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Late Cenomanian–Turonian (Cretaceous) ammonites from Wadi Qena, central Eastern Desert, Egypt: taxonomy, biostratigraphy and palaeobiogeographic implications

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ABSTRACT:

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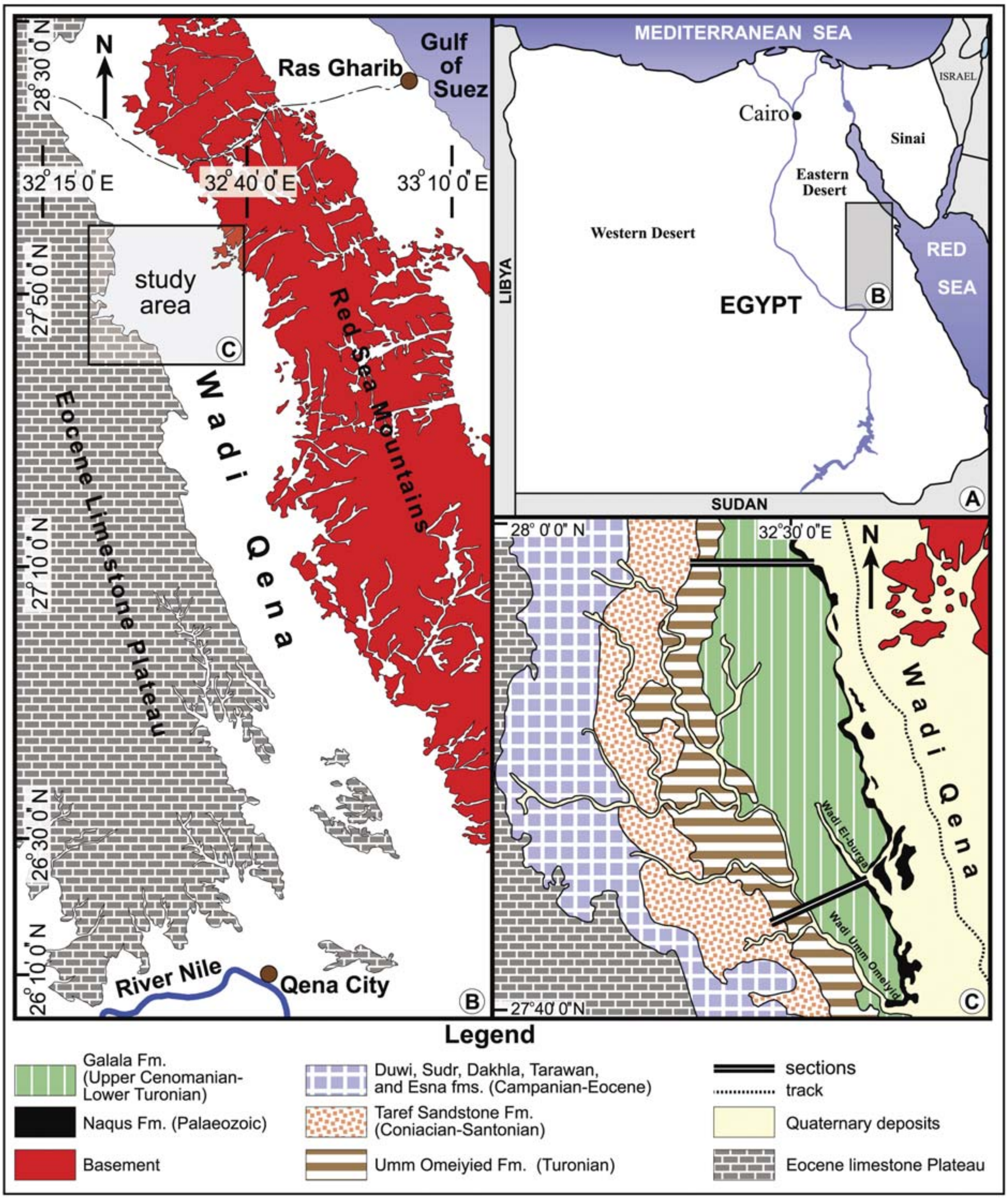
In Egypt, marine Upper Cenomanian–Turonian strata are well exposed in the Eastern Desert. The southernmost outcrops are located in the central part of Wadi Qena, where the lower Upper Cretaceous is represented by the fossiliferous Galala and Umm Omeiyid formations. From these strata, numerous ammonites have been collected bed-by-bed and 13 taxa have been identified, which are systematically described herein. Four of them (*Euomphaloceras costatum*, *Vascoceras globosum globosum*, *Thomasites gongilensis* and *Pseudotissotia nigeriensis*) are recorded from Egypt for the first time. The ammonite ranges are used for a biostratigraphic zonation of the lower Upper Cretaceous succession in the northern and central part of Wadi Qena: the Upper Cenomanian–Lower Turonian has been subdivided into five biozones (including a new upper Lower Turonian biozone based on the occurrence of *Pseudotissotia nigeriensis*), and one biozone has been recognized in the Upper Turonian. Palaeobiogeographically, the ammonite assemblage has a Tethyan character. During the Early Turonian, influences of the Vascoceratid Province were predominant with strong affinities to typical Nigerian faunas. This shows the significance of faunal exchange between Egypt and Central and West Africa via the Trans-Saharan Seaway. Compared to contemporaneous ammonoid faunas from the northern part of the Eastern Desert, Boreal influences are much less obvious in Wadi Qena. Thus, the present study greatly enhances the knowledge of the Late Cretaceous palaeobiogeography and biostratigraphy of Egypt and adjacent areas.

Key words: Upper Cretaceous; Ammonites; Systematic palaeontology; Biostratigraphy; Palaeobiogeography; Egypt.

INTRODUCTION

Marine lower Upper Cretaceous successions are well exposed in the northeastern part of Egypt (Sinai and Eastern Desert; Text-fig. 1). The southernmost exposures of Upper Cenomanian–Turonian sediments are preserved in the central part of the Eastern Desert in Wadi Qena, and ammonites are among the most important faunal elements in these strata. However, only three papers from the last century have dealt with this topic (Eck 1914; Douvillé 1928; Luger and Gröschke 1989). Therefore, this paper aims to enhance the knowledge of the taxonomy of the Late Cenomanian–Turonian ammonite fauna in Wadi Qena by means of a modern systematic approach and description of a large fauna of ammonites collected bed-by-bed from the Galala and Umm Omeiyid formations. In total, 90 ammonites have been collected during two field campaigns (April and June 2011) from two sections in Wadi Qena, forming the basis of the study. In addition, a detailed biostratigraphic framework is proposed for the succession based on the ranges of the ammonites. Finally, the palaeobiogeographic affinities of the ammonite assemblage are briefly discussed.



Text-fig. 1. Geographical and geological framework. A: map of Egypt with position of Wadi Qena (B); B map of Wadi Qena with position of study area (C); C: geological map of study area (modified after Conoco, 1987)

GEOLOGICAL SETTING

Wadi Qena is located in the central part of the Egyptian Eastern Desert (Text-fig. 1A, B). The main part of Wadi Qena is about 200 km long and runs from the southern slopes of the Southern Galala Plateau, near the Gulf of Suez, towards the south southeast. Near the town of Qena City it grades into the River Nile valley. Wadi Qena is bordered by the uniform, elevated and flat-topped Eocene limestone Plateau in the west and the serrated, varicoloured basement rocks of the Red Sea Mountains range in the east (Text-fig. 1B). Wadi Qena clearly developed along faults that run parallel to the Gulf of Suez and the Red Sea Mountains, which are well exposed at numerous places within the wadi, especially on the eastern side (Bandel *et al*. 1987). Sedimentary successions are well exposed on the western flank of the wadi while Quaternary alluvial fans predominate in the centre (Text-fig. 1C).

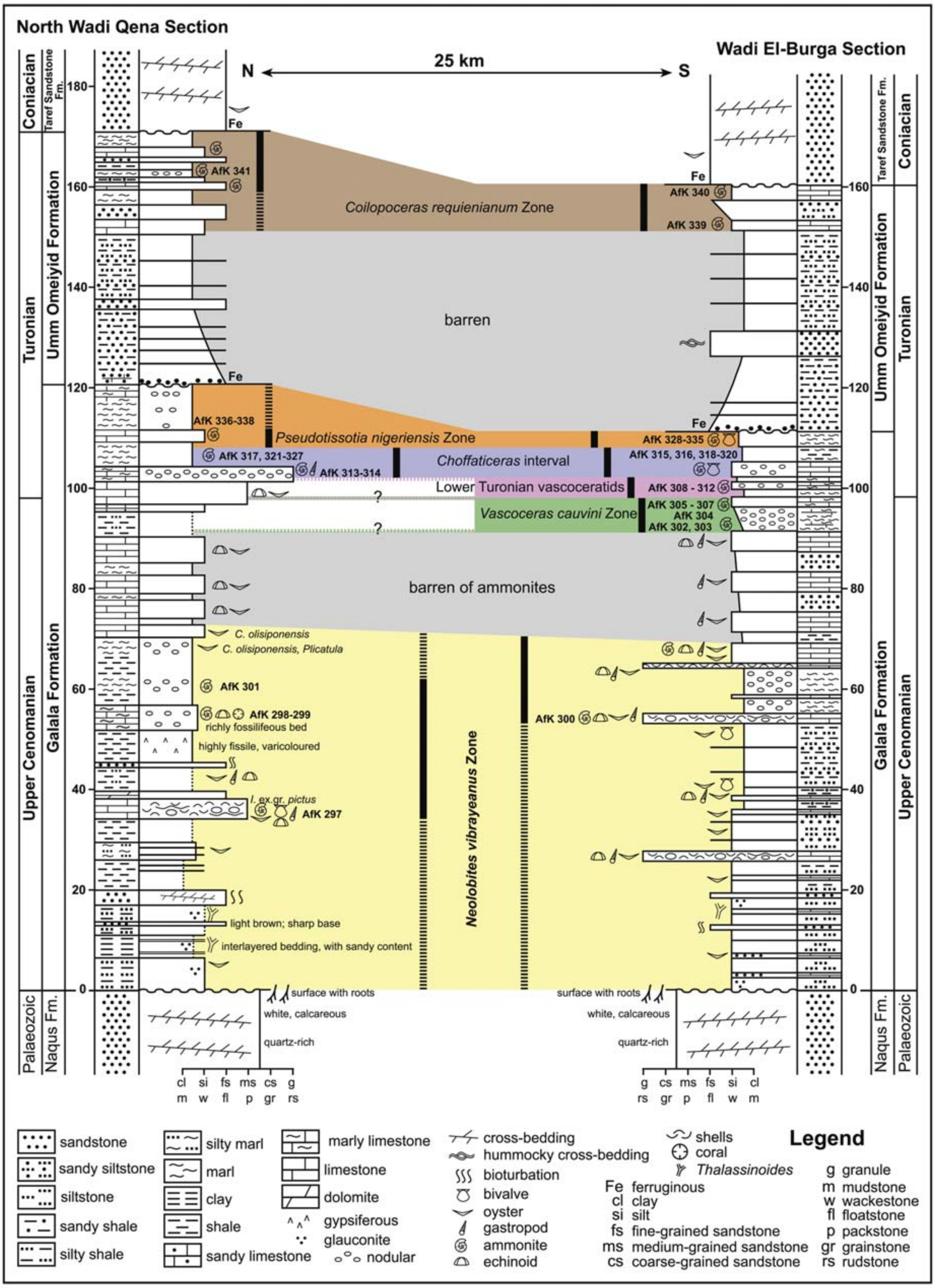
The sedimentary rocks of Wadi Qena range in age from Palaeozoic to Quaternary (Text-fig. 1C). Most of the Palaeozoic rocks are non-marine and well developed in the northern part of the wadi. The distribution of the Palaeozoic sediments was more or less controlled by older, pre-Cenomanian structural events (Said 1990; Issawi *et al*. 1999). The first marine transgression took place during the Late Cenomanian. This resulted in the deposition of shallow marine, mixed siliciclastic and carbonate sediments. During Late Cenomanian–Turonian times, the southern shoreline of the Tethyan seaway was situated immediately south of the study area. The marine transgression continued with some phases of regression during the later parts of the Late Cretaceous and Tertiary, leaving Coniacian–Eocene strata in the study area (see Text-fig. 1C).

SECTIONS

Two sections, located on the western margin in the northern part of Wadi Qena (Text-fig. 1C), have been measured bed-by-bed. One section, measured at N 27º 57` 57``, E 32º 30` 58``, is termed the north Wadi Qena section (Text-fig. 2). The other section, located 25 km south of the north Wadi Qena section, was measured at the mouth of Wadi El-Burga entering Wadi Qena at N 27º 44` 51``, E 32º 33` 55`` and is consequently termed the Wadi El-Burga section (Text-fig. 2).

The sedimentary succession starts with the Palaeozoic Naqus Formation (non-marine, kaolinitic, medium- to coarse-grained sandstones; see Abdallah *et al*. 1992 and Issawi *et al*. 1999) which, in places, overlies basement rocks unconformably. Along a truncated palaeosol, the Naqus Formation is overlain by the Galala Formation. The Galala Formation (Text-fig. 2) starts with silty, glauconitic sandstones rich in the trace fossil *Thalassinoides* isp. and fragmented mollusc shells, indicating shallow marine conditions. Higher up-section, shale beds are common (especially in the north), with a few sandy limestone and thin bioturbated sandstone intercalations. The lower part of the Galala Formation (35 m in the north and 25 m in the south) is terminated by a fossiliferous limestone bed, yielding a Late Cenomanian faunal assemblage including *Inoceramus* ex gr. *pictus* Sowerby (Nagm *et al.* 2011). The following interval consists of gypsiferous shale in the north and silty shale with thin sandstone interbeds in the south. It contains a highly fossiliferous limestone bed around the ~55-m-level (from the base of the Galala Formation) in both sections. This bed is characterized by a typical Late Cenomanian fauna represented by oysters [*Ceratostreon flabellatum* (Goldfuss), *Curvostrea rouvillei* (Coquand), *Ilymatogyra africana* (Lamarck)], nautiloids [*Angulithes mermeti* (Coquand)], ammonites [*Neolobites vibrayeanus* (d'Orbigny)] and echinoids (*Hemiaster cubicus* Desor) indicating a fully marine, lagoonal environment (cf. Nagm 2009; Wilmsen and Nagm 2012). Marls with calcareous nodules are common in the following part, which ends at a sharp and more or less irregular surface at 70 m and 64 m respectively in the two sections. The upper part of the Galala Formation (50 m in the north and 45 m in the south) is characterized by a high carbonate content and consists of thick limestone beds intercalating with marl containing calcareous nodules and/or sandy siltstone (in the south). These sediments are highly fossiliferous, containing abundant latest Cenomanian and Early Turonian ammonites (most of the studied specimens have been collected from this interval). The Galala Formation is truncated along a prominent unconformity at the base of the Umm Omeiyid Formation. This unconformity has also been recognized in Wadi Araba and placed in the Lower–Middle Turonian boundary interval (Nagm *et al*. 2010a, b). The thickness of the Galala Formation is about 120 m in the North Wadi Qena section and about 112 m in the Wadi El-Burga section.

The Umm Omeiyid Formation overlies the Galala Formation unconformably, attaining a thickness of about 50 m in both sections. It consists of unfossiliferous fissile siltstone with thin, medium-grained, in part hummocky cross-stratified sandstone intercalations. The upper part of the formation is also characterized by siliciclastic facies, but additionally contains a few fossiliferous limestone beds and/or marl inter-



Text-fig. 2. Graphic logs of the North Wadi Qena and Wadi El-Burga sections with stratigraphic distribution of the zonal ammonite markers. The dashed lines represent inferred ranges of taxa depending on other stratigraphic data. For location see Text-fig. 1C calations. The calcareous layers yield abundant early Late Turonian ammonites [*Coilopoceras requienianum* (d'Orbigny)]. The Umm Omeiyid Formation is overlain by the Coniacian Taref Sandstone Formation along a sharp, ferruginous surface.

SYSTEMATIC PALAEONTOLOGY

Repositories of specimens: 90 specimens (mostly composite internal moulds) form the basis of the study. Illustrated material is kept in the Museum für Mineralogie und Geologie (MMG) of the Senckenberg Naturhistorische Sammlungen Dresden (SNSD), Germany (repository AfK). Additional specimens are housed in the Department of Geology, Al-Azhar University, Egypt (repository AUEN).

Dimensions: All linear dimensions, taken with a Vernier Caliper, are given in millimetres. The abbreviations that are used in the present work are: maximum diameter (D), whorl breadth (Wb), whorl height (Wh), breadth of umbilicus (U). Figures in parentheses are dimensions as a percentage of diameters.

Suture terminology: The suture terminology follows Wedekind (1916) as applied by Kullman and Wiedmann (1970) and revised in parts by Korn *et al*. (2003): E=external lobe, A=adventive lobe (=lateral lobe, L, of former nomenclature), U=umbilical lobe, I=internal lobe.

Systematics: The ammonites studied are arranged systematically according to Wright *et al*. (1996). The terminology used for the description of the taxa follows the glossary in the Treatise on Invertebrate Paleontology, Part L, Mollusca 4 (Wright *et al*., 1996). In order to keep this article as short as possible, the synonymy lists only contain a few selected references which are important for the discussion.

Order Ammonoidea von Zittel, 1884
Suborder Ammonitina Hyatt, 1889
Superfamily Hoplitoidea Douvillé, 1890
? Family Engonoceratidae Hyatt, 1900
Genus *Neolobites* Fischer, 1882

TYPE SPECIES: *Ammonites vibrayeanus* d'Orbigny, 1841; by original designation.

Neolobites vibrayeanus (d'Orbigny, 1841)
(Text-figs 3, 6A)

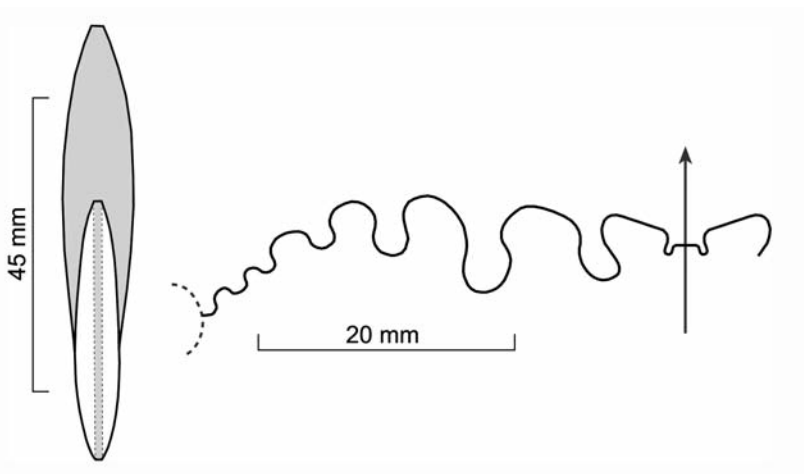
1841. *Ammonites vibrayeanus* d'Orbigny, 322, pl. 96, figs 1–3.
1981. *Neolobites vibrayeanus* (d'Orbigny); Kennedy and Juignet, 23, figs 3–4, 6a; text-fig. 5.
1989. *Neolobites vibrayeanus* (d'Orbigny); Luger and Gröschke, 366, pl. 39, fig. 3, text-fig. 5.
2005. *Neolobites vibrayeanus* (d'Orbigny); Wiese and Schulze, 933, figs 4–9. [with synonymy]
2010a. *Neolobites vibrayeanus* (d'Orbigny); Nagm *et al*., 475, figs 4, 5A–F.

MATERIAL: Twenty specimens (AfK 297–301, AUEN 1–15) from three different levels in the middle part of the Galala Formation in both sections (Text-fig. 2).

MEASUREMENTS:

Specimen	D	Wb	Wh	Wb/Wh	U
AfK 298	86.4 (100)	20.6 (23.8)	51.0 (59.0)	0.40	8.1 (9.3)
AfK 299	92.9 (100)	20.2 (21.7)	51.7 (55.6)	0.39	8.8 (9.4)
AfK 300	57.3 (100)	16.1 (28.0)	33.7 (58.8)	0.47	4.9 (8.5)
AfK 301	72.5 (100)	18.3 (25.2)	46.9 (64.6)	0.39	4.4 (6.0)

DESCRIPTION: Most of the specimens are fully septate internal moulds with very involute coiling. The



Text-fig. 3. Whorl section and suture line of *Neolobites vibrayeanus* (d'Orbigny, 1841), Upper Cenomanian of the Galala Formation, specimen AfK 301 small umbilicus, comprising about 6% of the diameter, is shallow, with low and rounded umbilical walls. The flanks are slightly convex with a narrow and flat venter. The whorl section (Text-fig. 3) is highly compressed, elevated, and has a lanceolate shape with greatest breadth around mid-flank. The suture lines (Text-fig. 3) are poorly preserved and characterized by broad saddles with somewhat narrower and lanceolate lobes that become shallower towards the umbilicus. The ornamental features are also poorly preserved except for some delicate clavi at the ventrolateral margin (e.g., Text-fig. 6A4–5).

REMARKS: Despite the imperfect preservation, the specimens collected from the Galala Formation of Wadi Qena can be assigned to *N. vibrayeanus* without any doubt. *Neolobites* includes several species and many morphological variants, the differences between which have been discussed by Kennedy and Juignet (1981) and Wiese and Schulze (2005). Most, if not all, *Neolobites* specimens that have been recorded from Egypt are representatives of one species, i.e., *N. vibrayeanus*. The morphological variation in the Egyptian material (presence or absence of very weak ribs and ventrolateral clavi) is related to different taphonomic conditions (for more details on *N. vibrayeanus* from Egypt see Nagm *et al*. 2010a).

OCCURRENCE: *Neolobites vibrayeanus* is a widespread and characteristic early Late Cenomanian species, occurring in France, Spain, Portugal, Morocco, Algeria, Tunisia, Egypt, Israel, Lebanon, Syria, Saudi Arabia, Oman, Niger, Bolivia, Colombia, Peru and Venezuela. According to Wiese and Schulze (2005), the species preferred shallow-water environments in subtropical/tropical areas. In the study area, *N. vibrayeanus* characterizes the lower Upper Cenomanian *Neolobites vibrayeanus* Zone, which is (as defined by Nagm *et al*. 2010b) equivalent to the Cenomanian standard ammonite Zone of *Calycoceras* (*Proeucalycoceras*) *guerangeri* (cf. Kennedy 1984; Wright *et al*. in Wright and Kennedy 1984; Hancock 1991).

Superfamily Acanthoceratoidea de Grossouvre, 1894
Family Acanthoceratidae de Grossouvre, 1894
Subfamily Euomphaloceratinae Cooper, 1978
Genus *Euomphaloceras* Spath, 1923

TYPE SPECIES: *Ammonites euomphalus* Sharpe, 1855; by monotypy.

Euomphaloceras costatum Cobban, Hook and Kennedy, 1989
(Text-figs 4, 6B)

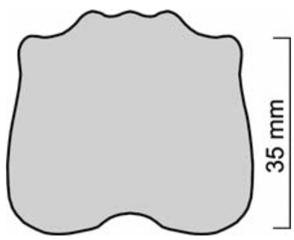
1989. *Euomphaloceras costatum* Cobban, Hook and Kennedy, 37, figs 37, 77S–EE, 78A–H.
2005. *Euomphaloceras costatum* Cobban, Hook and Kennedy; Gale *et al*.

MATERIAL: Three specimens (AfK 305–307) from the upper part of the Galala Formation (97 m above the base) at the Wadi El-Burga section (Text-fig. 2).

MEASUREMENTS:

Specimen	D	Wb	Wh	Wb/Wh	U
AfK 306	64.8 (100)	32.3 (49.8)	25.7 (39.6)	1.25	23.8 (36.7)

DESCRIPTION: The coiling is evolute, with a large umbilicus and rounded umbilical walls. The whorl section (Text-fig. 4) is quadratic, with the greatest breadth at the umbilical tubercles. Flanks are narrow, flattened and ribbed, with strong umbilical and ventrolateral tubercles occurring on all main ribs. The venter is broad and slightly convex, showing a weak ridge at the site of the siphuncle, and carries three rows of blunt tubercles (the middle one on the siphonal ridge). The suture line is poorly preserved.



Text-fig. 4. Whorl section of *Euomphaloceras costatum* Cobban, Hook and Kennedy, 1989, Upper Cenomanian of the Galala Formation, specimen AfK 305

REMARKS: The specimens described herein are very close to the holotype as described by Cobban *et al*. (1989). They differ in their less dense ribbing. In spite of their imperfect preservation, they are assigned to *E. costatum* without reservation.

OCCURRENCE: Upper Cenomanian of New Mexico (USA), southern England and Brazil. In the study area, the species has been collected from the upper part of the *Vascoceras cauvini* Zone, which is (as defined by Nagm *et al*. 2010b) equivalent to the *Neocardioceras juddii* Zone, in the standard ammonite zonation (Kennedy 1984; Wright *et al*. in Wright and Kennedy 1984; Hancock 1991). This is the first record of *E. costatum* from Egypt, which confirms the temporal equivalence of the *V. cauvini* Zone to the *N. juddii* Zone (see below).

Genus *Pseudaspidoceras* Hyatt, 1903

TYPE SPECIES: *Ammonites footeanus* Stoliczka, 1864; by original designation.

Pseudaspidoceras sp.
(Text-figs 5, 6C)

MATERIAL: One specimen (AfK 304) from the upper part of the Galala Formation (95 m above the base) at the Wadi El-Burga section (Text-fig. 2).

MEASUREMENTS:

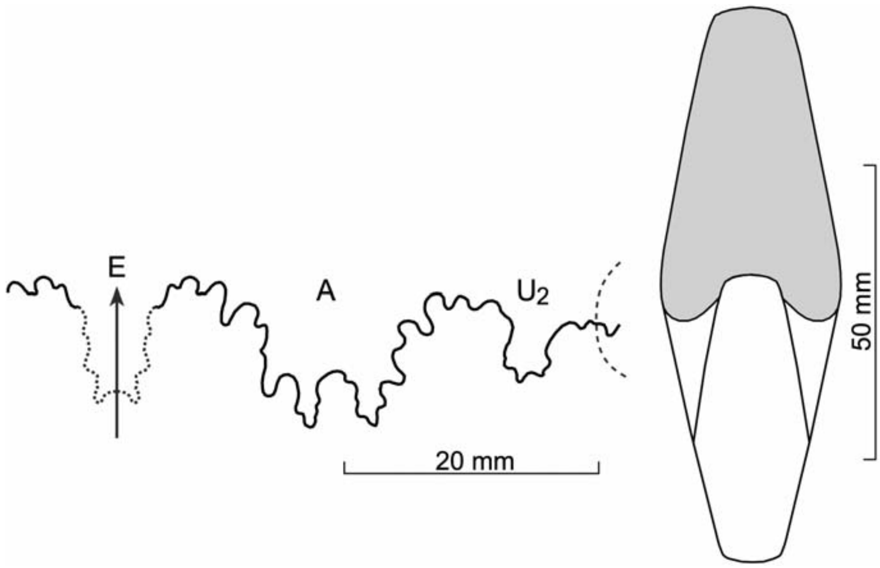
Specimen	D	Wb	Wh	Wb/Wh	U
AfK 304	95.0 (100)	36.9 (38.8)	53.5 (56.3)	0.68	29.3 (30.8)

DESCRIPTION: The coiling is moderately evolute, with a large umbilicus (ca. 30%). The whorl section (Text-fig. 5) is trapezoidal, with the strongest inflation at the umbilical shoulders. From the umbilical shoulders, the flanks converge towards a feebly convex venter with narrowly rounded ventrolateral shoulders. The ornamentation consists of distant, rounded and sometimes branched ribs carrying umbilical bullae. Each rib ends at the ventrolateral shoulder with a strong tubercle. Ribbing weakens towards the outer whorl. The suture line (Text-fig. 5) is well preserved and characterized by a broad adventive lobe.

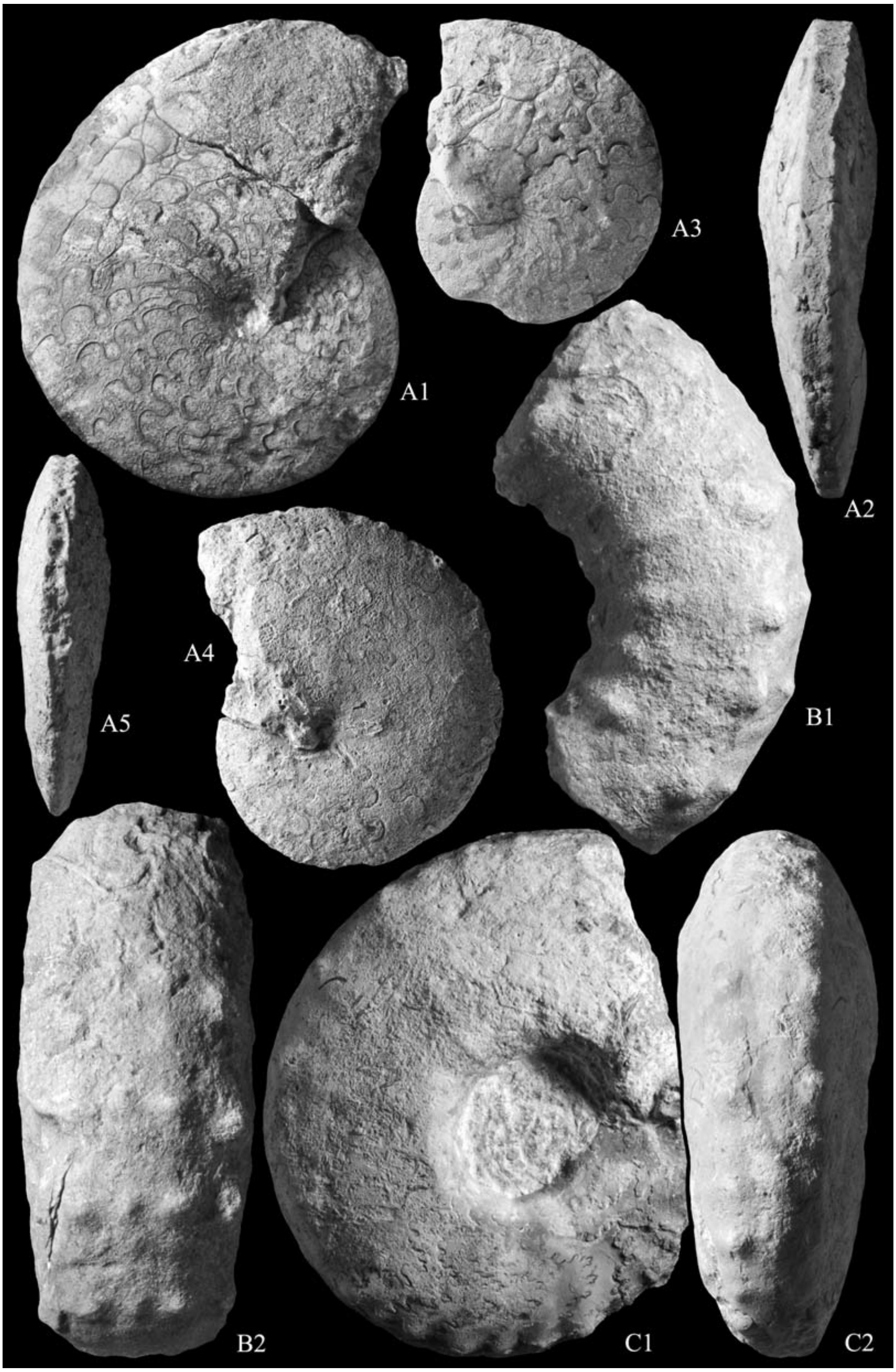
REMARKS: This well preserved specimen has all the diagnostic characters of the genus *Pseudaspidoceras*. However, it is difficult to identify at the specific level because of the inadequate match of its morphological characters with those of known species of the genus. In fact, there are only two species that come close to the present specimen, i.e., *P. conciliatum* Stoliczka var. *ampakabensis* Collignon (1965, p. 36, fig. 1669) and *P. pseudonodosoides* Choffat (1898, p. 65, pl. 16, figs 5–8; pl. 22, figs 32–33). However, *P. conciliatum* Stoliczka var. *ampakabensis* differs from our specimen in a slightly concave venter and highly indented sutures; furthermore, it is known from the Lower Turonian whereas the specimen from Wadi Qena was collected from uppermost Cenomanian strata. In stratigraphic position, *P. pseudonodosoides* matches our specimen, but it differs morphologically in its depressed whorl section with a very broadly rounded venter. The Wadi Qena specimen possibly represents a new species of the genus *Pseudaspidoceras*, but this conclusion cannot be based on a single specimen.

OCCURRENCE: The specimen was collected from the upper Galala Formation at the Wadi El-Burga section, 2 m above the level with *Vascoceras cauvini* and 2 m below the level with *Euomphaloceras costatum*. Therefore, its stratigraphic position is equivalent to the upper Upper Cenomanian *Neocardioceras juddii* standard ammonite Zone (*sensu* Wright *et al*. in Wright and Kennedy 1984).

Family Vascoceratidae Douvillé, 1912
Genus *Vascoceras* Choffat, 1898



Text-fig. 5. Suture line and whorl section of *Pseudaspidoceras* sp., Upper Cenomanian of the Galala Formation, specimen AfK 304



Text-fig. 6. **A** – *Neolobites vibrayeanus* (d'Orbigny, 1841) (A1, A2 – lateral and ventral views of AfK 298, ×1; A3 – lateral view of AfK 300, ×1; A4, A5 – lateral and ventral views of AfK 301, ×1). **B** – *Euomphaloceras costatum* Cobban, Hook and Kennedy, 1989 (B1, B2 – lateral and ventral views of AfK 305, ×1). **C** – *Pseudaspidoceras* sp. (C1, C2 – lateral and ventral views of AfK 304, ×1). All specimens from the Upper Cenomanian of the Galala Formation

TYPE SPECIES: *Vascoceras gamai* Choffat, 1898; by the subsequent designation of Diener, 1925.

Vascoceras cauvini Chudeau, 1909
(Text-figs 7, 9A)

1909. *Vascoceras cauvini* Chudeau, 67, pl. 1, figs 1a, 2a; pl. 2, figs 3, 5; pl. 3, figs 1b, 2b, 4.
1969. *Paravascoceras cauvini* (Chudeau); Freund and Raab, 20, pl. 3, figs 1–3; text-fig. 5a, b.
1989. *Vascoceras cauvini* Chudeau; Luger and Gröschke, 374, pl. 40, figs 3, 6, 8, 9; pl. 41, figs 1–4; pl. 42, fig. 1; text-figs 6g,h, 8c.
2010a. *Vascoceras cauvini* Chudeau; Nagm *et al*., 483, figs 9A–B, 10B.

MATERIAL: Two specimens (AfK 302, 303) from the upper part of the Galala Formation (93 m above the base) at the Wadi El-Burga section (Text-fig. 2).

MEASUREMENTS:

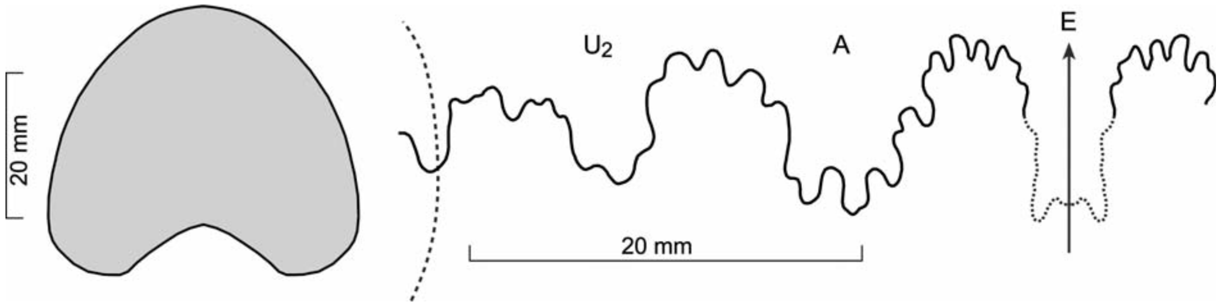
Specimen	D	Wb	Wh	Wb/Wh	U
AfK 302	96.3 (100)	41.3 (42.8)	36.1 (37.4)	1.14	33.4 (34.6)
AfK 303	98.0 (100)	34.3 (35.0)	41.5 (42.3)	0.82	37.1 (37.8)

DESCRIPTION: Both specimens are fragmentary internal moulds with relatively evolute coiling as well as a deep and wide umbilicus (ca. 35%). The umbilical shoulders are feebly rounded with vertical walls. Flanks are short and convex with a broadly rounded to nearly flat venter (in the latter case, faintly defined ventrolateral shoulders are present). The whorl section is compressed to slightly depressed (Text-fig. 7, specimen AfK 302). The ornamentation is not preserved in specimen AfK 302 (Text-fig. 9A3–4), while very weak, shallow ribs, especially towards the venter, occur in specimen AfK 303 (Text-fig. 9A1–2, a fragment of a body chamber). The suture line, characterized by a deep external lobe and a wide, deep adventive lobe, is clearly visible in specimen AfK 302 (see Text-fig. 7).

REMARKS: In *Vascoceras cauvini* two forms are known (see Chudeau 1909); i.e. the smooth form (e.g. Luger and Gröschke 1989; Zaborski 1996; Aly *et al*. 2008; Barroso-Barcenilla and Goy 2010; Nagm *et al*. 2010a); and the ribbed form (e.g., Freund and Raab 1969; Zaborski 1990, 1996; Meister *et al*. 1992). Two different forms also occur in the study area: specimen AfK 302 is a typical representative of the smooth form (Text-fig. 9A3–4) while specimen AfK 303 (Text-fig. 9A1–2) shares characters of both the smooth and ribbed forms in terms of dimensions and suture line. On the other hand, it has its own characters, i.e., a flat venter and the absence of the pronounced ornamentation typical of the ribbed form (very weak, shallow ribs occur only at the venter). Therefore, this specimen is considered here as a transitional morph between the smooth and ribbed form of *V. cauvini*.

Vascoceras pioti (Peron and Fourtau, 1904; in Fourtau, 1904) likewise has a flat venter, but its umbilicus is very small and the suture is different: the lobes of *V. cauvini* are deeper and wider than those of *V. pioti*, especially the A-lobe (Text-fig. 7). In addition, the suture line of *V. cauvini* has three saddles, while that of *V. pioti* has four (see Freund and Raab 1969, p. 30, text-fig. 6f). The sutures of *V. cauvini* from Wadi Qena (Text-fig. 7) are identical to sutures in the type material as illustrated by Chudeau (1909). Furthermore, *V. pioti* is from a higher stratigraphic level, coming from the Lower Turonian.

OCCURRENCE: *Vascoceras cauvini* is widely known from the Upper Cenomanian of Nigeria, Niger, Angola, Morocco, Algeria, Egypt, Israel, Spain and Peru. In the study area, *Vascoceras cauvini* characterizes the uppermost Cenomanian *Vascoceras cauvini* Zone, which is (cf. Nagm *et al*. 2010b) equivalent to the *Neocardioceras juddii* Zone in the standard ammonite zonation of Kennedy (1984), Wright *et al*. in Wright and Kennedy (1984) and Hancock (1991).



Text-fig. 7. Whorl section and suture line of *Vascoceras cauvini* Chudeau, 1905, Upper Cenomanian of the Galala Formation, specimen AfK 302

Vascoceras globosum globosum (Reyment, 1954)
(Text-figs 8, 9B)

1954. *Pachyvascoceras globosum* Reyment, 259, pl. 3, fig. 3; pl. 5, fig. 4; text-figs 3e, 7.
1957. *Vascoceras globosum globosum* (Reyment); Barber, 21, pl. 7, figs 1a, b; pl. 9, figs 4a, b; pl. 28, figs 1, 2.
2005. *Vascoceras globosum globosum* (Reyment); Gale *et al*., 182, fig. 9.

MATERIAL: A single specimen (AfK 308) from the upper part of the Galala Formation (102 m above the base) at the Wadi El-Burga section (Text-fig. 2).

MEASUREMENTS:

Specimen	D	Wb	Wh	Wb/Wh	U
AfK 308	80.3 (100)	69.2 (86.1)	41.5 (51.6)	1.66	10.1 (12.5)

DESCRIPTION: The specimen is a completely smooth, globose, very involute phragmocone with a maximum preserved diameter of 80.3 mm. The umbilicus is small (12.5% of diameter) and very deep, with a narrowly rounded umbilical shoulder. The flanks are short and strongly convex, grading without ventrolateral shoulders into a broadly rounded venter. The whorl section (Text-fig. 8) is depressed and globose, with a whorl-breadth to whorl-height ratio of 1.66. The suture line is well preserved and illustrated in Text-fig. 8.

REMARKS: Barber (1957) erected five subspecies of *Vascoceras globosum* based on variations in the degree of inflation. Of those subspecies, *V. globosum globosum* is the most inflated. The specimen from Wadi Qena is strongly depressed and globose in shape, with a small and deep umbilicus. These characters are diagnostic of *Vascoceras globosum globosum* as described and illustrated by Barber (1957) and Zaborski (1996).

OCCURRENCE: Uppermost Cenomanian of Nigeria and Lower Turonian of Brazil. In the study area, it has been recorded from the Lower Turonian, i.e., the lower part of the *Choffaticeras* spp. Zone. This zone is (as defined by Nagm *et al*. 2010b) equivalent to the upper part of the standard ammonite Zone of *Watinoceras coloradoense* (Kennedy 1984; Wright *et al*. in Wright and Kennedy 1984) or *Watinoceras* spp. (Hancock 1991). This is the first record of *Vascoceras globosum globosum* from Egypt.

Vascoceras kossmati Choffat, 1898
(Text-figs 9C, 10, 13A)

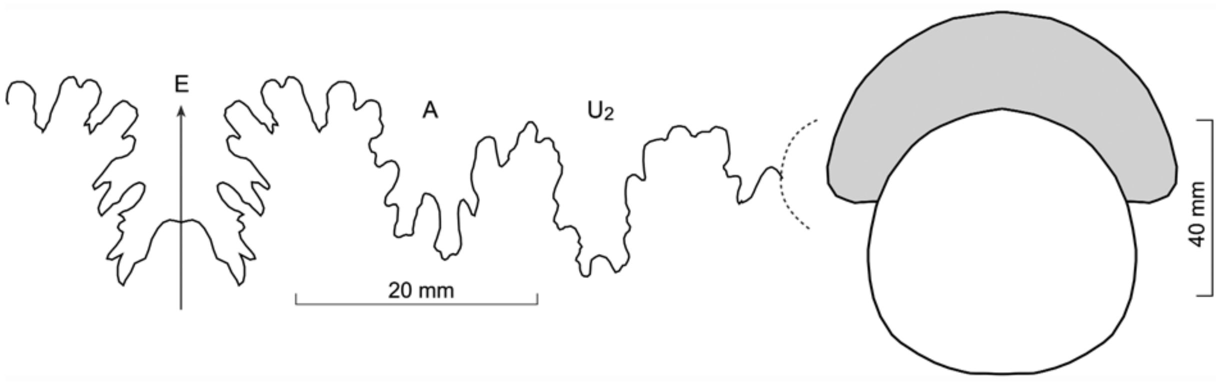
1898. *Vascoceras kossmati* Choffat, 63, pl. 13, figs 8, 9; pl. 14, figs 1, 2; pl. 21, figs 26, 27.
1992. *Paravascoceras kossmati* (Choffat); Thomel, 225, pl. 119, figs 2, 3.
2010. *Vascoceras kossmati* Choffat; Barroso-Barcenilla and Goy, 219, pl. 5, figs F–H; text-fig. 6B. [with synonymy].

MATERIAL: Four specimens (AfK 309–312) from the upper part of the Galala Formation (102 m above the base) at the Wadi El-Burga section (Text-fig. 2).

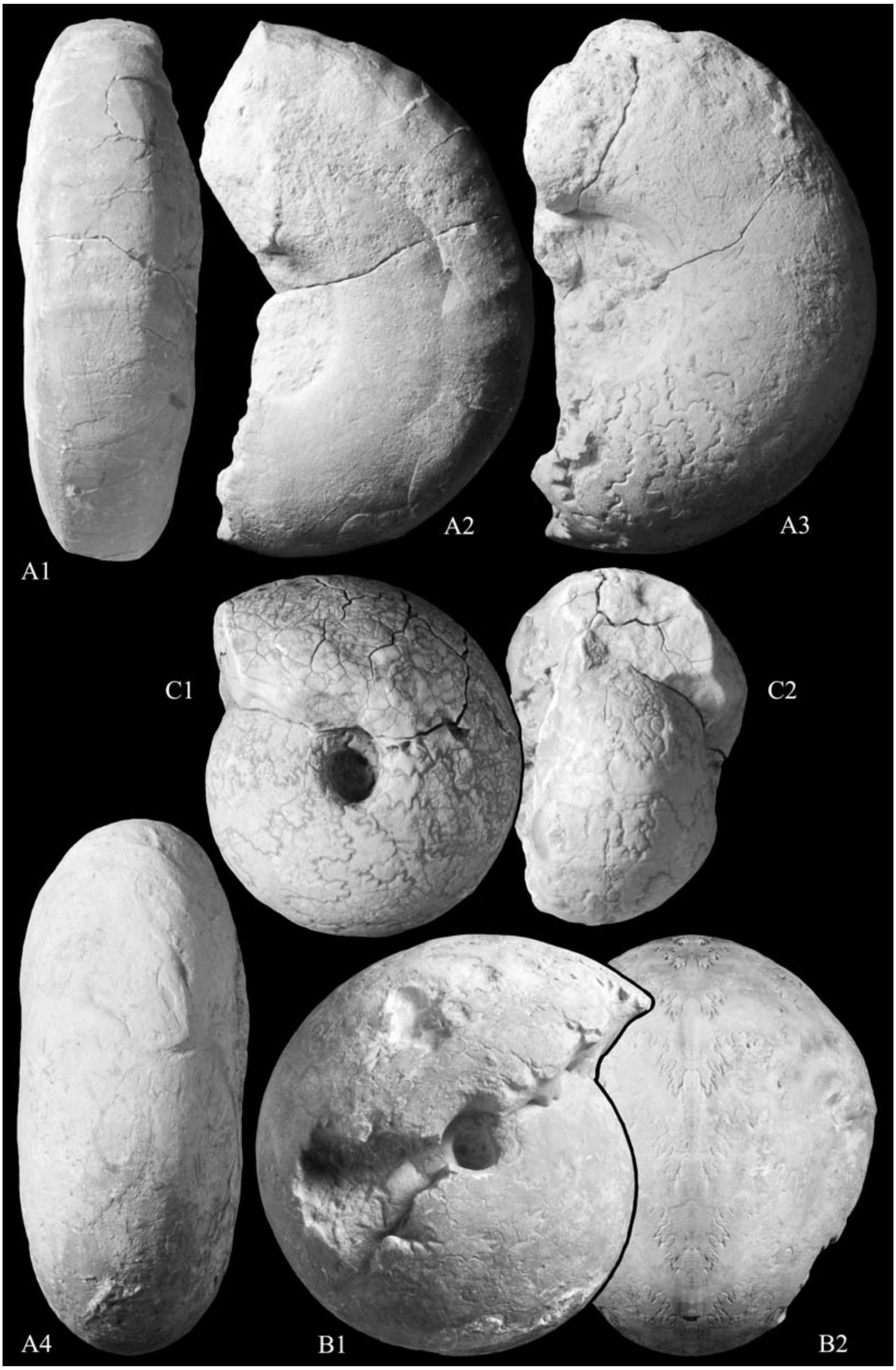
MEASUREMENTS:

Specimen	D	Wb	Wh	Wb/Wh	U
AfK 309	65.5 (100)	48.0 (73.2)	30.2 (46.1)	1.58	13.2 (20.1)
AfK 310	52.5 (100)	39.6 (75.4)	27.4 (52.1)	1.44	9.0 (17.1)
AfK 311	59.9 (100)	46.4 (77.4)	33.0 (55.0)	1.40	7.8 (13.0
AfK 312	66.4 (100)	45.6 (68.6)	35.2 (53.0)	1.29	9.1 (13.7)

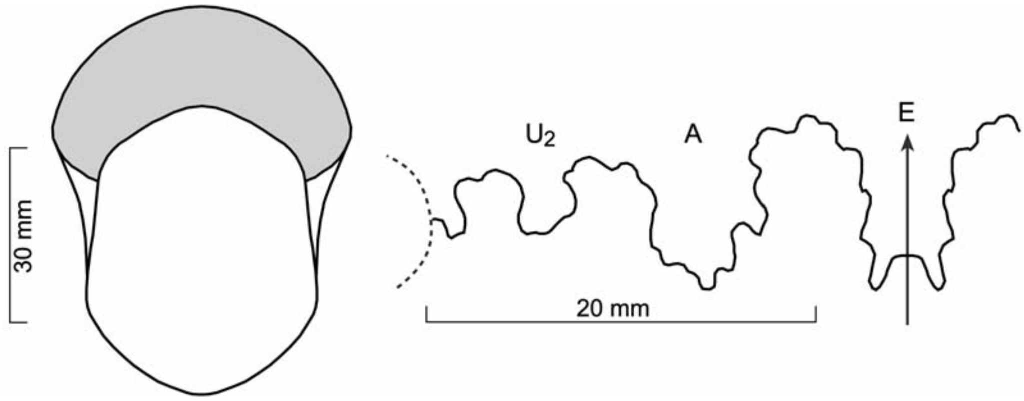
DESCRIPTION: All specimens are smooth internal moulds characterized by strongly involute coiling. The umbilicus is narrow and deep, showing vertical walls and sharp margins. The flanks are strongly convex, grading into a broadly rounded venter. Some specimens (AfK 311, 312) have wide and flat venters that are clearly separated from the flanks by ventrolateral shoulders (Text-fig. 13A2). The whorl section (Text-fig. 10) is depressed, with an incipiently triangular



Text-fig. 8. Whorl section and suture line of *Vascoceras globosum globosum* (Reyment, 1954), Lower Turonian of the Galala Formation, specimen AfK 308



Text-fig. 9. **A** – *Vascoceras cauvini* Chudeau, 1909 (A1, A2 – ventral and lateral views of AfK 303, ×1; A3, A4 – lateral and ventral views of AfK 302, ×1; Upper Cenomanian of the Galala Formation). **B** – *Vascoceras globosum globosum* (Reyment, 1954) (B1, B2 – lateral and ventral views of AfK 308, ×1; Lower Turonian of the Galala Formation). **C** – *Vascoceras kossmati* Choffat, 1898 (C1, C2 – lateral and apertural views of AfK 309, ×1; Lower Turonian of the Galala Formation)



Text-fig. 10. Whorl section and suture line of *Vascoceras kossmati* Choffat, 1898, Lower Turonian of the Galala Formation, specimen AfK 309

shape. The suture line (Text-fig. 10) is simple and characterized by a wide and deep adventive lobe.

REMARKS: Barroso-Barcenilla and Goy (2010) discussed the similarities between *Vascoceras kossmati* and *Vascoceras hartti* (Hyatt). They regarded the subspherical shape, the small umbilical width and the depressed whorl section as the key characters of *V. kossmati*. The material from Wadi Qena is very close to the Spanish material, and we thus assign it to Choffat's species without hesitation.

OCCURRENCE: Lower Turonian of Portugal, Spain and France (see Barroso-Barcenilla and Goy 2010). Eck (1914) noted the species from Egypt without illustration. Therefore, this is the first properly documented record from Egypt. In the study area, it occurs in the Lower Turonian, in the lower part of the *Choffaticeras* spp. Zone, the equivalent of the upper part of the standard ammonite Zone of *Watinoceras coloradoense* (Kennedy 1984; Wright *et al*. in Wright and Kennedy 1984) or *Watinoceras* spp. (Hancock 1991) (see Nagm *et al*. 2010b for further details).

Genus *Neoptychites* Kossmat, 1895

TYPE SPECIES: *Ammonites telinga* Stoliczka, 1865; by the subsequent designation of Solger 1904 (= *Ammonites cephalotus* Courtiller 1860).

Neoptychites cephalotus (Courtiller, 1860)
(Text-figs 11, 13B)

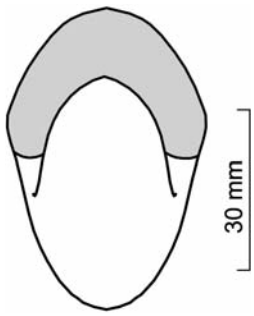
1860. *Ammonites cephalotus* Courtiller, 248, pl. 2, figs 1–4.
1907. *Neoptychites cephalotus* (Courtiller); Pervinquière, 393, pl. 27, figs 1–4, text-fig. 152.
1994. *Neoptychites cephalotus* (Courtiller); Chancellor *et al*., 70, pl. 16, figs 1–9; pl. 17, figs 1–5; pl. 18, figs 1–3; pl. 26, figs 2–4. [with synonymy]
2008. *Neoptychites cephalotus* (Courtiller); Kennedy *et al*., 159, pl. 3, figs 6–8; pl. 6, figs 1–5.
2010a. *Neoptychites cephalotus* (Courtiller); Nagm *et al*., 489, figs 11G–H, 12A–B, 13A–B.

MATERIAL: Three specimens (AfK 313, AUEN 16–17) from the upper part of the Galala Formation at the north Wadi Qena section, co-occurring with *Choffaticeras segne* (Text-fig. 2).

MEASUREMENTS:

Specimen	D	Wb	Wh	Wb/Wh	U
AfK 313	63.3 (100)	42.9 (67.7)	32.9 (51.9)	1.30	5.1 (8.0)

DESCRIPTION: All three specimens are characterized by very involute coiling with a small and shallow umbilicus (U ~8% of the diameter). The greatest whorl breadth is situated shortly above the umbilical shoulder. Whorls are generally depressed, with a subtrigonal section (Text-fig. 11). The flanks are strongly convex, converging to a rounded venter. Ornamentation and suture line are not seen due to the poor preservation.



Text-fig. 11. Whorl section of *Neoptychites cephalotus* (Courtiller, 1860), Lower Turonian of the Galala Formation, specimen AfK 313

REMARKS: Large collections of *Neoptychites cephalotus* have been described from Tunisia (Pervinquière 1907; Chancellor *et al*. 1994), France (Kennedy and Wright 1979), and New Mexico, USA (Cobban and Hook 1983). The last authors demonstrated a wide range of intraspecific variation and dimorphism in the species. This variation has also been documented in Egyptian material by Nagm *et al*. (2010a). The present material falls within the range of variation described in the literature; it is close to the Tunisian material (Chancellor *et al*. 1994) and material described recently from Morocco (Kennedy *et al*. 2008).

OCCURRENCE: Known from France, northern Spain, Morocco, Algeria, Tunisia, Egypt, Israel, Syria, Jordan, Cameroon, Madagascar, southern India, Colorado, New Mexico (USA), northern Mexico, Trinidad, Venezuela, Colombia, Brazil, Niger and Nigeria. In the study area, this species co-occurs with *Choffaticeras segne* and *Thomasites rollandi* which are dominant in the Lower Turonian of Egypt (Nagm *et al*. 2010a, b). It ranges into the basal Middle Turonian *Collignoniceras woollgari* Zone (Kennedy *et al*. 2008).

Family Pseudotissotiidae Hyatt, 1903
Subfamily Pseudotissotiinae Hyatt, 1903
Genus *Thomasites* Pervinquière, 1907

TYPE SPECIES: *Pachydiscus rollandi* Thomas and Peron, 1889; by subsequent designation of Diener, 1925.

Thomasites gongilensis (Woods, 1911)
(Text-figs 12, 13C)

1911. *Vascoceras gongilensis* Woods, 282, pl. 21, fig. 7; pl. 22, fig. 1.
1981. *Thomasites gongilensis* (Woods); Wright and Kennedy, 100, pl. 24, fig. 1; pl. 25, fig. 1; including varieties *tectiformis* Barber 1957, and *lautus* Barber 1957. [with full synonymy]
1989. *Thomasites gongilensis* (Woods); Meister, 38, pl. 16, figs 3–5; pl. 17, figs 1–6; pl. 18, figs 1–3; pl. 19, figs 1–5; pl. 20, figs 1–5; pl. 21, figs 1–3.
2003. *Thomasites gongilensis* (Woods); Kennedy *et al*., 12, pl. 5, figs 1–3.

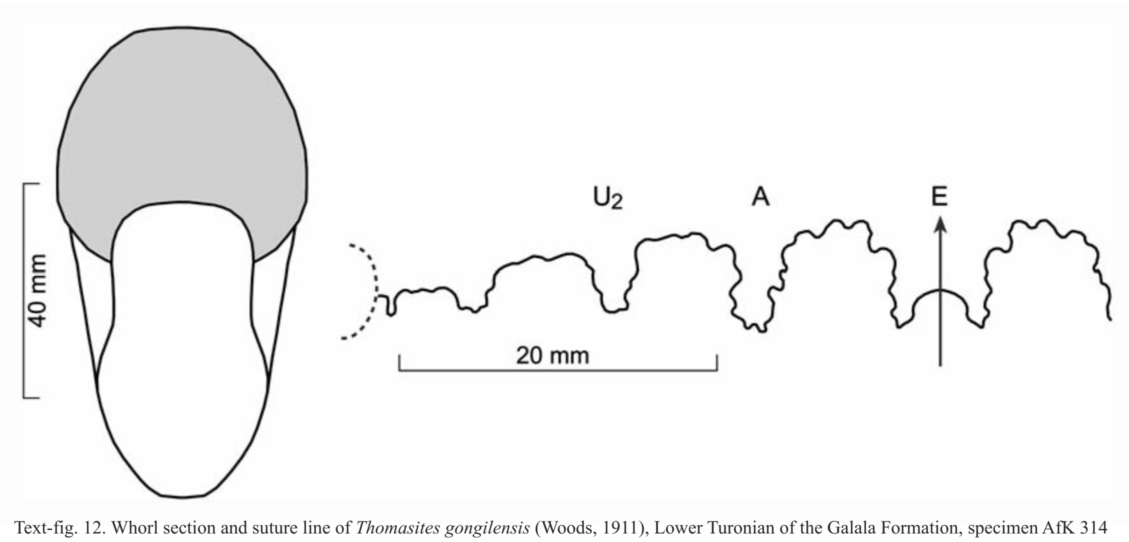
MATERIAL: One specimen (AfK 314) from the upper part of the Galala Formation at the north Wadi Qena section, co-occuring with *Choffaticeras segne* (Text-fig. 2).

MEASUREMENTS:

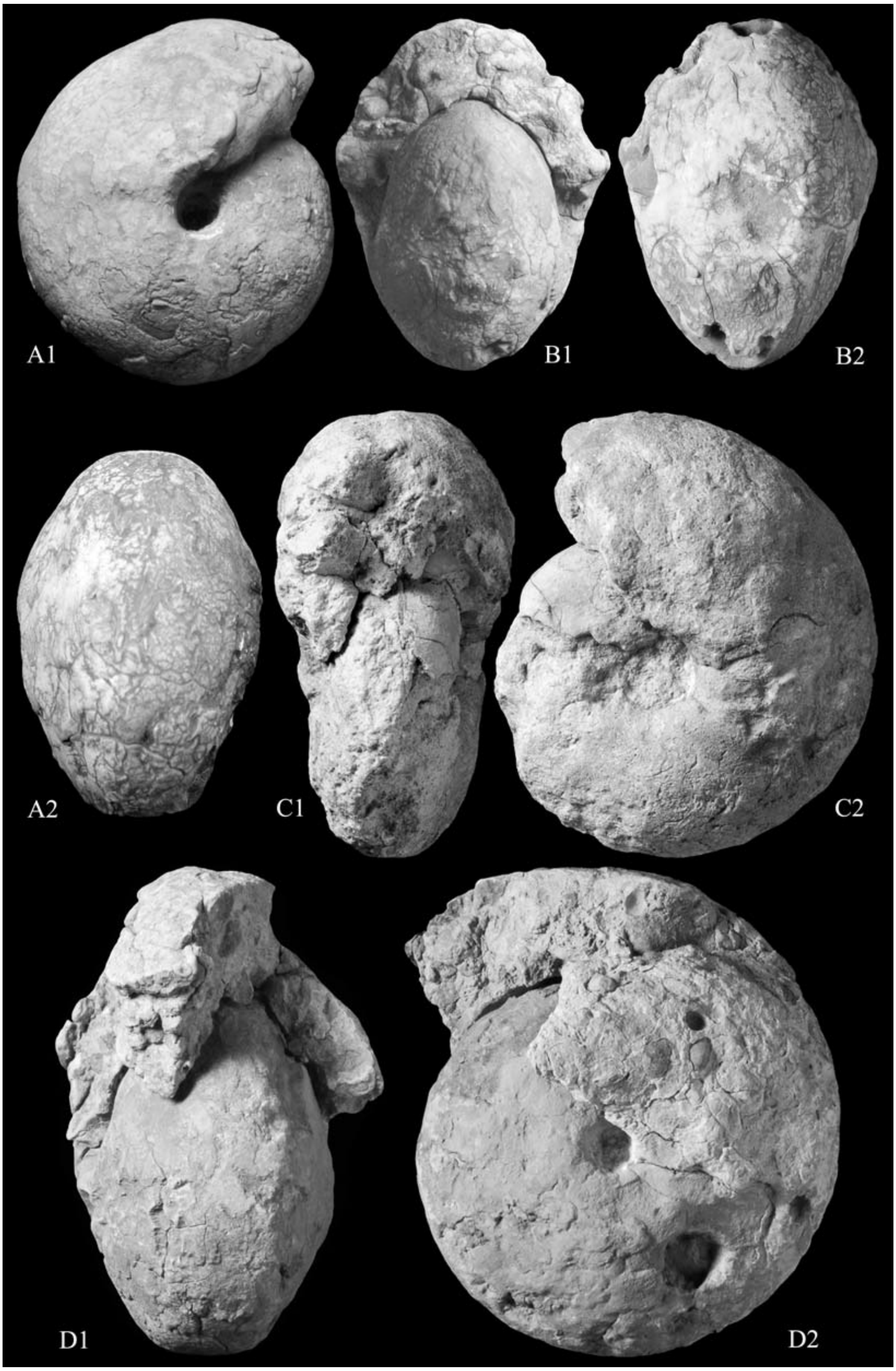
Specimen	D	Wb	Wh	Wb/Wh	U
AfK 314	81.8 (100)	42.3 (51.7)	43.5 (53.1)	0.97	19.3 (23.5)

DESCRIPTION: The specimen has a preserved diameter of ~82 mm and a moderately wide, deep umbilicus with broadly rounded umbilical shoulders. The whorl section (Text-fig. 12) is only slightly compressed (Wb/Wh = 0.97), with the greatest width at the umbilical shoulders. The flanks are convex, ending at rounded ventrolateral shoulders. The venter is fairly broad and flat. The suture line (Text-fig. 12) shows narrow lobes and broad, weakly incised saddles. Ornamental features are not preserved.

REMARKS: Wright and Kennedy (1981) revised the genus *Thomasites* and discussed the relationship of the present species to other species referred to the genus. West African faunas of *T. gongilensis* (e.g.,



Text-fig. 12. Whorl section and suture line of *Thomasites gongilensis* (Woods, 1911), Lower Turonian of the Galala Formation, specimen AfK 314



Text-fig. 13. **A** – *Vascoceras kossmati* Choffat, 1898 (A1, A2 – lateral and ventral views of AfK 311, ×1). **B** – *Neoptychites cephalotus* (Courtiller, 1860) (B1, B2 – apertural and ventral views of AfK 313, ×1). **C** – *Thomasites gongilensis* (Woods, 1911) (C1, C2 – apertural and lateral views of AfK 314, ×1). **D** – *Thomasites rollandi* (Thomas and Peron, 1889) (D1, D2 – apertural and lateral views of AfK 316, ×1). All specimens from the Lower Turonian of the Galala Formation

Barber 1957) have been compared with Tunisian material of *T. rollandi* by Chancellor *et al*. (1994). They noted that *T. gongilensis* rarely shows coarse umbilical tubercles (in contrast to juveniles of *T. rollandi)*, and generally has a less inflated, less triangular whorl section as well as a simpler suture line. The present specimen of *T. gongilensis* differs from *T. rollandi* in a wider umbilicus and a simple suture. The Sinai specimen of *T. gongilensis* of El-Hedeny (2002, fig. 4d, e) most probably represents *Vascoceras cauvini*.

OCCURRENCE: *Thomasites gongilensis* (Woods 1911) is common in the Lower Turonian of West Africa. Kennedy *et al.* (2003) recorded it from the Upper Cenomanian of France. In the study area, it has been recorded from the Lower Turonian *Choffaticeras* spp. Zone, which is (see Nagm *et al.* 2010b) equivalent to the upper part of the standard ammonite Zone of *Watinoceras coloradoense* (Kennedy 1984; Wright *et al.* in Wright and Kennedy 1984) or *Watinoceras* spp. (Hancock 1991). This is the first unequivocal record of *T. gongilensis* from Egypt.

Thomasites rollandi (Thomas and Peron, 1889)
(Text-figs 13D, 14, 16A)

1889. *Pachydiscus Rollandi* Thomas and Peron, 25, pl. 17, figs 1–3.
1994. *Thomasites rollandi* (Thomas and Peron); Chancellor *et al*., 75, pl. 19, figs 1–2; pl. 20, figs 1–12; pl. 21, figs 1–9; pl. 22, figs 1–6; pl. 23, figs 1–9; text-fig. 14a–f. [with synonymy]
2010a. *Thomasites rollandi* (Thomas and Peron); Nagm *et al*., 493, figs 13E–G, 14A–D, 15A–D.

MATERIAL: Seven specimens (AfK 315, 316; AUEN 18–22) from the upper part of the Galala Formation at the Wadi El-Burga section, co-occuring with *Choffaticeras segne* (Text-fig. 2).

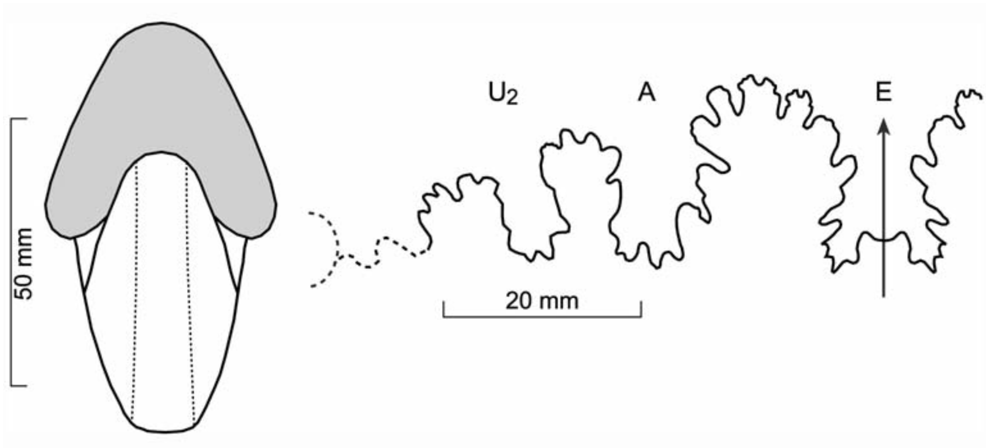
MEASUREMENTS:

Specimen	D	Wb	Wh	Wb/Wh	U
AfK 315	88.7 (100)	47.1 (53.1)	50.2 (56.5)	0.93	10.3 (11.6)
AfK 316	88.9 (100)	49.6 (55.7)	51.1 (57.4)	0.97	9.3 (10.4)

DESCRIPTION: The incompletely preserved internal moulds are smooth and characterized by involute coiling (U ~10% of diameter). The umbilical wall is high, subvertical and ends at narrowly rounded umbilical shoulders. The greatest whorl breadth is at the umbilical shoulder. The flanks are generally weakly convex and converge strongly to a narrowly rounded venter. The whorl section is compressed to slightly depressed and shows a trigonal (Text-fig. 14) to ovoidal shape (specimen AfK 316; Text-fig. 13D). The suture line (Text-fig. 14) is characterized by four saddles, the one between the external and adventive lobes being high, broad and strongly incised.

REMARKS: *Thomasites rollandi* has been extensively revised by Chancellor *et al*. (1994). They clarified the range of its intraspecific variation and discussed its relationship to other species of the genus. Into synonymy of *Th. rollandi* they put numerous varieties and species of Pervinquière (1907) and Douvillé (1928). The preservation of the specimens studied is not good but they clearly belong to *T. rollandi*, especially specimen AfK 316 (Text-fig. 13D), which is very close to the holotype as re-figured in Chancellor *et al*. (1994, pl. 19).

OCCURRENCE: The species is well known from



Text-fig. 14. Whorl section and suture line of *Thomasites rollandi* (Thomas and Peron, 1889), Lower Turonian of the Galala Formation, specimen AfK 315 the Lower Turonian of Morocco, Tunisia, Algeria, Egypt, Israel, Jordan, Syria, Lebanon, France and Spain. It may also occur in England, Colombia and Tadzhikistan (Chancellor *et al*. 1994). In the study area, *T. rollandi* co-occurs with Lower Turonian *Choffaticeras segne*, the range of which equates to the upper part of the *Watinoceras coloradoense* Zone of Kennedy (1984) and Wright *et al*. in Wright and Kennedy (1984) (see Nagm *et al*. 2010b for details).

Genus *Pseudotissotia* Peron, 1897

TYPE SPECIES: *Ammonites galliennei* d'Orbigny, 1850; by subsequent designation of Pervinquière, 1907.

Pseudotissotia nigeriensis (Woods, 1911)
(Text-figs 15, 16B)

1911. *Hoplitoides nigeriensis* Woods, 284, pl. 23, fig. 3; pl. 24, fig. 15; text-fig. 1.
1989. »*Pseudotissotia*« *nigeriensis* (Woods); Meister, 44, pl. 21, figs 4–6; pl. 22, figs 1–4; pl. 23, figs 1–5; pl. 24, fig. 1; pl. 25, figs 1–7; pl. 26, figs 1–3; pl. 27, figs 1–3.
2005. *Pseudotissotia nigeriensis* (Woods); Gale *et al*., 186, figs 10D–E, 12A–B, E, 13A–B.

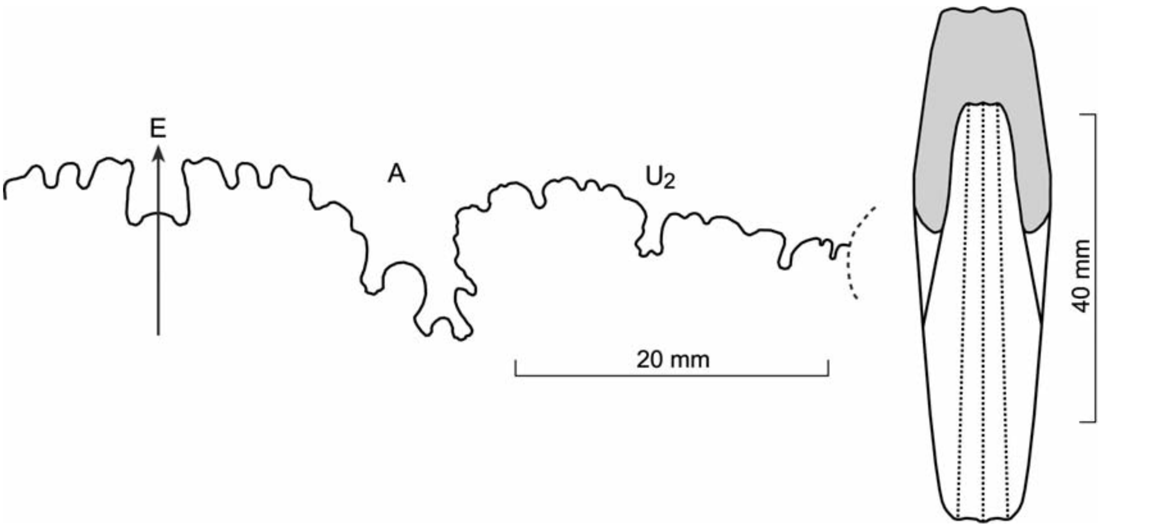
MATERIAL: Eleven specimens (AfK 328–338) from the uppermost part of the Galala Formation, in both sections studied (~110 m above the base of the formation; Text-fig. 2).

MEASUREMENTS:

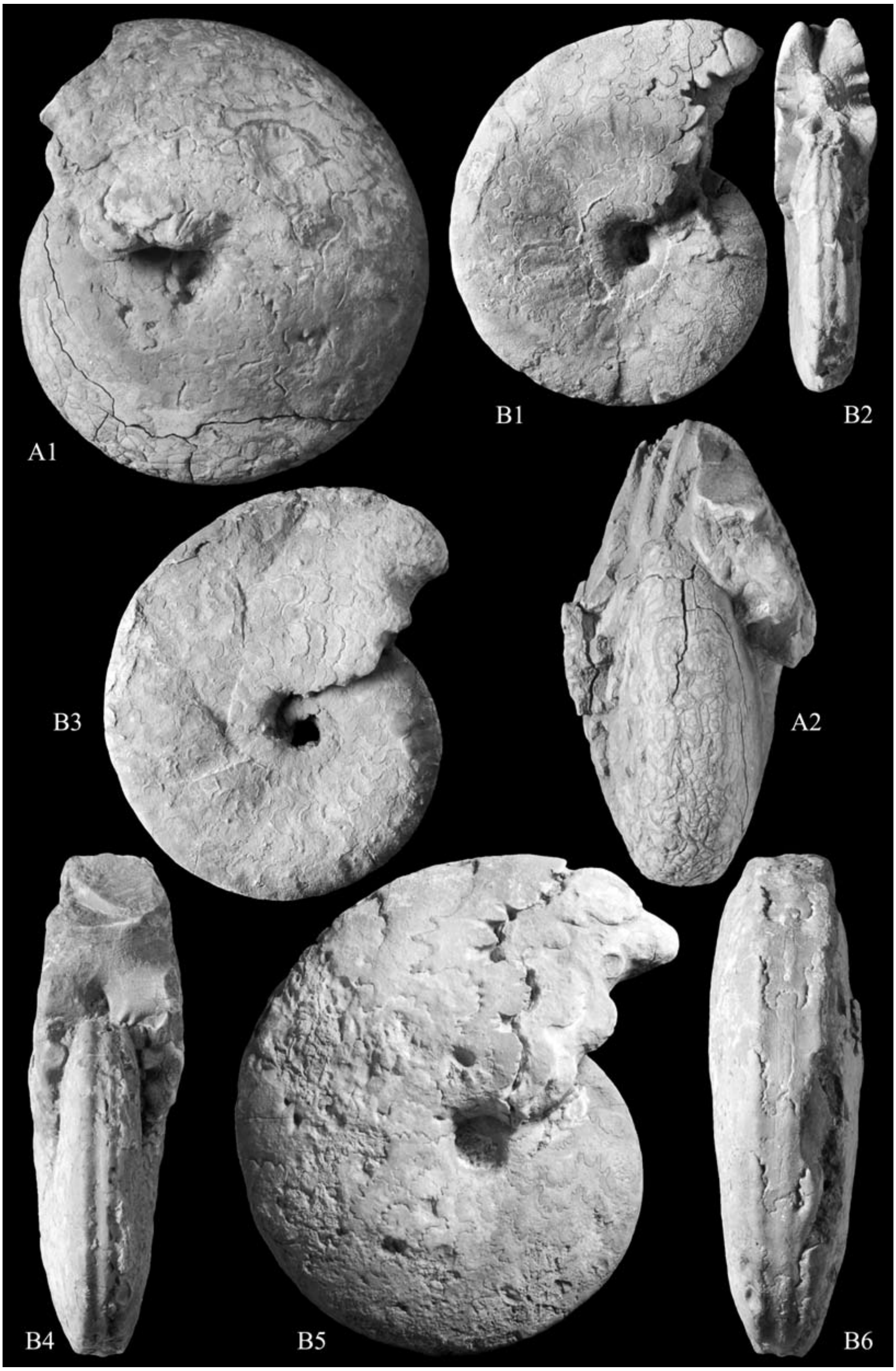
Specimen	D	Wb	Wh	Wb/Wh	U
AfK 328	68.5 (100)	19.7 (28.7)	37.5 (54.7)	0.36	6.0 (8.7)
AfK 329	91.1 (100)	33.4 (36.6)	50.3 (55.2)	0.66	11.7 (12.8)
AfK 330	84.0 (100)	20.1 (23.9)	43.0 (51.1)	0.46	9.8 (11.6)
AfK 331	85.8 (100)	27.3 (31.1)	47.0 (54.7)	0.58	7.7 (9.0)
AfK 332	78.5 (100)	23.4 (29.8)	42.3 (53.8)	0.55	8.2 (10.4)

DESCRIPTION: All specimens are smooth, fully septate internal moulds with a maximum preserved diameter of 91 mm (specimen AfK 329, Text-fig. 16B4–6). Coiling is involute (U ~10%) with a moderately deep umbilicus and feebly rounded umbilical walls. The flanks are high, subparallel, with convex inner and converging outer parts. Two prominent keels at the ventrolateral shoulders mark the contact with the venter, which is characterized by a siphonal keel, resulting in the distinctive tricarinate appearance of the ventral area (Text-fig. 15). The three keels have the same relative height in all specimens. The whorl section (Text-fig. 15) is compressed, with the maximum breadth directly above the umbilical shoulder. The suture line (Text-fig. 15) is characterized by very broad saddles and narrow lobes; the adventive lobe is deeply incised.

REMARKS: The flat, tricarinate venter, the compressed whorl section and a suture line with broad saddles and narrow lobes (deeply incised adventive lobe) are characteristic of *Pseudotissotia nigeriensis* (e.g., Meister 1989). Based on these characters, the specimens from the upper Galala Formation of Wadi Qena are unequivocally attributed to Woods' species and represent its first proven occurrence in Egypt. Our specimens closely match the Nigerian material as described by Woods (1911) and Meister (1989).



Text-fig. 15. Whorl section and suture line of *Pseudotissotia nigeriensis* (Woods, 1911), Lower Turonian of the Galala Formation, specimen AfK 328



Text-fig. 16. **A** – *Thomasites rollandi* (Thomas and Peron, 1889) (A1, A2 –lateral and apertural views of AfK 315, ×1). **B** – *Pseudotissotia nigeriensis* (Woods, 1911) (B1, B2 – lateral and apertural views of AfK 328, ×1; B3 – lateral view of AfK 334, ×1; B4, B5, B6 – apertural, lateral and ventral views of AfK 329, ×1). All specimens from the Lower Turonian of the Galala Formation

OCCURRENCE: The species is known from the Lower Turonian of Nigeria, Algeria, Israel, northern Mexico and Brazil. In the study area, it occurs in the Lower Turonian, above the mid-Lower Turonian *Choffaticeras* spp. Zone. The *P. nigeriensis* horizon is thus considered to be equivalent to the lower part of the standard ammonite Zone of *Mammites nodosoides* (cf. Kennedy 1984; Wright *et al*. in Wright and Kennedy 1984; Hancock 1991), since the last appearance of *Choffaticeras* in Egypt is very close to the interpolated first occurrence of *Mammites nodosoides* (Nagm *et al*. 2010b; see Text-fig. 22 and discussion below).

Genus *Choffaticeras* Hyatt, 1903

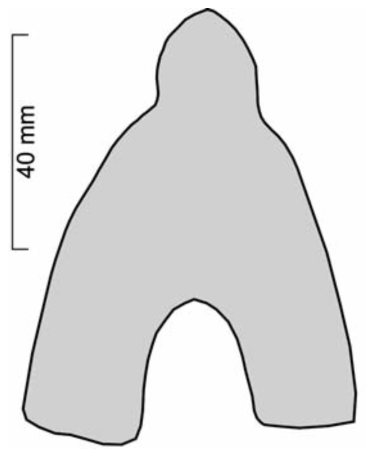
TYPE SPECIES: *Pseudotissotia meslei* Peron, 1897, by original designation.

Subgenus *Choffaticeras* Hyatt, 1903

Choffaticeras (*Choffaticeras*) *securiforme* (Eck, 1909)
(Text-fig. 17)

1909. *Tissotia securiformis* Eck, 187, figs 9–13.
1969. *Choffaticeras securiforme* (Eck); Freund and Raab, 60, pl. 9, fig. 1; text-fig. 11i–k.
1996. *Choffaticeras* gr. *securiforme* (Eck); Meister and Abdallah, 15, pl. 9, fig. 1; text-fig. 6g.
2009. *Choffaticeras* (*Choffaticeras*) *securiforme* (Eck); Nagm, 91, text-figs 5.19, 5.20A, 5.23H, I.

MATERIAL: Two fragmentary specimens (AUEN 23–24) from the upper part of the Galala Formation



Text-fig. 17. Whorl section of *Choffaticeras* (*Choffaticeras*) *securiforme* (Eck, 1909), Lower Turonian of the Galala Formation, specimen AUEN 23 from north Wadi Qena Section

(102 m above the base of the formation) at the North Wadi Qena section (Text-fig. 2).

DESCRIPTION: The specimens are large and characterized by a wide and fairly deep umbilicus, with vertical walls and a sharp umbilical shoulder. The flanks converge to a narrow venter with a strong median, obtuse keel. The whorl section (Text-fig. 17) is compressed, lanceolate in shape and with the maximum breadth at the umbilical shoulder. Ornament and suture line are not preserved.

REMARKS: Freund and Raab (1969) described a large collection (49 specimens) of *Choffaticeras securiforme* from Israel, and discussed its relationship to *C.* (*Leoniceras*) *luciae* (Pervinquière) and *C.* (*L.*) *massipianum* (Pervinquière). Although the specimens studied are very poorly preserved, their whorl section (Text-fig. 17) and the narrow venter, with a conspicuous median obtuse keel, allow their safe assignment to *C. securiforme*.

OCCURRENCE: The species is known from the Lower Turonian of Israel, Egypt and Tunisia. In the study area, it comes from the middle Lower Turonian *Choffaticeras* spp. Zone, which is (as defined by Nagm *et al*. 2010b), equivalent to the upper part of the standard ammonite Zone of *Watinoceras coloradoense* (Kennedy 1984; Wright *et al*. in Wright and Kennedy 1984) or *Watinoceras* spp. (Hancock 1991).

Choffaticeras (*Choffaticeras*) *segne* (Solger, 1903)
(Text-figs 18, 19)

1903. *Pseudotissotia segnis* Solger, 77, pl. 4, figs 1, 2; text-figs 16–21.
1904. *Schloenbachia quaasi* Peron, 255, pl. 1, figs 1–3.
2007. *Choffaticeras* (*Choffaticeras*) *quaasi* (Peron); Barroso-Barcenilla and Goy, 464, figs 4(4,5), 5(1).
2007. *Choffaticeras* (*Choffaticeras*) *segne* (Solger); Barroso-Barcenilla and Goy, 468, figs 5(5), 6(1–3).
2008. *Choffaticeras* (*Choffaticeras*) *segne* (Solger); Kennedy *et al*., 162, fig. 9; pl. 3, figs 4, 5; pl. 7, figs 1, 2; pl. 8, figs 1–6.
2009. *Choffaticeras* (*Choffaticeras*) *quaasi* (Peron); Nagm, 88, text-figs 5.18A, 5.23C.
2009. *Choffaticeras* (*Choffaticeras*) *segne* (Solger); Nagm, 94, text-figs 5.17B, 5.18C, 5.23E–G.

MATERIAL: Twenty-seven specimens (AfK 317–327, AUEN 25–33) from the upper part of the Galala Formation (103–104 m above the base of the formation) in both studied sections (cf. Text-fig. 2).

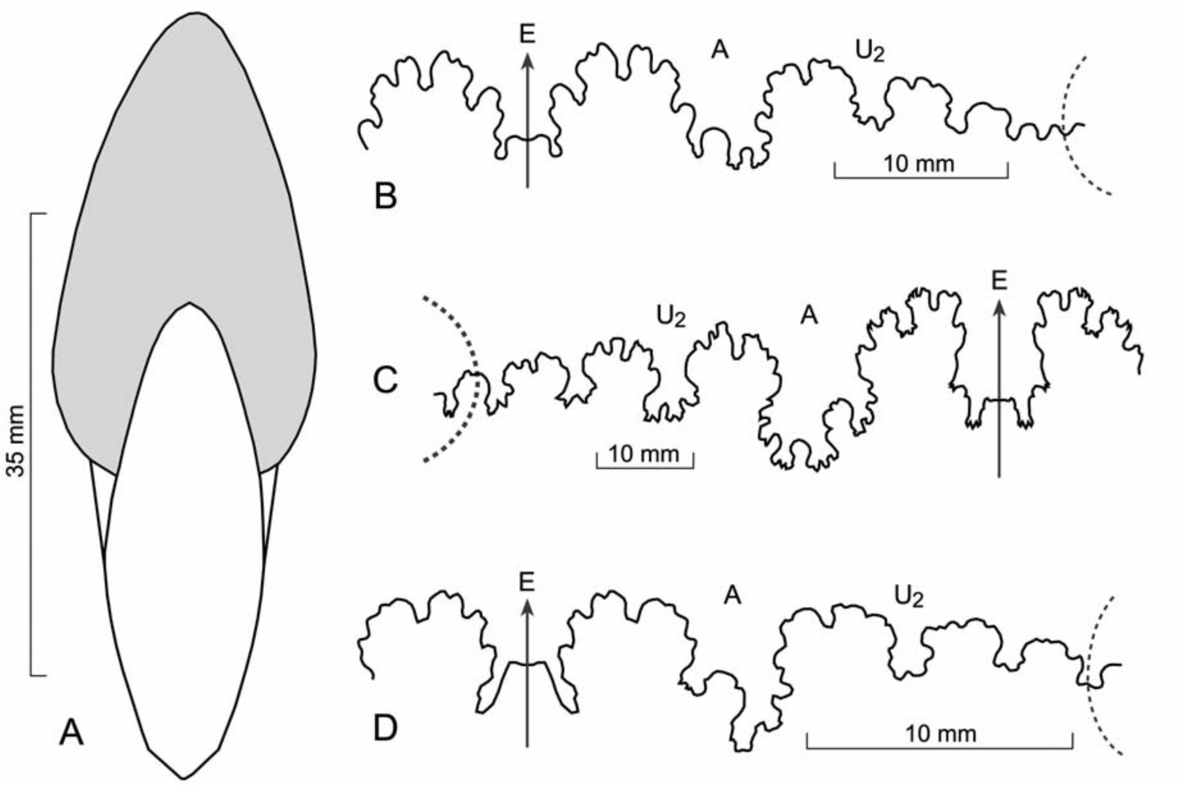
MEASUREMENTS:

Specimen	D	Wb	Wh	Wb/Wh	U
AfK 317	101.3 (100)	36.8 (36.3)	50.2 (49.5)	0.73	13.0 (12.8)
AfK 318	107.4 (100)	31.8 (29.6)	47.5 (44.2)	0.66	17.4 (16.2)
AfK 319	114.1 (100)	36.9 (31.9)	67.0 (56.2)	0.55	23.1 (20.2)
AfK 320	81.8 (100)	22.5 (27.5)	42.9 (52.4)	0.52	10.0 (12.2)
AfK 321	57.9 (100)	20.0 (34.5)	33.7 (58.2)	0.59	3.6 (6.2)
AfK 322	45.5 (100)	15.4 (33.8)	25.9 (56.9)	0.59	5.8 (12.7)
AfK 323	43.8 (100)	12.9 (29.4)	23.8 (54.3)	0.54	5.4 (12.3)

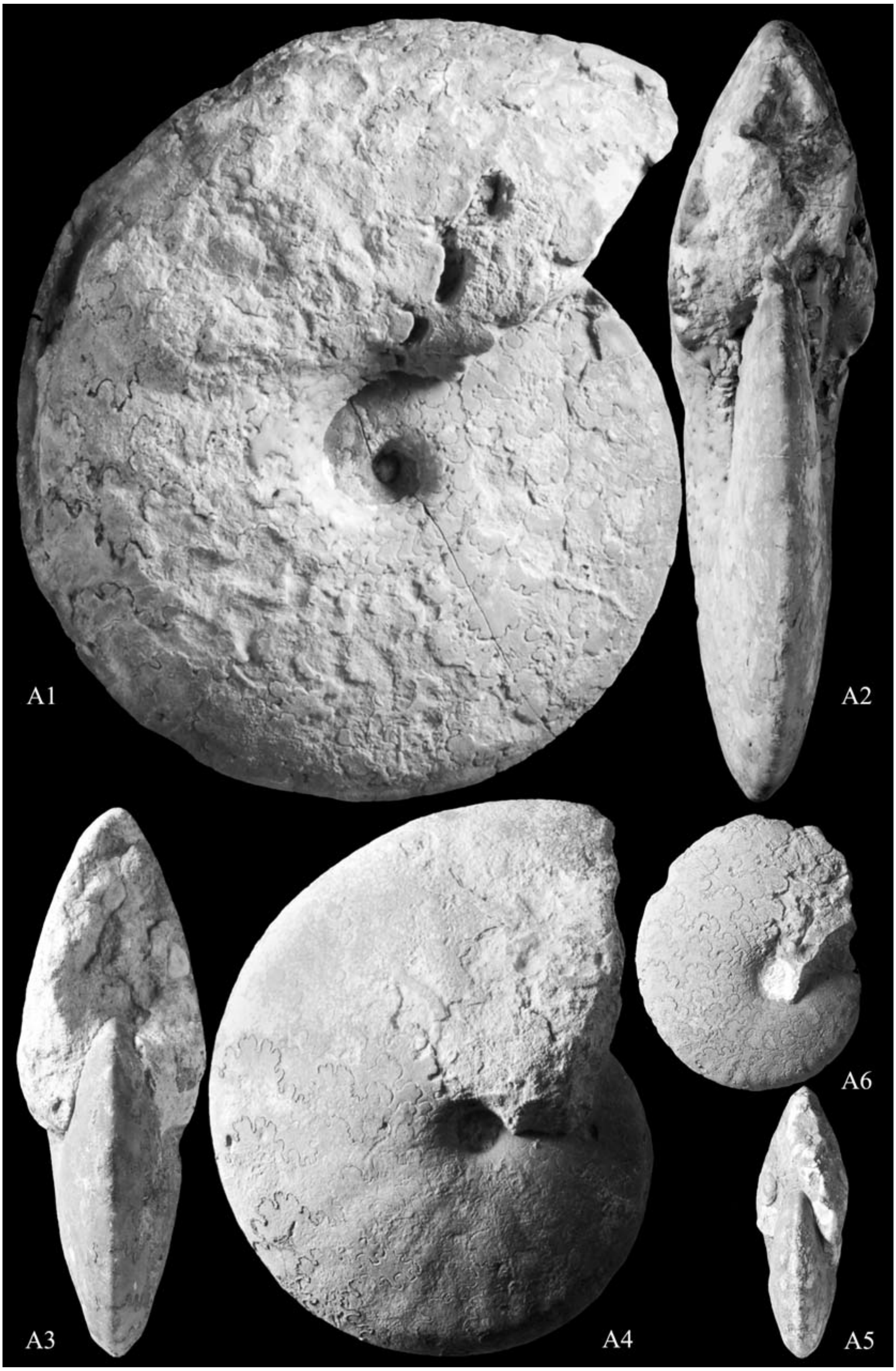
DESCRIPTION: Both small and large specimens are characterized by moderately involute coiling. The umbilicus has outward-inclined walls and rounded umbilical shoulders. The flanks are high and generally convex, especially on the inner parts. Early whorls are commonly ornamented by simple ribs and very weak ventrolateral tubercles that disappear during ontogeny. The venter is tricarinate in juvenile and sharp in adult stages. The whorl section is compressed, with an oxycone shape (Text-fig. 18) and the greatest breadth on the inner part of the flanks. The suture line is well preserved in all specimens and shows some variability (Text-fig. 18). However, the sutures are generally characterized by broad and high saddles with a deep and broad adventive lobe.

REMARKS: Barroso-Barcenilla and Goy (2007) described several species of *Choffaticeras* from Spain and discussed their relationship. The Lower Turonian of Egypt yielded abundant *Choffaticeras* (cf. Nagm 2009; Nagm *et al*. 2010a, b); however, only two species are represented in Wadi Qena, i.e., *Choffaticeras* (*Choffaticeras*) *securiforme* and *Choffaticeras* (*C.*) *segne* (and eight species are known in contemporaneous strata of Wadi Araba in the northern part of the Eastern Desert; Nagm 2009; Wilmsen and Nagm, in prep.). The well-preserved and large population of *C.* (*C.*) *segne* from the Eastern Desert confirms the view of Kennedy *et al*. (2008) that *C.* (*C.*) *quaasi* is a junior synonym of *C.* (*C.*) *segne* (Wilmsen and Nagm, in prep.).

OCCURRENCE: The species is known from the Lower Turonian of Tunisia, Israel, Syria, Jordan, France and Spain. In the study area, it characterizes the middle Lower Turonian *Choffaticeras* spp. Zone, which is (as defined by Nagm *et al*. 2010b) equivalent to the upper part of the standard *Watinoceras coloradoense* Zone (Kennedy 1984; Wright *et al*. in Wright and Kennedy 1984) or the *Watinoceras* spp. Zone (Hancock 1991).



Text-fig. 18. Whorl section and suture line of *Choffaticeras* (*Choffaticeras*) *segne* (Solger, 1903), Lower Turonian of the Galala Formation, A, B – specimen AfK 321; C – specimen AfK 317; D – specimen AfK 323



Text-fig. 19. *Choffaticeras* (*Choffaticeras*) *segne* (Solger, 1903) from the Lower Turonian of the Galala Formation. A1, A2 – lateral and apertural views of AfK 319, ×1; A3, A4 – apertural and lateral views of AfK 317 , ×1; A5, A6 – apertural and lateral views of AfK 325, ×1

Family Coilopoceratidae Hyatt, 1903
Genus *Coilopoceras* Hyatt, 1903

TYPE SPECIES: *Coilopoceras colleti* Hyatt, 1903, by original designation.

Coilopoceras requienianum (d'Orbigny, 1841)
(Text-figs 20, 21)

1841. *Ammonites requienianum* d'Orbigny, 315, pl. 93, figs 1–4.
1984. *Coilopoceras requienianum* (d'Orbigny); Kennedy and Wright, 282, pls. 35, 36, text-figs 1–5. [with synonymy]
1989. *Coilopoceras requienianum* (d'Orbigny); Luger and Gröschke, 388, pl. 46, text-figs 6a, e, 11, 12, 13a–c.
2010a. *Coilopoceras requienianum* (d'Orbigny); Nagm *et al*., 495, figs 16A–C, 17, 18A–C.

MATERIAL: Fifteen specimens (AfK 339–341, AUEN 34–45) from the upper part of the Umm Omeiyid Formation in both sections studied (Text-fig. 2).

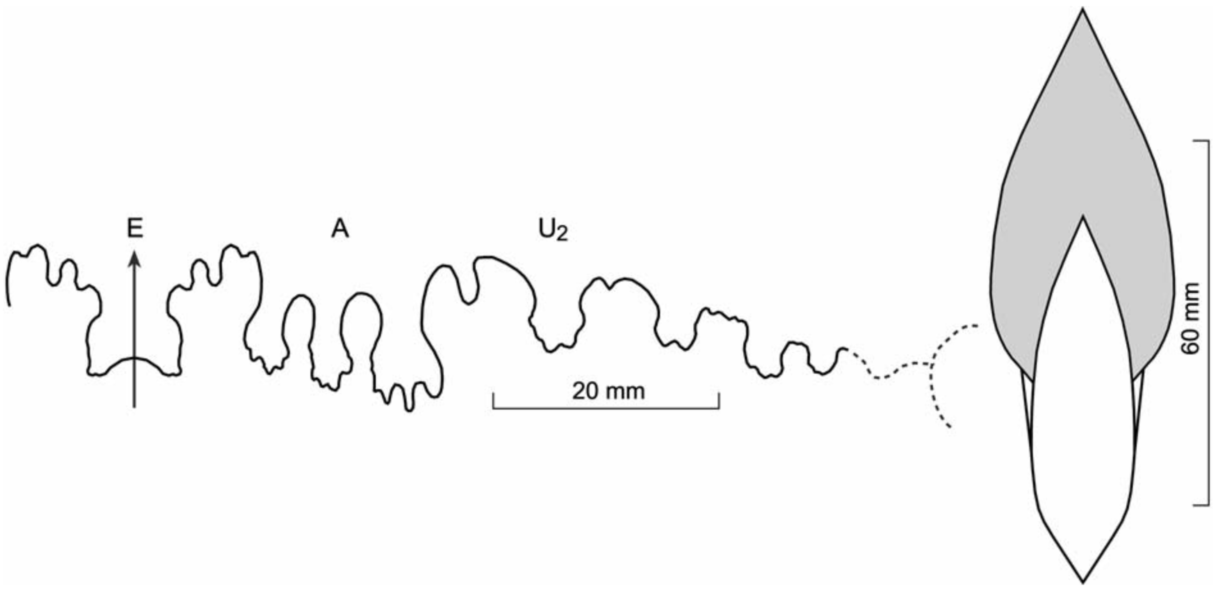
MEASUREMENTS:

Specimen	D	Wb	Wh	Wb/Wh	U
AfK 339	93.9 (100)	31.0 (33.0)	61.7 (65.7)	0.50	5.8 (6.1)
AfK 340	95.6 (100)	36.0 (37.6)	63.1 (66.0)	0.57	5.9 (6.1)
AfK 341	100.7 (100)	36.4 (36.1)	59.5 (59.0)	0.61	4.9 (4.8)

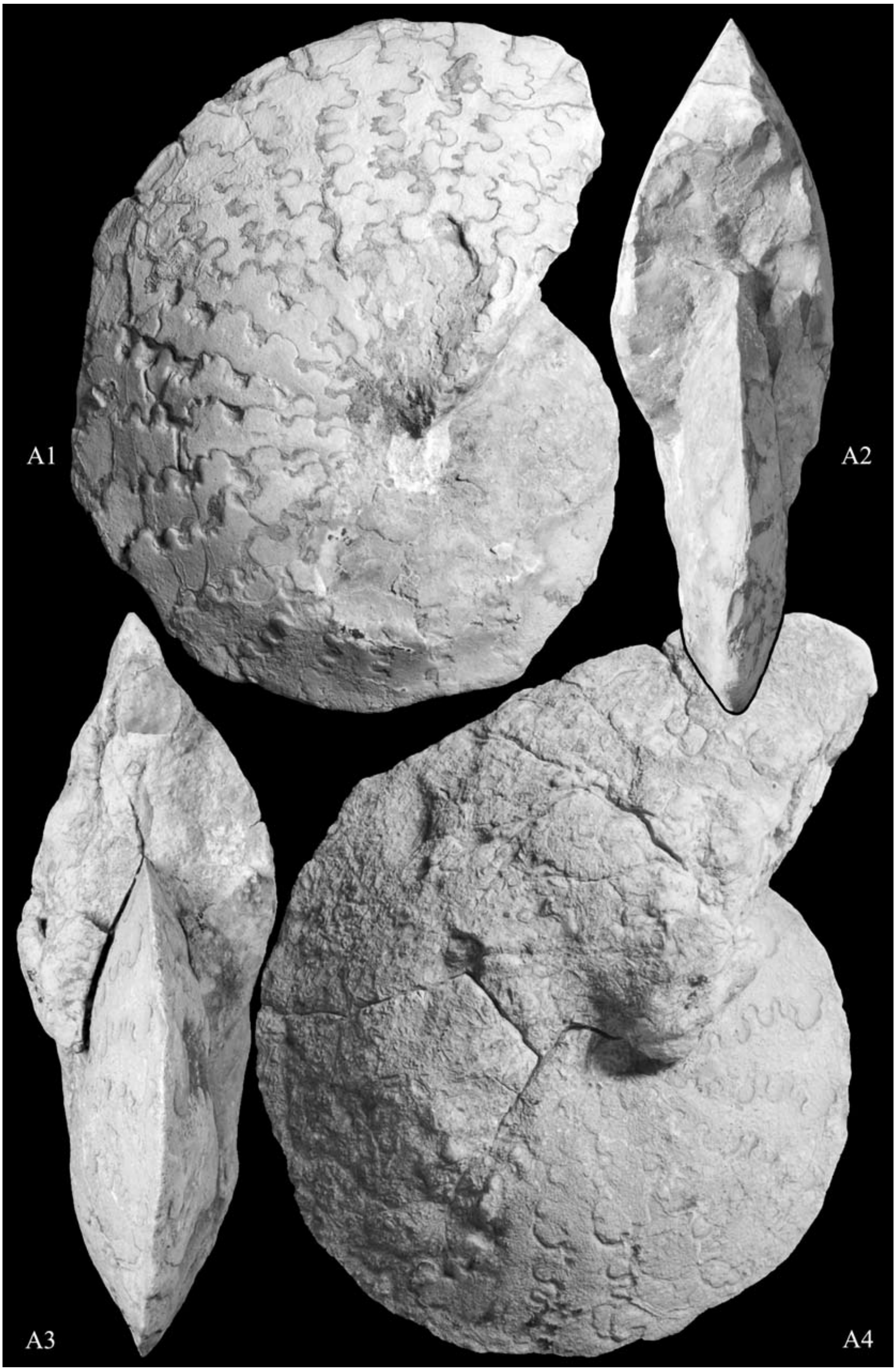
DESCRIPTION: All specimens are characterized by very involute coiling. The umbilicus is small (U ~5–6%) and narrow, with low and rounded shoulders. The flanks are convex and converge towards a pointed venter. The whorl section (Text-fig. 20) is compressed, with a lanceolate shape and the maximum breadth on the inner flanks. Most specimens are smooth but some of the small specimens have a few weak ribs on the inner whorls. The suture line (Text-fig. 20) shows a broad and shallow external lobe, and a very broad, open and bifid adventive lobe.

REMARKS: Cobban and Hook (1980) demonstrated that many of the described species of the genus *Coilopoceras* are probably synonyms, often being based on small differences in the suture lines. Their view is supported by the re-description of the type material of *C. requienianum* by Kennedy and Wright (1984), who suggested the existence of sexual dimorphism in *C. requienianum* shown by smooth and ribbed forms. The specimens from Wadi Qena closely correspond to the type material. However, some are more inflated and the smooth morphotype predominates.

OCCURRENCE: Upper Turonian of Madagascar, Egypt, North and South America, France and Spain. In the study area, *C. requienianum* characterizes the lower Upper Turonian zone of *Coilopoceras requienianum*, which is (as defined by Nagm *et al*. 2010b) equivalent to the lower part of the standard ammonite Zone of *Subprionocyclus neptuni* (Hancock 1991).



Text-fig. 20. Suture line and whorl section of *Coilopoceras requienianum* (d'Orbigny, 1841), Upper Turonian of the Umm Omeiyid Formation, specimen AfK 339

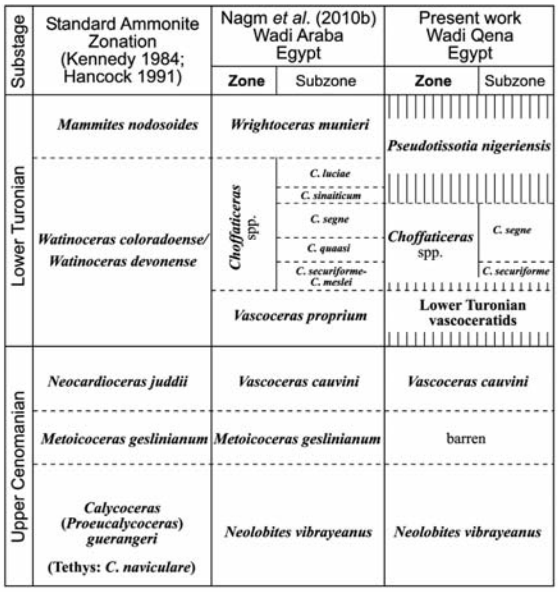


Text-fig. 21. *Coilopoceras requienianum* (d'Orbigny, 1841) from the Upper Turonian of the Umm Omeiyid Formation. A1, A2 – lateral and apertural views of AfK 339, ×1; A3, A4 – apertural and lateral views of AfK 341, ×1

BIOSTRATIGRAPHICAL AND PALAEOBIOGEOGRAPHICAL REMARKS

The first marine transgression in the study area took place during the Late Cenomanian, documented by the deposition of the shallow marine Galala Formation above the Palaeozoic Naqus Formation, with a prominent sequence boundary (major non-sequence) at the base of the Galala Formation. The early Late Cenomanian is known as a time of major eustatic sea-level rise (e.g., Wilmsen 2003; Wilmsen *et al.* 2005). The lower part of the Galala Formation is characterized by glauconitic, silty sediments, rich in oysters distinctive of Upper Cenomanian successions elsewhere in Egypt (Nagm 2009). Approximately 35 m above the base of the formation, the sediments have yielded the early Late Cenomanian ammonite *Neolobites vibrayeanus* (see Wiese and Schulze 2005 for details of the species). It defines the oldest ammonite zone in the study area (Text-fig. 2), equivalent to the northwest European standard ammonite Zone of *Calycoceras* (*Proeucalycoceras*) *guerangeri* (Kennedy 1984; Wright *et al.* in Wright and Kennedy 1984; Hancock 1991) and the Tethyan standard ammonite Zone of *Calycoceras naviculare* (Text-fig. 22; see Nagm *et al*. 2010b for full details). The beds of the Galala Formation below the first occurrence of *N. vibrayeanus* are included in the *N. vibrayeanus* Zone (cf. Nagm 2009; Nagm *et al*. 2010b). *N. vibrayeanus* ranges for about 35 m above its first occurrence, defining the top of the zone (Text-fig. 2). It is followed by an ammonite-barren 20–25 m interval rich in the oyster *Costagyra olisiponensis*. Based on the latest Cenomanian age of the overlying strata, the barren interval is regarded here as equivalent to the middle Upper Cenomanian *Metoicoceras geslinianum* Zone of Kennedy (1984), Wright *et al*. in Wright and Kennedy (1984) and Hancock (1991; see Text-fig. 22).

Above the barren interval, ammonites are common again. The lowest eight metres are characterized by high carbonate contents and yield, in the lower part, *Vascoceras cauvini*. This is the index of the eponymous uppermost Cenomanian ammonite zone in Egypt, largely equivalent to the *Neocardioceras juddii* Zone of Kennedy (1984), Wright *et al*. in Wright and Kennedy (1984) and Hancock (1991), in the Cenomanian standard ammonite zonation (Nagm *et al*. 2010b). *Euomphaloceras costatum* has been recorded from the upper part of the *Vascoceras cauvini* Zone, for the first time from Egypt. This species co-occurs with *Neocardioceras juddii* in the United States (Cobban *et al*. 1989). In the study area, the upper limit of this zone is considered to mark the Cenomanian–Turonian (C–T) boundary (cf. Nagm *et al*. 2010b).



Text-fig. 22. Ammonite biostratigraphy of the Upper Cenomanian and Lower Turonian. Vertically hatched fields represent stratigraphic gaps. See text for further explanations

Two metres above the inferred C–T boundary (a short distance below the 100-m-level above the base of the Galala Formation in both sections; Text-fig. 2), Early Turonian vascoceratids (*V. globosum globosum* and *V. kossmati*) become abundant in high-carbonate sediments. The absence of *Vascoceras proprium* and *Pseudaspidoceras flexuosum* suggests a stratigraphic gap at this level (see Text-fig. 22), comparable to the situation in some sections of Wadi Araba in the northern part of the Eastern Desert (Nagm *et al*. 2010b). Two horizons with representatives of the genus *Choffaticeras* have been recognized directly above the lowermost Turonian vascoceratid interval (Text-fig. 2): the lower one with *Choffaticeras* (*Choffaticeras*) *securiforme*; and the upper one with *C.* (*C.*) *segne*. The ~7 m thick *Choffaticeras* interval characterizes the middle Lower Turonian (Nagm *et al*. 2010b), equivalent to the upper part of the standard ammonite Zone of *Watinoceras devonense* (Kennedy 1984; Hancock 1991; see Text-fig. 22). This part is followed by the highly fossiliferous uppermost interval of the Galala Formation, yielding typical Nigerian ammonites, such as *Pseudotissotia nigeriensis* (Text-fig. 2), dated as late Early Turonian (Meister 1989). In agreement with this observation, Nagm *et al*. (2010b) proposed that the last appearance of the genus *Choffaticeras* approximates the first appearance of the index of the standard upper Lower Turonian *Mammites nodosoides* ammonite Zone of Kennedy (1984) and Hancock (1991). Therefore, the *P. nigeriensis* Zone (or horizon) seems to be equivalent to the lower part of the *M. nodosoides* Zone. The upper boundary of this zone is marked by a prominent unconformity in the Lower–Middle Turonian boundary interval (Text-fig. 2). The same unconformity has been recognized in the sections of Wadi Araba in the northern part of the Eastern Desert; Nagm *et al*. 2010b), and it also has its equivalent in shallow shelf settings of the northern Tethys margin (see Niebuhr *et al.* 2011). This unconformity also represents the contact of the Galala and Umm Omeiyid formations. The lower part of Umm Omeiyid Formation is dominated by siliciclastics and is barren of macrofauna. In the upper part of the formation, fossiliferous strata yielded the early Late Turonian ammonite *Coilopoceras requienianum*, the zone of which is (as defined by Nagm *et al*. 2010b) equivalent to the lower part of the Upper Turonian standard ammonite Zone of *Subprionocyclus neptuni* (Geinitz) (Kennedy 1984; Hancock 1991; see Text-figs 2, 22). This observation suggests that the unfossiliferous part of the lower Umm Omeiyid Formation corresponds, in a broad sense, to the Middle Turonian. Interestingly, also in the sections of Wadi Araba, Middle Turonian strata are barren of macrofossils (Nagm 2009; Nagm *et al*. 2010a, b).

The early Late Cretaceous eustatic transgression, with a significant sea-level rise that peaked during the Late Cenomanian and Early Turonian, has been well documented (Hancock and Kauffman 1979; Hardenbol *et al*. 1998; Sharland *et al*. 2001; Wilmsen 2003; Wilmsen *et al*. 2005, 2010). Rising sea level may be a straightforward explanation for the wide geographic distribution of many Cenomanian–Turonian ammonites (Wiedmann 1988; Lehmann and Herbig 2009; Nagm *et al*. 2010a). The palaeontological record documents ammonite geographic expansion during the Late Cenomanian, expressed by the presence of a single large Tethyan province, followed by biogeographic differentiation during the Early Turonian, expressed by Boreal, Vascoceratid and Puzosiid provinces (Wiedmann 1988; Lehmann and Herbig 2009). The palaeobiogeographic affinities of the studied fauna correspond to this pattern (see Nagm *et al.* 2010a for data from Wadi Araba). The early and mid-Late Cenomanian ammonite fauna is biogeographically not very diagnostic. The latest Cenomanian incipient provincialism is documented by the presence of the typically North and West African *Vascoceras cauvini*. The Early Turonian assemblage, studied herein, belongs to the Tethyan Vascoceratid Province, with strong influences of Nigerian faunas (*Vascoceras globosum globosum*, *Thomasites gongilensis*, *Pseudotissotia nigeriensis*), proving the faunal connection to Central and West Africa via the Trans-Saharan Seaway (see Collignon and Lefranc 1974; Meister *et al*. 1992). The palaeobiogeographic affinity to the Boreal Realm is much less noticeable in the study area, with only 50% of the ammonites of Wadi Qena known also from that Realm. It is noteworthy that, in the contemporaneous successions of the northern part of the Eastern Desert (Wadi Araba, ca. 130 km to the north), 85% of the Early Turonian ammonoids identified are also known from the Boreal Realm (Nagm *et al*. 2010a). This observation may indicate relatively steep north–south environmental gradients.

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