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Taxonomy, Paleoecology and Paleobiogeography of the Middle Eocene Nautiloid Cephalopods from the Midawara Formation, Fayum, Egypt

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Abstract

This paper focuses on the nautiloid fauna of the Middle Eocene (Lutetian) Midawara Formation in the Fayum Depression, Egypt. Four species belonging to four genera were identified: *Euciphoceras regale*, *Eutrephoceras (Simplicioceras) centrale*, *Aturoidea parkinsoni*, and *Deltoidonautilus sowerbyi*. Two species of them (*E. regale* and *D. sowerbyi*) are recorded for the first time in Egypt. Paleoecologic analysis reveals that these nautiloids were deposited in a shallow-marine environment and experienced various diagenetic processes. Evidence of abrasion, bioerosion, and encrustations suggests limited post-mortem transportation. Paleoecological reconstruction indicates a nekton-benthic lifestyle for these nautiloids. Furthermore, the presence of rhyncholites (calcic jaws of cephalopods) indicated that these nautiloids inhabited shallow-water areas, and most likely died during nocturnal migrations. Paleogeography of the studied nautiloid in the Lutetian Stage shows a widespread distribution, adaptability and resilience in diverse marine environments across the Tethys Sea, Africa, Asia and Europe. The co-occurrences of predators (such as whales, sharks, gastropods and cephalopods) and scavengers (e.g., crabs) indicate a complex food web and the prosperity of marine life. The significant turnover of the abundance and diversity of nautiloid assemblage from Lutetian to Bartonian ages may be corresponded to severe environmental conditions that dominate during brief warming event of the Middle Eocene Climatic Optimum (MECO).

Keywords: Nautiloid cephalopods, Eocene, Lutetian, Midawara Formation, Fayum, paleoecology, paleobiogeography, Tethys.

Introduction

This study presents a comprehensive analysis of Eocene cephalopod fossils from the Fayum, Egypt (Fig. 1). The Eocene Epoch in Egypt was characterized by a thriving marine ecosystem with diversified cephalopod fauna, mainly nautiloids. Previous studies in Egypt have documented the presence of various nautiloid species across different regions and periods within this epoch. Notable earlier recording of nautiloid backs to the identification of *Nautilus* cf. *mokattamensis* Foord in Gebel Gurna (Cuvillier in Hume 1965) and *Hercoglossa aegyptiaca* Foord in Gebel Mokattam (Fleming 1945).

Later studies reported nautiloid occurrences in the Middle Eocene deposits of the Fayum region (Beadnell 1905; Iskander 1943) and the Qattara Depression (Van Vliet and Abu el Khair 2010). Paleontological studies of the Eocene successions in the Kurkur Oasis (Hewaidy and Azab 2002) and the Fayum (Abd-Elshafy et al. 2007) revealed further understanding of nautiloid diversity and distribution during the Eocene Epoch. Moreover, recent investigations by Hewaidy et al. (2019), Aly and Sadek (2019) and Sayed et al. (2021) have contributed to taxonomy and description of some nautiloid species in Egypt.

Regionally, the Eocene nautiloid fossils have attracted significant and many researchers across the Mediterranean, Middle East and Europe regions as well as in the whole World. Notable studies of nautiloids include from oldest to youngest: The Eocene deposits of England (Edwards 1849; Jeffery and Tracey 1997; Lesport et al. 2021); the Lower Eocene deposits of Spain (Calzada and Viader 1983; Díaz 1989), Belgium (Dupuis and Robaszynski 1986), and Mexico (Morales-Ortega et al. 2023); The Lutetian-age nautiloids of Croatia (Mikuž and Bartol 2012), Qatar (LeBlanc 2019), and Argentina (Casadío et al. 1999); and the Middle Eocene (Lutetian) strata of Germany (Schultz 1976), Hungary Austria (Galácz 2004, 2008; Moosleitner 2004), and Somalia (Haas and Miller 1952). Additionally, these nautiloids were also studied from the Middle Eocene of India (Halder 2012) and Middle-Late Eocene of Australia (Darragh and Kendrick 2010).

Most of the earlier work focuses on the general geology, stratigraphy, paleontology, and sedimentology (e.g., Gingerich 1992, 2006, 2023; Abdel-Fattah et al. 2010; Abdel-Fattah 2016, 2018; Abdel-Fattah and Gingras 2020, Moneer et al. 2024, Hewaidy et al. 2024, etc.) mainly in the late Middle to Upper Eocene rock units such as Gehannam, Birket Qarun and Qasr El-Sagha formations. The strata in the Fayum province, especially in the Middle Eocene Midawara Formation, offer a unique opportunity to investigate the ancient marine ecosystems and paleogeography within the Tethyan realm during Eocene time. This paper focuses on the cephalopod assemblage from the Middle Eocene Midawara Formation. We aim to reveal valuable insights into the taxonomy, biodiversity and paleogeography of these important marine organisms in the Fayum area. A regional and global comparison of nautiloid occurrences is discussed too.

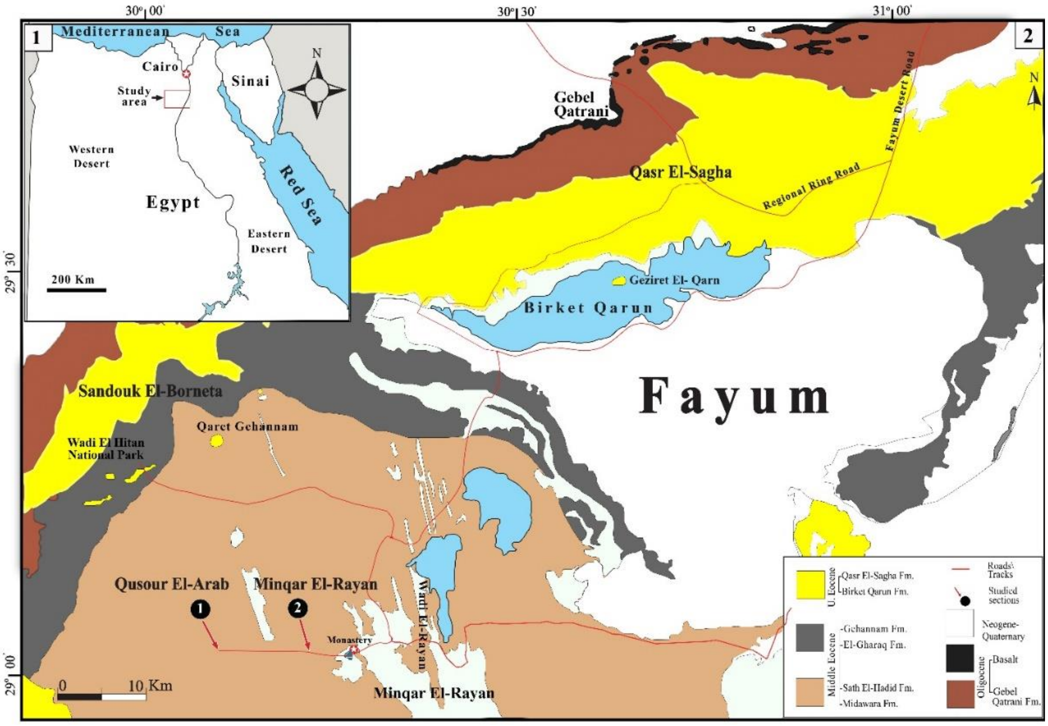

Fig. 1 Geologic map of the Fayum Depression, illustrating the locations of the investigated sections (modified and adapted from Beadnell 1905; Conoco 1987; Gingerich 1992; Abdel-Fattah et al. 2010).

Geological settings

This study focuses on nautiloid samples, which were collected from the Midawara Formation in the southern part of the Fayum Depression; mainly at Qusour El-Arab and Minqar El-Rayan sections (Figs. 1, 2). Thickness of the studied successions ranges between 26 and 57.5 m. The stratigraphic sequence at both sections includes three rock units: The basal Midawara Formation (with unexposed base) which is overlain by the Sath El-Hadid Formation that is topped by El-Gharaq Formation (Fig. 3a-b). Locally, the Midawara Formation conformably overlies the Middle Eocene Muweilih Formation in the southern part of the Fayum and Wadi Muweilih (Abu El Ghar 2012; Helal and Holcová 2017). Despite previous studies employing alternative stratigraphic names such as the Wadi El-Rayan series (Beadnell 1905) and the Rayan Formation (Issawi et al. 2009), the Midawara Formation, originally described by Iskander (1943), is widely used in literature as a famous rock unit in the Fayum Depression. A detailed chart (Fig. 2) has been added to show the stratigraphic framework, nomenclature and age of this important rock unit. The Midawara Formation is primarily composed of grey to dark gypsiferous shale, bioturbated and fossiliferous sandstones and limestone (Figs. 2, 3a-j).

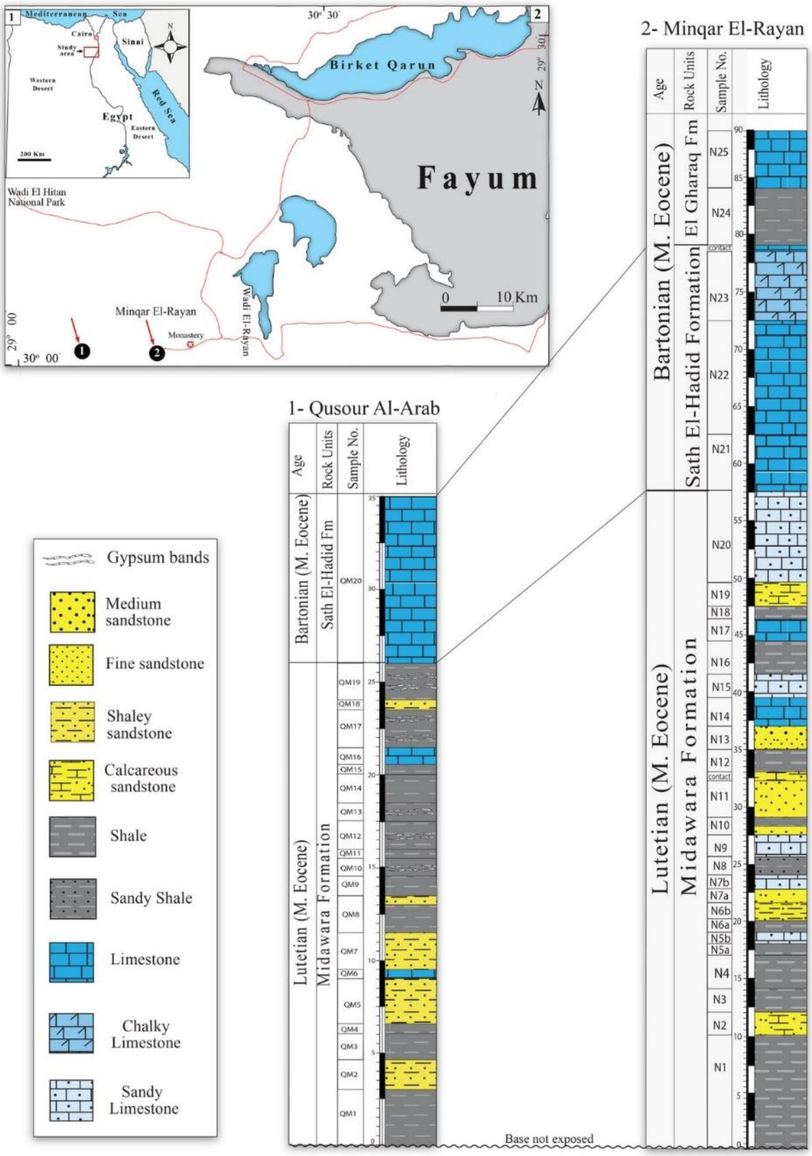

Fig. 2 The lithostratigraphic correlation chart of the investigated sections.

Fig. 3 (a) A field view of the Middle Eocene (Lutetian) succession at the Qusour El-Arab section showing the lower, thick-bedded unit of the Midawara Formation and the overlying carbonates of the Sath El-Hadid Formation. **(b)** Another view captures the stratigraphic relationships at the Minqar El-Rayan section exposing the Middle Eocene (Lutetian) Midawara Formation at the base, the Middle Eocene (Bartonian) Sath El-Hadid Formation at the top. **(c)** The grey to dark gypsiferous shale topped by bioturbated sandstone of the Midawara Formation at the Minqar El-Rayan section. **(d)** A close-up view of the gypsiferous shale and fossiliferous sandstone of the Midawara Formation at the Qusour El-Arab section. A magnified view of the common fossils of the Midawara Formation: **(e)** *Aturoidea parkinsoni* (Edwards), **(f)** *Schizaster* sp., **(g)** *Pecten* sp., **(h)** *Sigmesalia fasciata* (Lamarck), **(i)** *Nummulites midawaraensis* (Kenawy), and **(j)** shark tooth.

The bioturbated sandstones (Fig. 3c) are highly fossiliferous, particularly rich in large benthic foraminifera (LBF), especially *Nummulites* (Fig. 3i). Common invertebrate fauna include anthozoans (e.g., *Goniopora* sp.), arthropods (e.g., *Lobocarcinus lumacopius* Anderson and Feldmann) bivalves (e.g., *Ostrea* (*T.*) *multicostata* (Deshayes), *Wakullina* (*H.*) *lefevrei* (Fischer), and *Pecten* sp.), gastropods (e.g., *Sigmesalia fasciata* (Lamarck)), and echinoids (e.g., *Echinolampas africana* De Loriol and *Schizaster* sp.) (Fig. 3c-i). Marine vertebrate remains of whale bones, fish scales, and shark teeth (Fig. 3j) are commonly reported. The fossil content and stratigraphic position, as well as previous investigations are used to assign a Middle Eocene, mainly middle to late Lutetian age, of the Midawara Formation (see Said 1990; Zalmout and Gingerich 2012; Abu El Ghar 2012).

Study Locations and Methods

Two well-exposed Middle Eocene successions were investigated and spatially measured along the southern Fayum Depression: 1) Qusour El-Arab (N 29° 04' 49"-E 30° 06' 25") and 2) Minqar El-Rayan (N 29° 04' 06"-E 30°14' 53") (Figs. 1-3). Field measurements were carried out to delineate the boundaries and thicknesses of rock units. The collected fieldwork data included detailed measurements of rock unit thicknesses and lithological descriptions. Representative rocks and fossils have been also collected throughout the Midawara Formation. Specifically, a total of 14 samples of nautiloid fossils were collected from various stratigraphic horizons within these successions. Each sample was labeled and photographed in situ at its respective stratigraphic zone.

Field data were refined and analyzed through additional laboratory examination of the collected fossils and rock samples. Nautiloid shells were classified on the basis of the taxonomic scheme outlined by Edwards (1849), Flower and Kummel (1950), Haas and Miller (1952), Kummel (1956) and Teichert et al. (1964). The systematic analysis was primarily based on external morphological characteristics such as shell diameter, whorl height, whorl breadth, and umbilical width. Morphological data and photos were further analyzed and illustrated by using Adobe Photoshop and Adobe Illustrator software.

To ensure accurate and consistent documentation of the fossil assemblages, each specimen was assigned a unique identifier using the XYN–n format. The X component denotes the specimen type (e.g., C for Cephalopoda), Y represents the section of origin (e.g., QM for Qusour El Arab), N indicates the bed number, and n specifies the sequential specimen number within that bed. This identifier system provides a standardized and organized method for tracking individual fossils. All fossil samples, images, and measured data were deposited in the Geological Museum of the Department of Geology, Damietta University (GMDG-DU), under the prefixes QM (Qusour El Arab) and N (Minqar El Rayan).

Systematic Paleontology

Phylum: Mollusca LINNÉ 1758
Class: Cephalopoda CUVIER 1797
Order: Nautilida AGASSIZ 1847
Family: Nautilidae DE BLAINVILLE 1825
Genus: *Euciphoceras* SCHULTZ 1976
Type species: *Nautilus regalis* J. Sowerby 1823
Euciphoceras regale (J. SOWERBY 1823)
(Fig. 4a-d)
1823 *Nautilus regalis* J. Sowerby, p. 77, pl. 355.
1849 *Nautilus regalis* J. Sowerby; Edwards, p. 46, pl. IV, pl. VIII, fig. 5.
1976 *Eutrephoceras* (*Euciphoceras*) *regale* (J. Sowerby); Schultz, p. 9, text-fig. 1D.
2004 *Euciphoceras regale* (J. Sowerby); Galácz, p. 2, text-figs 2-3.
2021 *Euciphoceras allionii* (Michelotti); Lesport et al., p.60, figs. 8-9.

Materials*:* Two moderately-preserved specimens were collected from the Middle Eocene (Lutetian) Midawara Formation at the Qusour El-Arab section.

Description*:* The shell exhibits a moderately sized, involute morphology with a semi-spherical shape, a small and shallow umbilicus characterized by rounded shoulders and steeply convex walls, a semi-quadrate or trapezoidal aperture of relatively large size, and a whorl breadth slightly exceeding the whorl height. The shell's dimensions range from 42.0-75.0 mm in diameter, 25.0-46.0 mm in whorl height, 28.0-54.0 mm in whorl breadth, and 1.2-3.5 mm in umbilical width (Table 1; Fig. 4a-d). The siphuncle is likely small and central. Although the suture lines are poorly preserved in the available specimens, they appear to be simple, relatively undulating and straight, with slightly convex flanks that converge towards the venter.

Table 1. Dimensions of the *Euciphoceras regale* (J. Sowerby)

Specimen No.	Diameter (mm)	Whorl Height (mm)	Whorl Breadth (mm)	Umbilical Width (mm)
CQM8-4	75.0	46.0	54.0	~1.2
CQM8-5	42.0	25.0	28.0	3.5

Remarks: *Euciphoceras regale* is a distinctive species characterized by its flattened flanks and venter. The original specimen, described by

Sowerby from the Eocene of Britain, exhibits a relatively large size, reaching a diameter of approximately 200 mm. Septa are visible up to about 160 mm, and the whorl-section displays a characteristic trapezoidal shape (Galácz 2004). The current *E. regale* specimen closely resembles *Euciphoceras allionii* (Michelotti) as described by Lesport et al. (2021), particularly in its broad, quadrangular septum with a rounded abapical margin.

Distribution and age: *Euciphoceras regale* was documented in a wide range of Eocene-age deposits, including the Early to Late Eocene of England (Edwards 1849; Jeffery and Tracey 1997; Lesport et al. 2021), the Lower Eocene strata of Belgium (Dupuis and Robaszynski 1986), and the Middle Eocene (Lutetian) strata of Hungary (Galácz 2004).

Genus*:* *Eutrephoceras* HYATT 1894

Type-species: *Nautilus dekayi* Morton, 1834: 291, pl. 8, fig. 4, by original designation by Hyatt, 1894

Eutrephoceras (*Simplicioceras*) *centrale* (J. SOWERBY 1812)

(Fig. 4e-m)

1812 *Nautilus centralis* J. Sowerby, pl. III, fig. 1a-c.

1849 *Nautilus centralis* J. Sowerby; Edwards, p. 45, pl. VIII, fig. 2.

1906 *Nautilus mokattamensis* Foord; Oppenheim, p. 344, fig.35.

2012 *Eutrephoceras* (*Simplicioceras*) *centrale* (J. Sowerby); Mikuž and Bartol, p.267, pl. 1, figs. 1a-d.

2019 *Eutrephoceras* sp., Aly and Sadek, p. 3, fig. 4.4.

2019 *Eutrephoceras (Simplicioceras) centrale* (J. Sowerby); LeBlanc, p. 53, fig. 10-06 G.

Materials: Four samples, three moderately-preserved and one poorly preserved, were obtained from the Middle Eocene (Lutetian) Midawara Formation at the Minqar El-Rayan and Qusour El-Arab sections.

Description: The shell is characterized by a medium size, coiled and elongated shape with a narrow elongated aperture, involute coiling, and sutures that range from relatively straight to highly sinuous lines. The diameter ranges from 35.0-62.0 mm, the whorl height from 22.0-33.0 mm, the whorl breadth from 31.0-37.5 mm, and the umbilical width from 3.0-5.0 mm (Table 2; Fig. 4e-m). The flanks are convex, the umbilicus is rounded, somewhat wide and shallow, and the whorls are laterally flattened and ventrally rounded. Additionally, the ventral saddle is broadly rounded, the lateral lobe is narrowly rounded, and the siphuncle is located in a sub-dorsal position. The shell surface is smooth with fine and closely spaced lines that running longitudinally.

Table 2. Dimensions of the *Eutrephoceras* (*Simplicioceras*) *centrale* (J. Sowerby)

Specimen No.	Diameter (mm)	Whorl Height (mm)	Whorl Breadth (mm)	Umbilical Width (mm)
CQM6-3	54.0	31.0	37.5	4.0
CQM6-4	55.0	33.0	37.0	~5.0
CQM6-5	62.0	30.5	35.5	-
CN14-6	35.0	22.0	31.0	3.0

Remarks: *Nautilus centralis* is relatively large and rounded nautiloid, which is characterized by its ventricose shell shape, bluntly lunate aperture, narrow and deep umbilicus, simple and concave septa with broad dorsal lobes, small and central siphuncle, and prominent growth lines (Edwards 1849).

Distribution and age: *Eutrephoceras* (*Simplicioceras*) *centrale* was documented from the Eocene of England (Edwards 1849), the Lutetian of Germany (Schultz 1976), the Lower Eocene of Spain (Díaz 1989), Austria, England, Switzerland, Germany, and Italy, and the Upper Eocene of Romania, Austria, and Hungary (Moosleitner 2004), from the Lutetian stages of Croatia (Mikuž and Bartol 2012). Additionally, it has been reported from the Upper Eocene strata of the Siwa Oasis in the North Western Desert (Aly and Sadek 2019).

Family: Hercoglossidae SPATH 1927

Genus: *Aturoidea* VREDENBURG 1925

Type-species: *Nautilus parkinsoni* Edwards (1849)

Aturoidea parkinsoni (EDWARDS 1849)

(Fig. 5a-i)

1849 *Nautilus parkinsoni* Edwards, p. 49, pl. vii.

1947 *Aturoidea parkinsoni* (Edwards); Miller, p. 69, pl. 49, figs. 1, 2.

1951 *Aturoidea* aff. *parkinsoni* (Edwards); Miller, fig. 15 A.

2019 *Aturoidea parkinsoni* (Edwards); Aly and Sadek, p. 3, fig. 3(1-4).

Materials: Four moderately to well-preserved samples were collected from the Middle Eocene (Lutetian) Midawara Formation at the Qusour El-Arab and Minqar El-Rayan sections.

Description: The discoidal shell is characterized by its moderate size, regular convexity, and elongated elliptical aperture. It exhibits a slightly large and shallow umbilicus with rounded shoulders. Shell's dimensions range from 33.5 to 86.0 mm in diameter, 19.0 to 46.0 mm in whorl height, 16.0 to 39.0 mm in whorl breadth, and 2.0 to 10.0 mm in umbilical width (Table 3; Fig. 5a-i). The moderately concave septa possess angular lobes on either side, while the moderately large siphuncle is positioned dorsally, along the midway between the center and the margin of the septum. The shell features involute coiling with flattened flanks converging towards the slightly compressed and rounded venter. Sigmoidal suture lines and a siphuncle are poorly preserved in some specimens.

Fig. 4 *Euciphoceras regale* (J. Sowerby) and *Eutrephoceras* (*Simplicioceras*) *centrale* (Sowerby) from the Midawara Formation, Fayum Depression, Egypt. **(a-d)** *E. regale* specimens from the Qusour El-Arab section (CQM8-4, CQM8-5). **(e-m)** *E.* (*S.*) *centrale* specimens from the Minqar El-Rayan (CN14-1, 2) and Qusour El-Arab (CQM6-4, CN14-1, CQM6-3) sections. Black arrows in **(f)** refer to *Entobia* boring and in **(e and k)** refers to crystallization of celestite minerals.

Table 3. Dimensions of the *Aturoidea parkinsoni* (Edwards)

Specimen No.	Diameter (mm)	Whorl Height (mm)	Whorl Breadth (mm)	Umbilical Width (mm)
CQM8-2	76.5	40.0	39.0	~10.0
CQM8-3	86.0	46.0	39.0	8.0
CQM8-7	33.5	19.0	16.0	~2.0
CN71	35.0	20.0	16.5	2.5

Remarks: Overall, *Aturoidea parkinsoni* is a moderately sized, discoidal nautiloid characterized by its distinct shell morphology and suture patterns. It lacks the wide trumpet-mouthed funnel, typically associated with *Aturia* (Edwards 1849). The samples are moderately preserved and filled with a light-colored heavy mineral, most likely celestite (Gingerich 1992). Miller (1947) noted that the *Aturoidea parkinsoni* (Edwards), previously reported by Spath (1927) from the London Clay, was the only specimen among Spath's collection that exhibits a notable resemblance to an American form.

Distribution and age: *Aturoidea parkinsoni* is recorded for the first time from the Lower Eocene formations of England (Edwards 1849). It is also recorded from the Lower Eocene strata of Spain (Calzada and Viader 1983). Locally, *Aturoidea parkinsoni* is identified from the Upper Eocene strata of Siwa, North Western Desert, Egypt (Aly and Sadek 2019).

Genus: *Deltoidonautilus* SPATH 1927

Type-species: *Nautilus pompilius* Linné, 1758

Deltoidonautilus sowerbyi (J. SOWERBY 1843)

(Fig. 5j-l)

1843 *Nautilus sowerbyi* Wetherell 1836, in J. Sowerby, p. 35, pl. 627, figs. 1-3.

1849 *Nautilus sowerbyi* Wetherell; Edwards, p. 48, pl. viii, fig. 3.

1952 *Deltoidonautilus spathi* Haas and Miller, pl. 29, fig. 3; pl. 30, figs. 1, 2

1997 *Deltoidonautilus sowerbyi* (J. Sowerby); Jeffery and Tracey, p. 103, pl. 15, figs 9-10.

2008 *Angulithes sowerbyi* (Wetherell); Galácz, p. 161, pl. 5; pl. 6, fig. 1; text-fig. 8.

2019 *Deltoidonautilus sowerbyi* (J. Sowerby); LeBlanc, p. 50.

Materials: Four samples, moderately preserved, were collected from the Middle Eocene (Lutetian) Midawara Formation at the Qusour El-Arab section.

Description: The shell is moderately sized and exhibits involute oxycone morphology with a small, shallow umbilicus, characterized by rounded shoulders and sloping walls. Measurements range from 47.5-71.5 mm in diameter, 24.0-42.0 mm in whorl height, 19.0-39.0 mm in whorl breadth, and 3.0-4.5 mm in umbilical width (Table 4; Fig. 5j-l). The venter is distinctly egg-shaped or peak-shaped, while the aperture is narrow and elongated. Although poorly preserved, suture lines appear simple, relatively undulating, and straight. The flanks are slightly convex and converge toward the venter, where the whorls exhibit a narrowly rounded or subangular profile. The siphuncle, obscured by sediment, is likely small and dorsal. The shell surface is exhibiting fine, closely spaced longitudinal lines. The phragmocone, in a state of poor preservation, hinders the determination of chamber number and morphology.

Table 4. Dimensions of the *Deltoidonautilus sowerbyi* (Wetherell)

Specimen No.	Diameter (mm)	Whorl Height (mm)	Whorl Breadth (mm)	Umbilical Width (mm)
CQM6-1	60.0	40.0	28.0	3.0
CQM6-2	47.5	24.0	19.0	-
CQM8-1	71.5	42.0	39.0	4.5
CQM8-6	58.0	40.0	30.0	3.0

Remarks: Edwards (1849) noted that *D. sowerbyi* is characterized by its smooth, discoidal shell with a slightly lenticular shape. It differs from *Aturia zic-zac* in its narrower margins, which resulted in a triangular aperture. While Haas and Miller (1952) initially proposed *D. spathi* as a distinct species, recent researches (Jeffery and Tracey 1997; LeBlanc 2019) have suggested that these morphological differences may not be sufficient to warrant separate species status. Based on the analysis of available specimens, *D. spathi* and *D. sowerbyi* appear to be synonymous, and representing a single species. Furthermore, our study indicates that *Angulithes sowerbyi* (Wetherell), as described by Galácz (2008), is also synonymous with *D. sowerbyi*. This aligns with the taxonomic classification adopted by several previous authors (e.g., Haas and Miller 1952; Jeffery and Tracey 1997), supporting the use of the name *D. sowerbyi* for this species. The Paleocene *D. polymorphus* (Hewaidy and Azab 2002) closely resembles the *D. sowerbyi* of the current specimens, but the *D. polymorphus* exhibits a compressed platycone outline and slightly larger umbilicus.

Distribution and age: *Deltoidonautilus sowerbyi* was reported from the Lower Eocene strata of England (Edwards 1849), Middle

Eocene (Lutetian) of Somalia (Haas and Miller 1952), the Early Eocene of London (Jeffery and Tracey 1997), the Upper Eocene strata of Hungary (Galácz 2008), and the Early Eocene of Qatar (LeBlanc 2019).

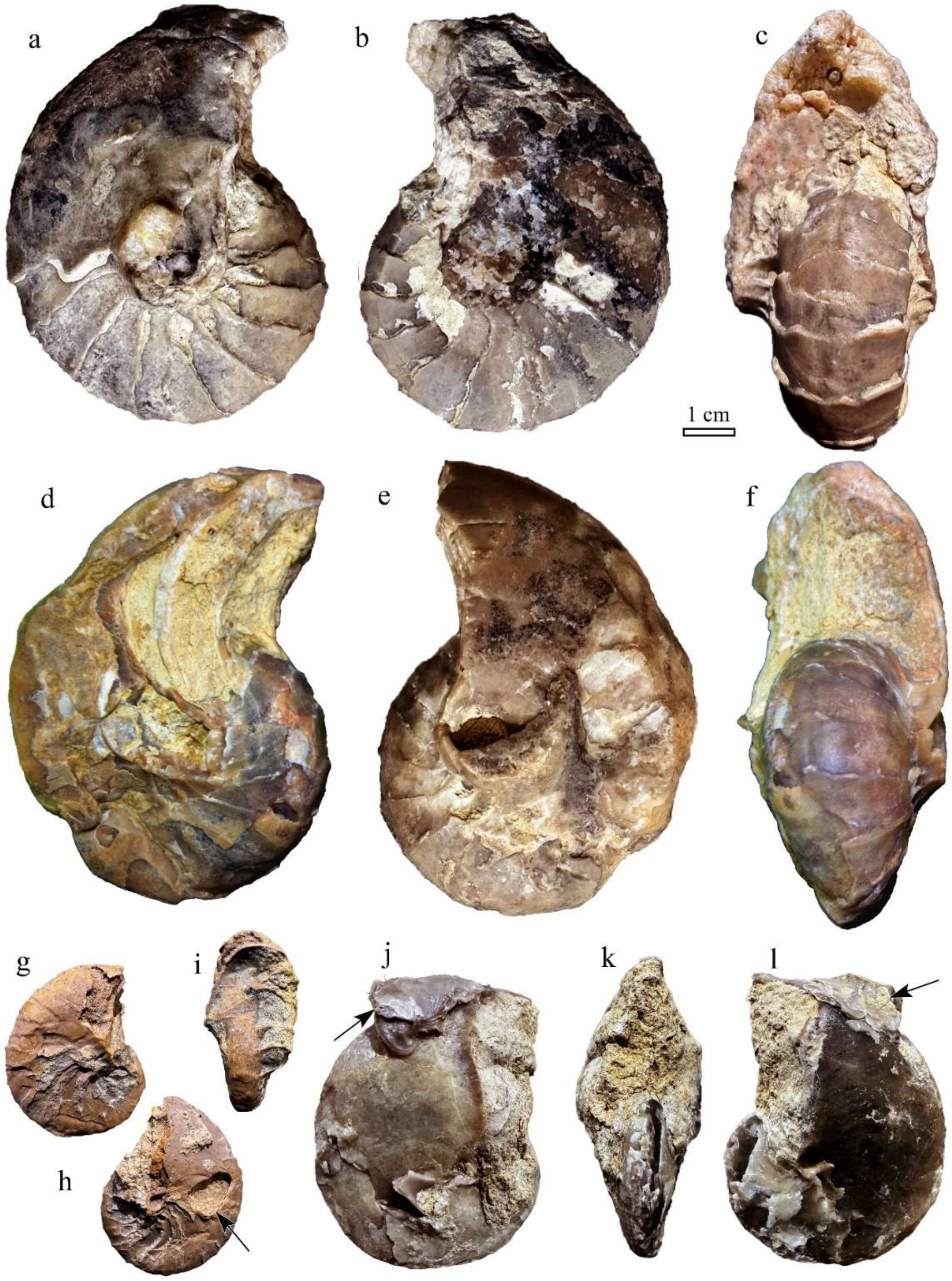

Fig. 5 *Aturoidea parkinsoni* (Edwards) and *Deltoidonautilus sowerbyi* (J. Sowerby), Midawara Formation at the Qusour El-Arab and Minqar El-Rayan sections. **(a-i)** *Aturoidea parkinsoni* (Edwards), sample no. CQM8-2, CQM8-3, and CN7-1, respectively. Black arrow in **(h)** refers to *Gastrochaenolites* boring. **(j-l)** *Deltoidonautilus sowerbyi* (J. Sowerby), sample no. CQM6-1. Black arrow in **(j and l)** refers to encrustations by small oyster shells.

Paleoecology

The paleoecology of cephalopods from the Lutetian Stage (Middle Eocene) of the Midawara Formation is deduced from the integration of sedimentary facies, the fossil assemblages and taphonomic / diagenetic features. The taphonomic features show varying degrees of fragmentation, erosion and transportation that observed in the nautiloid shells (Figs. 3-5). The paleoecology of nautiloids is a challenging task to be reconstructed due to post-mortem processes and the limited understanding of modern species of *Nautilus*. However, by analyzing factors like modern *Nautilus* ecology, in addition to the fossilized features such as aperture configuration, abrasion, encrustation and bioerosion (Figs. 4, 5), in addition to facies relationships, we concluded that nautiloids were likely active, deep-sea predators and scavengers with a nekton-benthic lifestyle. They were capable of swimming and interacting with the seafloor (Furnish and Glenister 1964).

The abrasion observed in some nautiloids is likely a result of repeated contact with the seafloor (Furnish and Glenister 1964). This abrasion is more likely preserved in active nekton-benthic nautiloids, as they could not add new shell material after reaching a full maturity. According to Iledgpeth and Ladd (1957), nautiloids are not pelagic but lives near or on the seafloor, although they are capable of free swimming as nektonic organisms. They can flourish in water-depth range of approximately 300–650 m deep. If they are found in shallower depths, it is most likely due to either nocturnal migration (50–70 m) in swarms or as the result of post-mortem transportation (Iledgpeth and Ladd 1957).

In the present study, we observed some rhyncholites (calcitic elements of the jaws), which provide valuable insights into the past food webs, and offered information that cannot be inferred solely from shells (Furnish and Glenister 1964). The distribution of rhyncholites often differs from that of associated conchs, potentially due to the detachment of rhyncholites from decaying nautiloids near their habitats, while empty shells underwent more extensive post-mortem dispersal (Furnish and Glenister 1964; Souquet et al. 2024). The presence of rhyncholites within the Midawara Formation suggests that these marine organisms were buried in or near their original habitats and the post-mortem transportation is weak to improbable. Furthermore, the shallow-water environment may be attributed to the reported fossil assemblages that indicate that the nautiloids most likely died during their nocturnal migrations.

The fossilized cephalopod shells exhibit moderate to high levels of diagenesis, which include cementation, dissolution and diagnostic crystallization of celestite minerals (Figs. 4a, 4e, 4k). The bioerosion in the nautiloid shells are represented by abundant borings of the *Gastrochaenolites* (Fig. 5h) and rare small-sized borings of *Entobia* (Fig. 4f). Frequent encrustations by small oyster shells are observed (Figs. 5j, 5l). The reported bioerosion and encrustations imply that these shells were exposed on the sea floor to various marine animals and possible transportation before buried in the substrate under low-sedimentation rates and weak wave / current velocities. Additionally, the presence of nautiloid shells within highly bioturbated and fossiliferous sandstone facies reflects a rich nutrient, calm environment and normal-marine salinities, possibly in an open-marine bay.

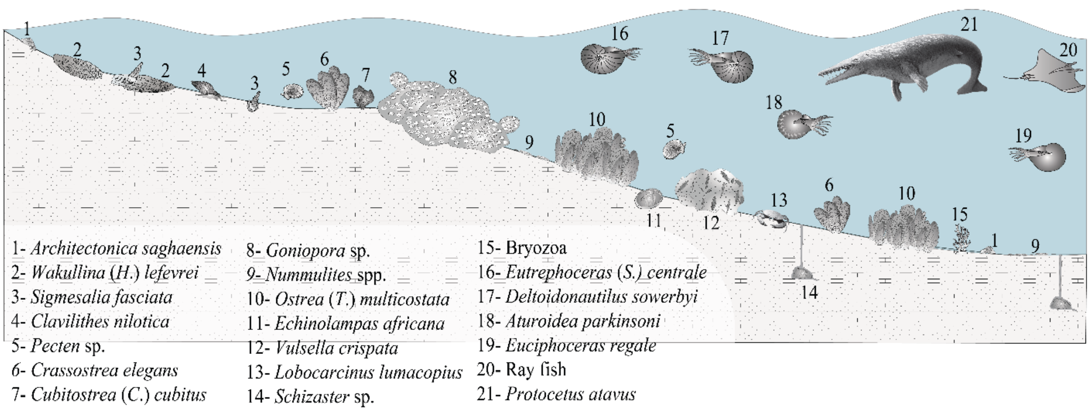

Fig. 6 Paleoecological reconstruction two-dimensional profile of the Middle Eocene Midawara Formation, Fayum, Egypt, depicting the shallow-marine habitat preferences and interactions of nautiloids and associated macrofauna. The diagram illustrates a productive, open-shelf environment with a diverse and interconnected food web.

Finally, the associated invertebrate assemblage is highly diversified (Fig. 6) and comprises abundant LBF (e.g., *Nummulites biarritzensis* D´Archiac and Haime, *N. midawaraensis* Kenawy); and rare to locally common Anthozoa (e.g., *Goniopora* sp.) and arthropods (*L. lumacopius*), common bivalves (e.g., *Cubitostrea* (*C.*) *cubitus* (Deshayes), *Crassostrea elegans* (Deshayes), *Ostrea* (*T.*) *multicostata* (Deshayes), *Vulsella crispata* Fischer *Wakullina* (*H.*) *lefevrei* (Fischer), and *Pecten* sp.), gastropods (e.g., *S. fasciata*, *Architectonica saghaensis* Abbass, and *Clavilithes nilotica* (Abbass)), and echinoids (e.g., *Echinolampas africana* De Loriol and *Schizaster* sp.; Notable vertebrate remains such as whale bones, fish scales, and shark teeth are also present. These faunal assemblages coincide with the stratigraphic occurrence of early ancient whales *Protocetus atavus* and *Eocetus schweinfurthi*. Most of the marine organisms such as LBF, anthozoa, bivalves, gastropods, and cephalopods, reported above, can thrive in temperatures between 0° and 35°C and an average salinity of approximately ~ 35% (Iledgpeth and Ladd 1957). The preceded diverse faunal invertebrate / vertebrate associations confirm that the cephalopod shells lived in clear and lighted water, under shallow-marine conditions, normal-marine salinity, and predominant calm habitats that are well oxygenated and nutrient-rich niches.

Paleogeography

The paleogeographic distribution of the reported cephalopod species (*Euciphoceras regale*, *Eutrephoceras* (*Simplicioceras*) *centrale*, *Aturoidea parkinsoni*, and *Deltoidonautilus sowerbyi*,) shows a widespread presence throughout the Eocene epoch in the Tethyan provinces. These species have been also documented from various localities across Africa (e.g., Egypt and Somalia), the Asia (Middle East and Qatar) and Europe (including England, Spain, Hungary, Romania, Austria, Italy, Germany and Belgium) (see Figs. 7–9). The geographic range of these species highlights the adaptability and resilience of cephalopods during the Eocene Epoch, as they inhabited diverse marine environments within the Tethys Sea, particularly during the Lutetian age.

Aturoidea parkinsoni has been documented in the Eocene formations of England (Edwards 1849) and Spain (Calzada and Viader 1983). Additionally, this species has been identified from the Upper Eocene strata of the Siwa Oasis, North Western Desert, Egypt (Aly and Sadek 2019) (Figs. 7–9). *Deltoidonautilus sowerbyi* has a wide geographic distribution, and it has been documented in the Eocene of England (Edwards 1849; *Kummel 1956*), the Middle Eocene (Lutetian) of Somalia (Haas and Miller 1952), the E arly Eocene of London (Jeffery and Tracey 1997), the Upper Eocene of Hungary (Galácz 2008), and the Early Eocene of Qatar (LeBlanc 2019). This species, along with D. somaliensis and D. moli, is found in the Eocene deposits of England and Sudan-Senegal (Haas and Miller 1952) (*Figs. 7-9*). Euciphoceras regale has a broad geographic distribution. It has been documented in various Eocene-age deposits, including the Early Eocene of England (Edwards 1849; Jeffery and Tracey 1997; Lesport et al. 2021), the Lower Eocene strata of Belgium (Dupuis and Robaszynski 1986), and the Middle Eocene (Lutetian) strata of Hungary (Galácz 2004) (Figs. 7-9).

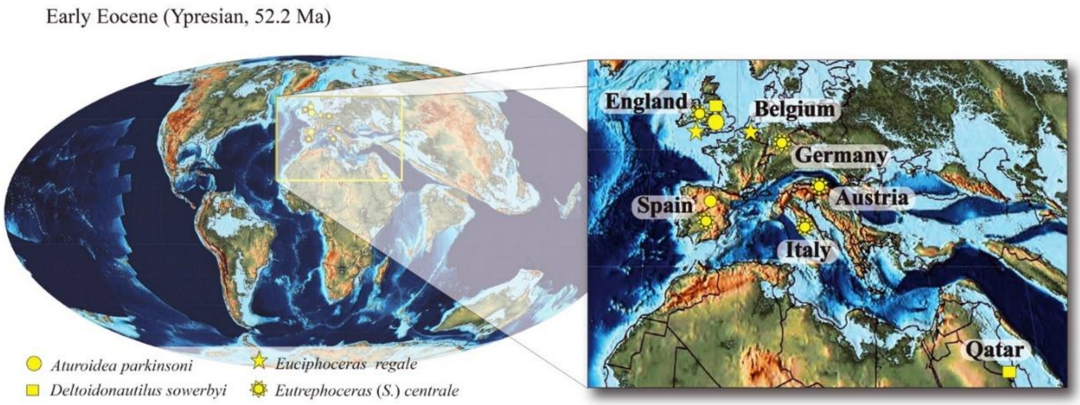

Fig. 7 A Paleogeographic map illustrating the distribution of Early Eocene nautiloids (Data based mainly on Edwards 1849; Calzada and Viader 1983; Dupuis and Robaszynski 1986; Díaz 1989; Jeffery and Tracey 1997; Moosleitner 2004; LeBlanc 2019).

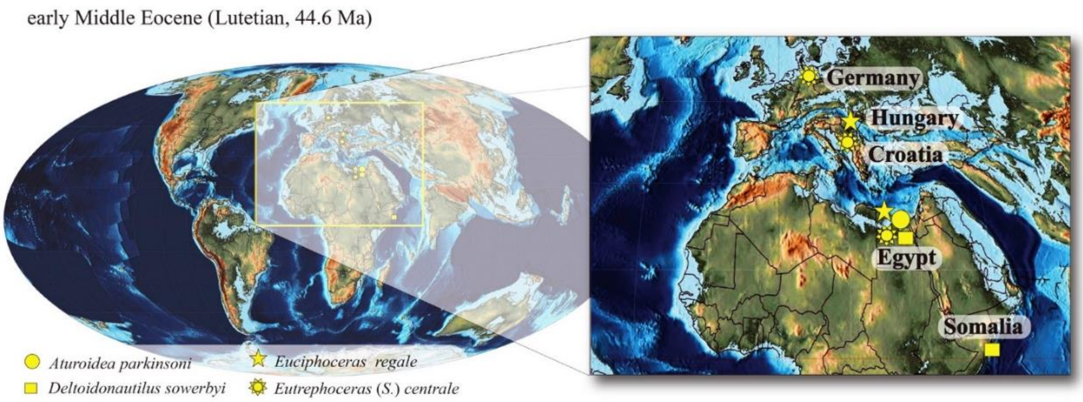

Fig. 8 Paleogeographic map, showing the distribution of Middle Eocene nautiloids (data from Edwards 1849; Haas and Miller 1952; Schultz 1976; Galácz 2004; Mikuž and Bartol 2012; and the present study).

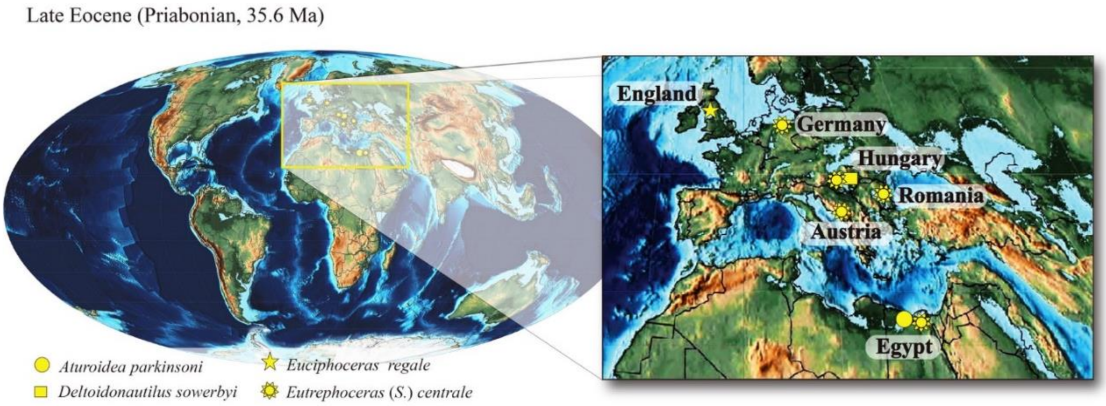

Fig. 9 Paleogeographic map depicting the distribution of Late Eocene nautiloids (data derived from the previous studies of Edwards 1849; Moosleitner 2004; Galácz 2008; Aly and Sadek 2019; Lesport et al. 2021).

The *Eutrephoceras* (*Simplicioceras*) *centrale* was documented from the Eocene strata of England (Edwards 1849), the Lutetian formations of Germany (Schultz 1976), and Lower Eocene strata of Spain, England, Switzerland, Germany and Italy (Díaz 1989). It is also reported from the Upper Eocene deposits from Romania, Austria and Hungary (Moosleitner 2004), and from the Lutetian-stage beds of Croatia (Mikuž and Bartol 2012). Importantly, it has been reported from the Upper Eocene strata of the Siwa Oasis in the North Western Desert (Aly and Sadek 2019) (Figs. 7–9).

Deltoidonautilus and *Aturoidea*, members of the aturiid clade, demonstrated a cosmopolitan distribution during the Eocene Epoch, inhabiting both shallow-water and near-surface oceanic environments (Dzik and Gaździcki 2001). Jeffery and Tracey (1997) reported a poorly preserved specimen tentatively identified as *Euciphoceras regale*. Due to the specimen's degraded condition and the associated uncertainty in identification, this record will not be included in our analysis. Dzik and Gaździcki (2001) documented a compressed specimen of *Euciphoceras* that closely resembles the modern *Nautilus* in terms of shell shape and siphuncle location. This specimen is housed at the Naturhistoriska Riksmuseet in Stockholm. This compressed type of the *Euciphoceras has been* collected from the Eocene tropical deposits of Fayum area, Egypt.

Discussion

The Eocene Epoch is characterized by significant climatic fluctuations that started with the Paleocene-Eocene Thermal Maximum (PETM), Early Eocene Climatic Optimum (EECO) and the subsequent cooling trend, which profoundly influenced the marine ecosystems and habitats of the cephalopods. Then, the Middle Eocene (Bartonian) witnessed a brief warming event that known as the Middle Eocene Climatic Optimum (MECO) (Bohaty and Zachos 2003; Gingerich 2006; Jovane et al.

2007). The dominance of large foraminifera in the Middle Eocene (Lutetian), especially *Nummulites*, suggests a relatively shallow, warm, and nutrient-rich marine environment (BouDagher-Fadel 2008; BouDagher-Fadel and Price 2014). The accompanied diverse assemblage including mollusks, bivalves, gastropods and cephalopods indicates a productive marine ecosystem with abundant food resources and a shallow-marine setting (Banerjee et al. 2019). Moreover, the presence of corals further suggests clear, well-oxygenated, and warm waters (Iledgpeth and Ladd 1957).

The diverse assemblage of benthic Mollusca, associated with the cephaolopd shells, preserved in the thin limestone bed of the Middle Eocene (Lutetian) Midawara Formation suggests a shallow-marine carbonate platform or ramp, which is characterized by nutrient-rich habitats, normal-marine salinity and open-shelf environment. The dominance of large foraminifera like *Nummulites midawaraensis* points to a relatively shallow continental shelf (BouDagher-Fadel 2008; BouDagher-Fadel and Price 2014). The presence of *Euciphoceras* sp., a species commonly inhabits shallower depths (e.g. Dzik and Gaździcki 2001) furtherly supports a shallow-marine environment in the Fayum area.

The diverse fauna within the Midawara Formation, including irregular echinoids, bivalves, gastropods, cephalopods, and corals, indicates a complex and productive marine ecosystem. Irregular echinoids like *E. africana* suggest shallow infaunal deposit-feeding lifestyles, while *Schizaster* sp. likely inhabited deeper sandy substrates (Kroh and Nebelsick 2003). *Crassostrea* sp., a filter feeder, played a crucial role in improving water quality and boosting primary productivity (Kasmini and Batubara 2022). Its dense populations may have formed reefs that provided habitat for diverse species. The co-occurrence of early whales with this assemblage further strengthens the evidence for abundant marine-food chains in this paleoenvironment. The presence of predators (such as gastropods, cephalopods, whales and sharks) and scavengers (e.g., crabs) suggests a complex food web, which reflects suitable conditions for the prosperity of marine life.

Although the Lutetian age was characterized by significant increase in cephalopod diversity, the Bartonian age witnessed a notable decline in cephalopod diversity. This decline might be attributed to severe environmental conditions analogous to those experienced during the MECO. The absence of the coral fossils of *Acropora* in the upper part of the Middle Eocene (Bartonian) Observatory Formation is contributed to the faunal changes observed during the MECO (El-Azabi 2023). Furthermore, Morabito et al. (2024) highlighted a shift towards dominance of LBF and a decline in corals during the early-late Bartonian, which is consistent with the environmental changes associated with the MECO event. It can be correlated to the extinction of benthic foraminifera during the PETM (Takeda and Kaiho 2007) as evidenced by the disaster of fauna, signifying a severe disruption of the marine ecosystem, which potentially led to deleterious conditions for cephalopods too.

Temperature-sensitive geochemical signatures preserved in sediments and fossil shells provided valuable insights into the environmental conditions that influenced cephalopod diversity during the Eocene (Jardine 2011). By analyzing these records, researchers can gain a deeper understanding of the intricate interplay between climate change and marine ecosystems, as well as the evolutionary history of cephalopods. The paleoecological evidence from the Middle Eocene (Lutetian) Midawara Formation suggests a shallow-marine environment with a diverse and productive ecosystem. The presence of various marine organisms, including cephalopods, highlights the favorable conditions for marine life during the Lutetian Stage of the Eocene. However, the decline in cephalopod diversity during the Bartonian age may be attributed to environmental disruptions linked to climate change events such as MECO.

Conclusion

The study identified four species of nautiloid cephalopods belonging to four distinct genera within the Nautilidae and Hercoglossidae families: *Euciphoceras regale*, *Eutrephoceras* (*Simplicioceras*) *centrale*, and *Aturoidea parkinsoni*, *Deltoidonautilus sowerbyi*. These species were described from the Middle Eocene Midawara Formation of the Fayum Depression, Egypt. The paleoecological analysis of cephalopods from the Midawara

Formation provides valuable insights into their lifestyle and habitat preferences during the Lutetian Stage. By integrating sedimentary facies, fossil assemblages, and taphonomic features, we can infer that these nautiloids were active, deep-sea predators and scavengers with a nektobenthic lifestyle, capable of swimming and interacting with the seafloor. The diverse associated fauna, including LBF, Anthozoa, arthropods, bivalves, gastropods, echinoids, and vertebrates, further supports a rich and dynamic marine ecosystem. The paleogeographic studies indicate that these species exhibited a widespread presence throughout the Tethys Sea during the Eocene Epoch. Their geographic range, encompassing Africa, Asia, and Europe, underscores their ability to thrive in various habitats, from shallow waters to deeper oceanic environments.

The paleoecological parameters deduced from the Middle Eocene (Lutetian) Midawara Formation indicate a shallow-marine environment and a marked diverse and productive ecosystem. Co-occurrences of diverse faunal association, including cephalopods, confirm favorable conditions for prosperity of marine life during the Lutetian age of the Middle Eocene. Less abundant cephalopod and general low diversity during the Bartonian age in the late Middle Eocene may be linked to the predominated climate change events MECO during this period of time.

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الملخص العربي

عنوان البحث: الوضع التصنيفي، بيئة الأحافير القديمة، والجغرافيا الحيوية القديمة للرأسقدميات النوتيلويدية من تكوين المدورة، الفيوم، مصر

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تَم التعرف على أربعة أنواع من الرأسقدميات (النوتيلويدات) تنتمي إلى جنسين: Nautilidae وHercoglossidae. وتشمل هذه الأنواع Euciphoceras regale، وEutrephoceras (Simplicioceras) centrale، وAturoidea parkinsoni، وDeltoidonautilus sowerbyi.. تم تجميع حفريات النوتيلويدات من تكوين المدورة في منطقتي قُصور العرب ومنقار الريان جنوب منخفض الفيوم، مصر، الذي يعود للعصر الإيوسيني الأوسط. تم وصف هذه الحفريات وصفًا تفصيلياً ودراسة بيئتها القديمة. حيث تشير الخصائص المورفولوجية و التحليل البيئي القديم للحفريات من تكوين المدورة إلى أن هذه النوتيلويدات كانت مفترسات نشطة في أعماق البحار وحيوانات تتغذى على المخلفات، تتمتع بأسلوب حياة مزدوج (سباح و قاعى)، قادرة على السباحة والتفاعل مع قاع البحر. تدعم الحفريات المصاحبة والمتنوعة، بما في ذلك الفورامنيفرا القاعية الكبيرة و المراجين والمفصليات والرخويات وقنافذ البحروعظام الفقاريات، وجود نظام بيئي بحري غني وديناميكي. كما يشير التوزيع الجغرافي الواسع لهذه الأنواع في بحر تيثيس إلى قدرتها على التكيف مع بيئات متنوعة في جميع أنحاء بحر تيثيس القديم خلال العصر الإيوسيني. وكذلك يبرز نطاقها الجغرافي، الذي يشمل إفريقيا وآسيا وأوروبا، قدرتها على الازدهار في مختلف البيئات، من المياه الضحلة إلى البيئات المحيطية العميقة. وتشير الخصائص البيئية القديمة المستنبطة من تكوين المدورة في العصر الإيوسيني الأوسط (اللوتيتي) إلى بيئة بحرية ضحلة ونظام بيئي متنوع. تؤكد التواجدات المشتركة والمتنوعة لتجمعات الحفريات، بما في ذلك النوتيلويدات، على الظروف المواتية لإزدهار الحياة البحرية خلال العصر اللوتيتي في الإيوسيني الأوسط.