct. Umbonal region slightly swollen.

Interior of ventral valve. Unknown.

Interior of dorsal valve. Septalium small. Dorsal median septum extends anteriorly about 1/3 of valve length. The remaining features have not been studied due to the paucity of material.

Stratigraphical and geographical occurrence. Bajocian to Callovian (Middle Jurassic) Saudi Arabia, Tel el Dhahab section, Bed S-10, Mughanniyya Formation, (Callovian), Jordan.

Discussion. *Daghanirhynchia angulocostata* differs from *D. susanae* in that it has 1 to 2 more costae on fold and sulcus and larger shells.

?*Daghanirhynchia triangulata* has 1 to 3 less costae on fold and sulcus and a subtriangular outline, whereas *D. angulocostata* is subpentagonal. Figs. 5B, 6C

2012b *Daghanirhynchia susanae* Feldman *et al.* p. 197-199, figs. 3C, 5.

Holotype. Articulated specimen housed at the AMNH under the repository number AMNH FI-72380; length 19.0mm, width 19.5mm, and thickness 15.4mm.

Type horizon and type locality. Bed S-7, Mughanniyya Formation, Callovian (upper Middle Jurassic), Wadi Zarqa, Arda Section, Jordan. (A detailed description is given in Feldman *et al.* (2012b) and herein.)

Material. 24 specimens. Tel el Dhahab section: AMNH FI-72380 (holotype), FI-72381- FI-72392 (bed s-7); GSI M731, GSI M 732, GSI M 741, GSI M 743, GSI M 4506, GSI M 4552, GSI M 4558 (all collected from the Tel el Dhahab section but beds not identified); Arda section: AMNH FI-72382, FI-72384, FI-72385, FI-72389.

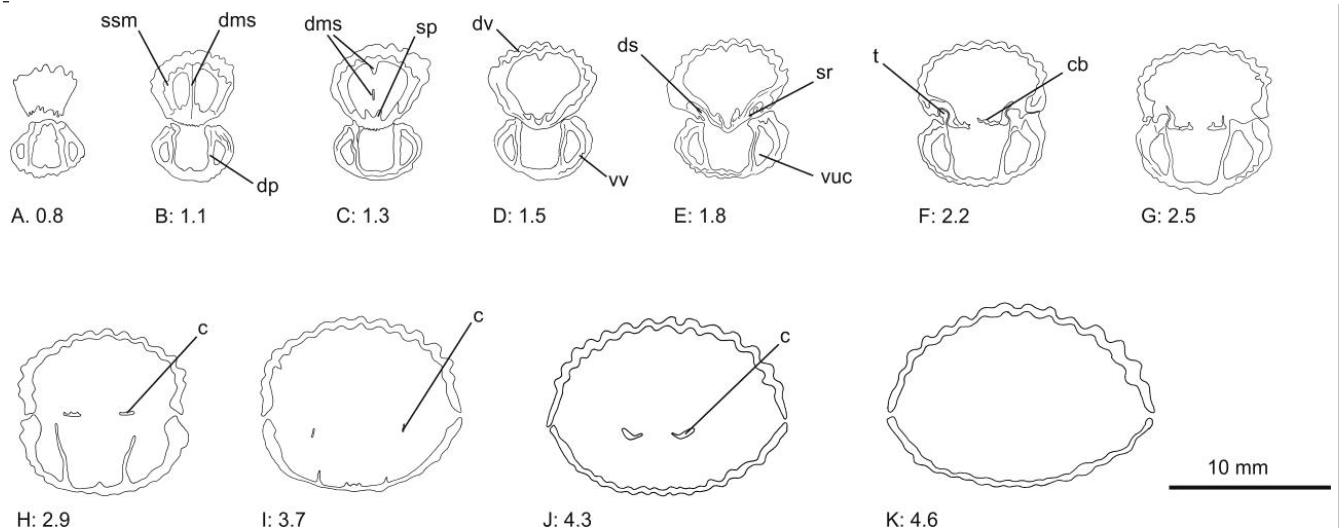


FIGURE 11. Drawings of grinding surfaces of serial sections perpendicular to commissural plane of articulated shell of *Daghanirhynchia susanae* Feldman *et al.* (2012b) (AMNH 72410). Numbers show section distance from apex in mm. All figures magnified (x2.0). c: crus, cb: crural base, dms: dorsal median septum, dp: dental plate, ds: dental socket, dv: dorsal valve, sp: septalial plate, sr: socket ridges, ssm: secondary shell material, t: tooth, vuc: ventral umbonal cavity, vv: ventral valve.

TABLE 1. Morphological comparison of *Daghanirhynchia* species from the Jordan Valley

	<i>D. rawyaensis</i> n. sp.	<i>D. jordanicana</i> n. sp.	<i>D. daghaniensis</i> Muir-Wood, 1935	<i>D. susanae</i> Feldman <i>et al.</i> , 2012b	<i>D. macfadyeni</i> Muir-Wood, 1935	? <i>D. triangulata</i> Cooper, 1989	<i>D. angulocostata</i> Cooper, 1989
size	medium	medium	medium to large	small to medium	medium to large	medium	medium
outline	subpentagonal	subpentagonal	subtriangular to subpentagonal	subpentagonal	subtriangular	subtriangular	subpentagonal
apical angle			95°		80°		
n° costae/shell	11 to 15	14 to 16	17 to 21	12 to 16	18	16 to 18	14 to 16
n° costae/sulcus	3 to 4	4 to 5	2 to 5	2 to 3	3 to 4	2 to 3	3 to 4
n° costae/fold	4 to 5	5	3 to 6	3	4 to 5	3 to 4	4 to 6
secondary shell material	moderate	hardly	moderate	few	hardly	?	?
dental plates	thick divergent	thin parallel	posteriorly thickened divergent	thick divergent	thin parallel	?	?
dorsal median septum	long thick	short blade-like	short fine	short fine	short fine	?	?
septalium	imbedded	weakly developed	imbedded	imbedded	small, short	?	small
septalial plates	imbedded	narrow parallel	short, almost parallel	parallel	almost parallel	?	?
crura	short gently curved ventrally	short gently curved ventrally	long in ventral direction strongly curved	long in anterior direction hardly curved	short in ventral direction strongly curved	?	?

Diagnosis. As in Feldman *et al.* (2012b, p. 198).

Description: Shells small to medium-sized, subpentagonal, dorsibiconvex with maximum width at about midlength. Apical angle is 96 degrees. Costae strong, angular, and coarse, numbering 12 to 16 on each shell, 2 to 3 in sulcus and 3 on fold. Fold and sulcus originating anterior to umbonal region of shell. Sulcus tongue high, mostly reaching to maximum curvature of dorsal valve, and with rounded to straight anterior margin. Ventral beak suberect to erect. Beak ridges rounded, strongly uniplicate anterior commissure, linguiform extension moderate, anterior margins end abruptly and a slightly stubby. Foramen small with disjunct deltidial plates.

Interior of ventral valve. Little development of secondary shell material, slightly filling the umbonal cavities. Ventral median septum lacking. Dental plates short and gently divergent leading into short and bulbous teeth that extend dorsally. Denticular cavities rounded and short.

Interior of dorsal valve. Little development of secondary shell material in apical region. Dorsal median septum short, but posteriorly imbedded into secondary shell material. Septalium imbedded or lacking, septalial plates parallel to each other. Dental sockets imbedded

into secondary shell material. Hinge plates horizontal and thick. Crura slightly curved ventrally but extending far anteriorly.

Stratigraphical and geographical occurrence. Mughanniyya and Hamam formations, Bathonian to Callovian (Middle Jurassic), Jordan.

Discussion. *Daghanirhynchia susanae* differs from ?*D. triangulata* in its smaller shell size, a subpentagonal outline and 2 to 4 less costae on the shell.

?*Daghanirhynchia triangulata* Cooper, 1989

Fig. 6E

1989 ?*Daghanirhynchia triangulata* Cooper, p. 28-29, pl. 7 figs. 6-21, pl. 11 figs. 12-16.

2012b *Daghanirhynchia? triangulata* Feldman *et al.* p. 199-200, fig. 3E.

Holotype. Articulated shell housed at the USNM under the repository number USNM 380246; length 23.7mm, width 20.6mm, thickness 20.0mm. Remark: The shell is laterally broken, and width gives the measurement of the actual fossil specimen and not of the reconstructed original width.

Type horizon and type locality. S1444, Hisyan Member, Upper Dhurma Formation, Callovian; Dhurma quadrangle, Saudi Arabia (detailed description is given in Cooper, 1989, appendix 2).

Material. 4 specimens. USNM 380246 (holotype), USNM 380198, USNM 380250a, USNM 380380.

Diagnosis. As in Cooper (1989: 28).

Description. Triangular shells anteriorly rounded and narrow with maximum width located at the anterior margin. Gently dorsibiconvex. Apical angle is acute. Lateral commissure straight, anterior commissure strongly uniplicate. Ventral valve slightly swollen medially. Sixteen to 18 costae on each shell, 2 to 3 on sulcus, 3 to 4 costae on fold. Sulcus originating in umbonal region occupying nearly half the width, depressed below flanks throughout, strongly so on anterior half. Fold narrow, moderately

elevated above flanks, and originating posterior to midvalve. Ventral beak fairly long and suberect. Foramen large. Deltoidal plates narrow and disjunct.

Interior of ventral and dorsal valve. Unknown due to paucity of material.

Stratigraphical and geographical occurrence. Middle and Upper Dhurma Formation, Bathonian to Callovian (Middle Jurassic); Saudi Arabia, Jordan.

CONCLUSIONS

Owing to their strongly dorsibiconvex shells, outline, number of costae, and form of sulcus tongue, taxa of *Daghanirhynchia* are easy to recognize. The three-dimensional reconstructions of the internal shell morphology confirm the species assignments and diversity.

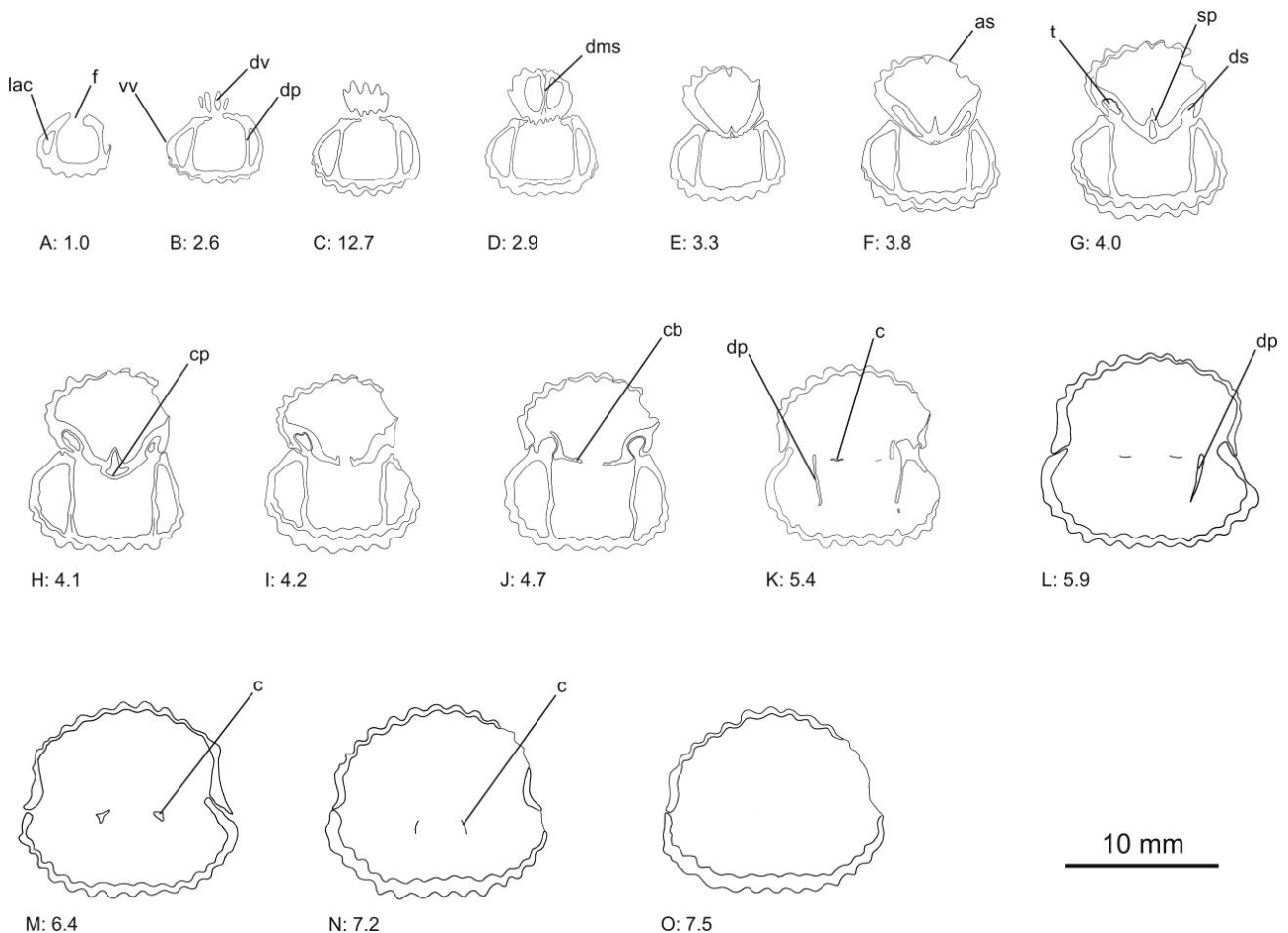


FIGURE 12. Drawings of grinding surfaces of serial sections perpendicular to commissural plane of articulated shell of *Daghanirhynchia macfadyeni* Muir-Wood, 1935 (unnumbered specimen). Numbers show section distance from apex in mm. All figures magnified (x2.0). As: abraded shell, c: crus, cb: crural base, dms: dorsal median septum, dp: dental plate, ds: dental socket, dv: dorsal valve, f: foramen, hp: hinge plate, s: septalium, t: tooth, vv: ventral valve, vuc: ventral umbonal cavity.

The comparison of the *Daghanirhynchia* fauna from Jordan with the *Daghanirhynchia* fauna from different regions within the Ethiopian Province indicate that the maximum diversity of this genus occurs in the center of the Province (today's Jordan, Saudi Arabia, and Somalia).

ACKNOWLEDGMENTS

We thank Jann Thompson, Mark Florence, and Daniel Levin (National Museum of Natural History/Smithsonian Institution, Washington DC, USA) and Lee Davies and Martin Munt (Natural History Museum, London, UK) for providing access to the brachiopod collection and literature. Many thanks are due to Tina Emmel, Michael Ricker, and Erika Scheller-Wagner (all Senckenberg Forschungsinstitut and Naturmuseum, Frankfurt am Main, Germany) for technical help. H.R.F. would like to acknowledge the Touro College Faculty Research Fund for supporting this project and thank the members of its peer review panel. This research received support from the SYNTHESYS Project <http://www.synthesys.info/>, which is financed by European Community Research Infrastructure Action under the FP6 'Structuring the European Research Area' Programme (GB-TAF-5141) and (DE-TAF-1111). The visit of M. S.-G. to the American Museum of Natural History, New York, was supported by a Lerner Grey Award. M.S.-G. thanks Russell Garwood (Manchester University, UK) and Mark Sutton (Imperial College, London, UK) for instructions, help, and endless patience in solving SPIERS problems related to German and Portuguese computer systems.

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Manuscript received May 2013;

revision accepted February 2014;

published Online February 2014.