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Eocene nautiloids from the Baja California Peninsula, Mexico: records, description of a new species, and biogeographic implications

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EOCENE NAUTILOIDS FROM THE BAJA CALIFORNIA PENINSULA, MEXICO: RECORDS, DESCRIPTION OF A NEW SPECIES, AND BIOGEOGRAPHIC IMPLICATIONS

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Abstract. Several cephalopods from the Eocene have been recorded along the Pacific coast of North America. Each new record incorporates relevant knowledge to infer the paleobiology of this group. In this study, we report two nautiloids (subclass Nautiloidea) from the Ypresian found in the Tepetate Formation. One specimen was identified as *Eutrephoceras hannai,* and the other was designated as *species nova*, *Nautilus sudcalifornianus*. We found that the suture shape, especially in the lateral lobe, is the most conspicuous diagnostic feature to discriminate nautiloids. Moreover, the biological material evaluated in our study constitutes the southernmost geographic distribution of the two species and the most ancient record of Nautilidae for the Eocene. Due to the characteristics detected in the specimens analyzed here and previous studies that describe the faunal diversity of the formation, we hypothesize that this area was an idoneous site for spawning and growth of young stages of *E. hannai* and *N. sudcalifornianus* sp. nov. during the Eocene. Thus, our study supports the hypothesis that extant nautiloids migrate towards warm shallow water areas for spawning and growth of the juvenile stage and suggests that this migratory behavior is ancient within the subclass. With this research, we provide new insights into the taxonomy, biology, ecology, and biogeography of nautiloids from the Eocene. Additionally, the Tepetate Formation has great geological and paleontological relevance given the faunal diversity discovered in this area increases the malacological record for the northeastern Pacific.

Key words. Cephalopoda. Ypresian. *Nautilus*. Tepetate Formation. Nautilidae.

Resumen. NAUTILOIDEOS DEL EOCENO DE LA PENÍNSULA DE BAJA CALIFORNIA, MÉXICO: REGISTROS, DESCRIPCIÓN DE UNA NUEVA ESPECIE E IMPLICANCIAS BIOGEOGRÁFICAS. Se han reportado varios cefalópodos del Eoceno a lo largo de la costa del Pacífico de Norteamérica. Cada registro nuevo incorpora conocimiento relevante para inferir la paleobiología de este grupo. En este estudio reportamos dos nautiloideos (subclase Nautiloidea) del Ypresiense encontrados en la Formación Tepetate. Un espécimen fue identificado como *Eutrephoceras hannai* y otro fue designado como *species nova*, *Nautilus sudcalifornianus*. Encontramos que la forma sutural, especialmente en el lóbulo lateral, es el carácter diagnóstico más conspicuo para discriminar nautiloideos. Asimismo, el material biológico evaluado en nuestro estudio constituye tanto la distribución geográfica más sureña de ambas especies, como el registro más antiguo de Nautilidae para el Eoceno. Otro aspecto que considerar es que, debido a las características detectadas en los especímenes aquí analizados y también a estudios previos que describen la diversidad faunística de la Formación Tepetate, hipotetizamos que esta área era un sitio idóneo para el desove y crecimiento de la etapa juvenil de *E. hannai* y *N. sudcalifornianus* sp. nov. durante el Eoceno. En este sentido, nuestro estudio apoya la hipótesis de que los nautiloideos actuales migran hacia aguas cálidas someras para el desove y crecimiento de la etapa juvenil, y sugiere que este comportamiento migratorio es antiguo dentro de la subclase. Esta investigación proporciona nuevas perspectivas sobre taxonomía, biología, ecología y biogeografía de los nautiloideos del Eoceno. Adicionalmente, la Formación Tepetate ha demostrado tener gran relevancia geológica y paleontológica dado que la diversidad faunística de esta área incrementa el registro malacológico para el Pacífico nororiental.

Palabras clave. Cephalopoda. Ypresiense. *Nautilus*. Formación Tepetate. Nautilidae.

THE ORIGIN of modern nautiloids (Nautiloidea Agassiz, 1847) is very recent (1–5 Ma) compared with the origin proposed for the subclass (≈ 500 Ma) (Teichert & Matsumoto, 2010; Kröger *et al.*, 2011). At present, all species belong to the family Nautilidae Blainville, 1825, and their distribution is restricted to the Indo-Pacific (Boyle & Rodhouse, 2005). There is substantial knowledge concerning their biology (*e.g.*, Barord & Basil, 2014; Ward *et al.*, 2016a; Barord *et al.*, 2023), although there are certain aspects that still require endorsement. This could be attained by analyzing the paleontological record, especially from strata where extinct cephalopods are newly discovered.

In general, the cephalopod record in the Western North American Province (WNAP) (Das & Halder, 2018) during the Paleogene is scarce. Previous to our work, in the Baja California Peninsula, only two nautiloid families (Aturiidae Chapman, 1857 and Hercoglossidae Spath, 1927) and genera (*Aturia* Bronn, 1838 and *Hercoglossa* Conrad, 1866), were detected; these specimens were discovered in the Bateque Formation (26° N) with an Early Eocene age (Squires & Demetrion, 1992). Besides from these records, other Paleogene cephalopods (all nautiloids) have been reported in the WNAP, specifically from California to Washington, USA (32–47° N), where the genera *Aturia, Cimomia* Conrad, 1866*, Eutrephoceras* Hyatt, 1894, and *Nautilus* Linnaeus, 1758 (including formerly *Kummelonautilus*) were identified (Anderson & Hanna, 1935; Miller, 1947; Miller & Downs, 1950; Palmer, 1961; Hickman, 1969; Squires, 1983, 1988, 2001; Goedert & Kiel, 2016). In this view, any new record for this biogeographic province contributes to the understanding of the evolutionary history and biogeography of the Cephalopoda Cuvier, 1795 at large.

In this study, we report two nautiloid specimens found in the Tepetate Formation (24° N), recovered in the southern portion of the State of Baja California Sur, between 70 and 150 km (Mexican Federal Highway 1) northwest of the La Paz city (Schwennicke *et al.*, 2004; Miranda-Martínez & Carreño, 2008; Morales-Ortega & González-Barba, 2018) (Fig. 1). The Tepetate Formation belongs to the group of the oldest Paleogene sedimentary units of marine and terrestrial origin in the State (Servicio Geológico Mexicano, SGM, 1999). This area is characterized by mudstone, siltstone, and sandstone sequences with ages ranging from the Late Cretaceous (Maastrichtian?) to the Middle Eocene (Heim, 1922; Mina-Uhink, 1957; Fulwider, 1976; Coleman, 1979; Galli-Olivier *et al.*, 1986; Schwennicke *et al.*, 2004, 2005; Miranda-Martínez & Carreño, 2008; García-Cordero & Carreño, 2009). While over ≈ 70% of the fauna identified in the Tepetate Formation comprises marine mollusks (Squires & Demetrion, 1991; Squires, 1992; Perrilliat, 1996; Morales-Ortega & González-Barba, 2018), our work is the first to report cephalopods.

GEOLOGICAL SETTING

Arroyo El Conejo

A portion of the Tepetate Formation crops out above the arroyo El Conejo (at kilometer 76 of the Mexican Federal Highway 1) (Vázquez-García, 1996; González-Barba, 2002; Schweitzer *et al.*, 2002, 2005; Morales-Ortega, 2010) (Fig. 1). In this locality, the outcrop is composed of Ypresian deposits (51±2 Ma, Eocene) from the continental shelf to the backshore (Vázquez-García, 1996). Its estimated age was obtained from zircon U-Pb in sandstone samples collected at ≈ 600 m in sites Te9 (24°09.7′ N, 100°55.5′ W) and Te14 (24°10.1′ N, 110°55.1′ W) (sandstone sample No. 75 in Fletcher *et al.*, 2007, tab. 1, p. 1322). In addition, this estimated age (51±2 Ma) was also confirmed through calcareous nannofossil sample analyses (Schwennicke, pers. comm.).

The sedimentary sequence is a shallow marine regressive sequence comprising continental shelf (≈ 50 m maximum depth) to upper shoreface depositional environments on an active continental margin (Figs. 2, 3). The lower part of the sedimentary sequence (the layer bearing marine specimens) is composed of clay, silt, and mudstone, was deposited below the lowest tide level, and was highly impacted by storm waves (Vázquez-García, 1996). The middle part of the sedimentary sequence was deposited above the lowest tide level and exhibits coarse material, probably transported from the upper to lower shoreface by rip currents, which caused erosion of the seabed and the formation of channels (later filled by regular sedimentation) (Vázquez-García, 1996). The upper part of the sedimentary sequence, composed of fine–to medium–grained sandstones, shows a high content of volcanic material, which could indicate moderate to high energy levels (Vázquez-García, 1996).

SAMPLING AND IDENTIFICATION

Two internal molds of nautiloids were collected at Arroyo El Conejo, Tepetate Formation (Fig. 1). The specimens were labelled and deposited in the paleontological reference

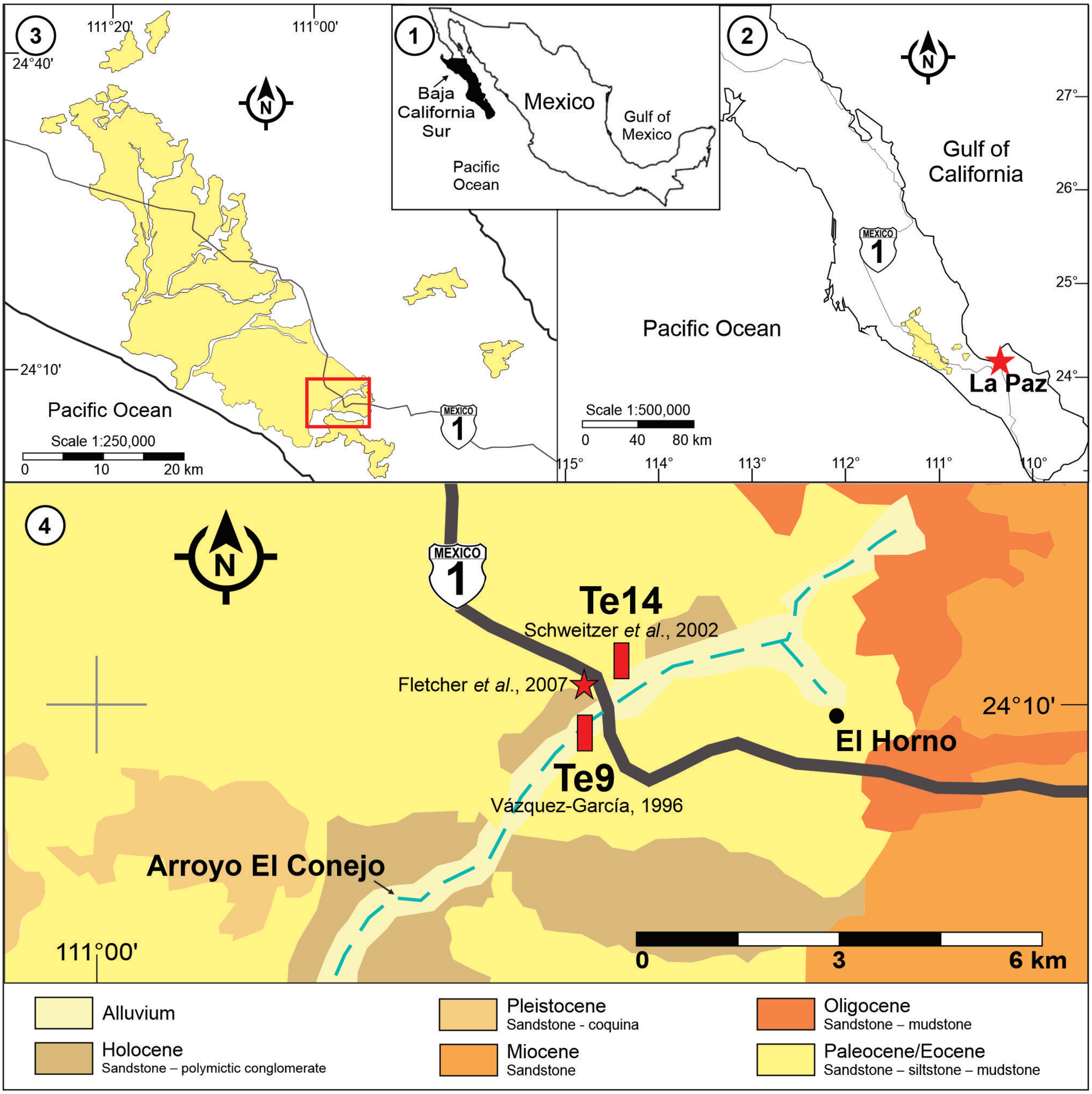

Figure 1. Study area; **1,** geographic location of the state of Baja California Sur, Mexico; **2,** proximity of the La Paz city to the outcrops of Tepetate Formation; **3,** outcrops of the Tepetate Formation depicting the location of the study area (red rectangle); **4,** Te14 site (northeast side) and Te9 site (southwest side) at Arroyo El Conejo; stratigraphic sections (red rectangles), and dating location by Fletcher *et al.*, (2007) (red star) (modified from SGM, 1999).

collection of marine invertebrates of the Museo de Historia Natural, Universidad Autónoma de Baja California Sur under acronym MHN-UABCS Te9/49/27 and MHN-UABCS Te14/66/65. The collection manager is Dr. Gerardo González-Barba, co-author of this research. Additionally, the record of the sampled specimens is publicly available at the Paleobiology Database (PBDB, https://paleobiodb.org/).

For taxon determination, the morphological features of the specimens collected were compared to those mentioned in original descriptions and specialized literature of candidate nautiloids (*i.e.* Linnaeus, 1758; Blainville, 1825; Hyatt, 1894; Vokes, 1937; Ruzhentsev *et al.*, 1962; Kummel, 1964;

Jereb & Roper, 2006). Measurements were recorded for each specimen using a vernier caliper (Tabs. 1, 2).

To depict morphological features, the specimens were photographed with a semi-professional camera and an X-ray image of each specimen was obtained (Figs. 4, 6). Digitized versions of the specimens were drawn for comparison with digitized versions of reference nautiloids (Figs. 5, 7, 8).

SYSTEMATIC PALAEONTOLOGY

Class CEPHALOPODA Cuvier, 1795
Subclass NAUTILOIDEA Agassiz, 1847
Order NAUTILIDA Agassiz, 1847
Family NAUTILIDAE Blainville, 1825

Genus ***Eutrephoceras*** Hyatt, 1894

Type species. *Eutrephoceras dekayi* Morton, 1834 (pl. VIII, fig. 4), by original designation. Upper Cretaceous, New Jersey, USA.

Eutrephoceras hannai

Figures 4, 5

1937. *Eutrephoceras hannai* Vokes, pp. 6–7, pl. 2, figs. 13, 14.

Material examined. Specimen MHN-UABCS Te9/49/27.

Description. Almost complete internal mold, 23 mm shell diameter (Tab. 1). The ventral view exhibits two incomplete, well-marked, slightly inclined sutures (Fig. 4.1). The small inclination is probably due to the burial or relocation of the specimen at the time of death or during the fossilization process. Sutures almost straight (Figs. 4.2–4.3, 6.4). Venter round; body chamber slightly displaced from the rest of the shell (post-mortem displacement) (Figs. 4.3–4.4, 5.4). Umbilicus closed. Longitudinal ridges visible over the coils (Fig. 4.2, 4.5).

Remarks. *Eutrephoceras* is strongly represented in the Pacific coast of USA. In Washington State, *E. eyerdami* Palmer, 1961 from the Middle Eocene (Bartonian) was reported in the Cowlitz Formation. In addition, fragments of

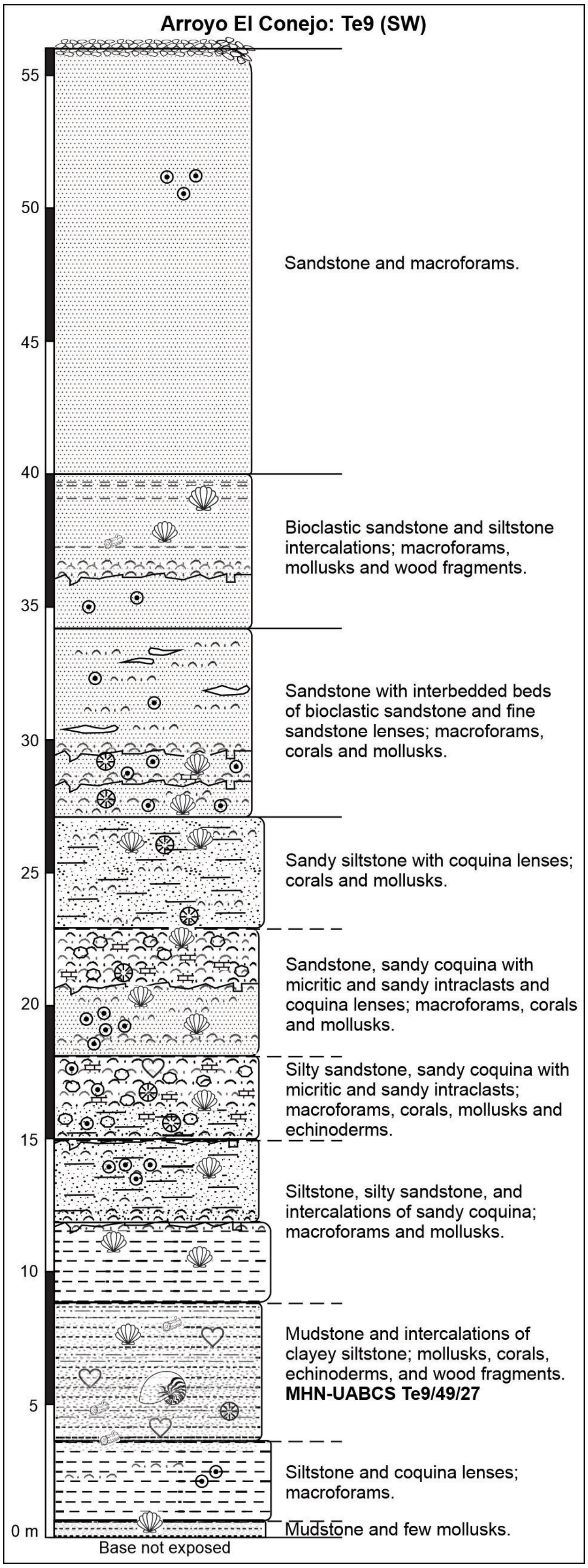

Figure 2. Stratigraphic section of locality Te9, modified from Vázquez-García (1996). The stratigraphic position where specimen **MHN-UABCS Te9/49/27** (***Eutrephoceras hannai***) was collected is depicted.

E. oregonense Miller, 1947 were recorded from the Oligocene in Oregon. In California, *E. hallidayi* Waring, 1914 and *E. stephensoni* Dickerson, 1914 were recorded from the Paleocene; *E. marksi* Miller, 1947 from the Middle Eocene (Bartonian) Tejon Formation; and *E. hannai* Vokes, 1937 from the Middle Eocene (Lutetian) Ardath Formation. The specimen MHN-UABCS Te9/49/27, found and described in this study, resembles *E. hannai* (Figs. 4, 5).

Among the main characteristics differentiating *E. hannai* from its congeners are the shell with a globular shape (wider than long) and the small umbilicus (covered by sediment in specimen MHN-UABCS Te9/49/27; Fig. 4.2–4.3). Chambers are markedly short. The external sutures are transversal, almost straight. The siphuncle is small and in subcentral position, closer to the dorsum compared with the venter (Fig. 5.3). Furthermore, while most of the morphological features characterizing *E. hannai* apply to *Eutrephoceras* in general, in this species, these characters are exacerbated, being easily discriminated from the rest of the species in the genus.

Moreover, specimen MHN-UABCS Te9/49/27 is at the juvenile stage, as it shows longitudinal ridges (Fig. 4.2, 4.5). Additionally, previous to our work, *E. hannai* was only known from four specimens exhibiting a maximum shell diameter of 50 mm (mean 40.1 mm shell diameter), which could be considered the size at maturity (adult stage) (Miller, 1947). Hence, the juvenile stage proposed for specimen MHN-UABCS Te9/49/27 is also confirmed by its shell diameter (23 mm).

In view of the taxonomic information available and of the preservation condition of specimen MHN-UABCS Te9/49/27, we were able to identify *E. hannai* with a high degree of certainty. However, we acknowledge that more accurate species discriminations will be achieved when more specimens and in better conditions are available for the genus *Eutrephoceras*, with which new taxonomic consensus should be made.

Finally, specimen MHN-UABCS Te9/49/27 is the most ancient record for *E. hannai* in the Eocene (Ypresian), which

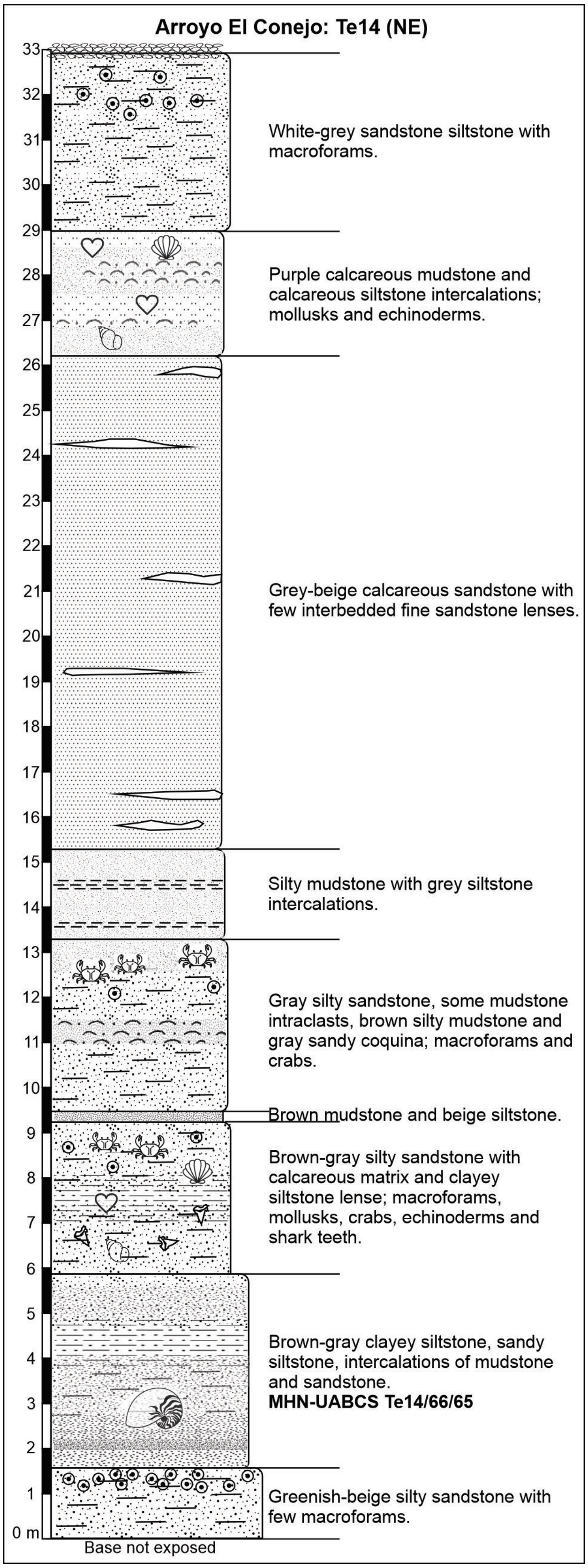

Figure 3. Stratigraphic section of locality Te14, modified from Schweitzer *et al.* (2002). The stratigraphic position where specimen **MHN-UABCS Te14/66/65** (***Nautilus sudcalifornianus*** sp. nov.) was collected is depicted.

TABLE 1 – Measurements of *Eutrephoceras hannai*

Character	Dimensions (mm)
Umbilicus diameter	–
Shell diameter	23
Whorl height	12
Whorl width	15
Dorso-ventral height	9
Siphuncle	0.9
Distance from the siphuncle to the venter	6
Distance from the siphuncle to the dorsum	2

TABLE 2 – Measurements of *Nautilus sudcalifornianus* sp. nov.

Character	Dimensions (mm)
Umbilicus diameter	16
Shell diameter	150
Whorl height	77
Whorl width	67
Dorso-ventral height	70
Siphuncle	–
Distance from the siphuncle to the venter	–
Distance from the siphuncle to the dorsum	–

increases both its age range, from Ypresian to Lutetian, and its geographic distribution range, from California, USA to Baja California Sur, Mexico.

Locality. Arroyo El Conejo, at kilometre 76 of the Mexican Federal Highway 1. Station Te9, southwest side (24°09.7′ N, 100°55.5′ W; Figs. 1.4, 2).

Age. Early Eocene, Ypresian (51±2 Ma).

Genus ***Nautilus*** Linnaeus, 1758

Type species. *Nautilus pompilius* Linnaeus, 1758, by subsequent designation by Montfort, 1808.

Nautilus sudcalifornianus sp. nov.

Figures 6, 7

LSID urn:lsid:zoobank.org:act:C187F469-25AC-4DA7-A8B9-1E3E3C427076

Derivation of name. *Nautilus sudcalifornianus* is designated due to the demonym used for Baja California Sur.

Diagnosis. Planispiral shell form of coiled chambered with involute growth. The suture shape is slightly less sinuous than other species of Eocene *Nautilus*. In particular, the lateral lobe is the most conspicuous diagnostic feature to discriminate nautiloids.

Type material. Specimen MHN-UABCS Te14/66/65.

Description. Internal mold almost complete. Planispiral shell shape. Maximum shell diameter 150 mm. Shell width ≈ 45% of shell diameter, shell height ≈ 54% of shell diameter, and umbilicus closed, ≈ 10% of shell diameter (Tab. 2). In apertural view, coils compressed and venter convex (Fig. 6.4). In lateral view, sutures (three incomplete, from umbilicus to venter) are slightly sinuous; a portion of a septum is

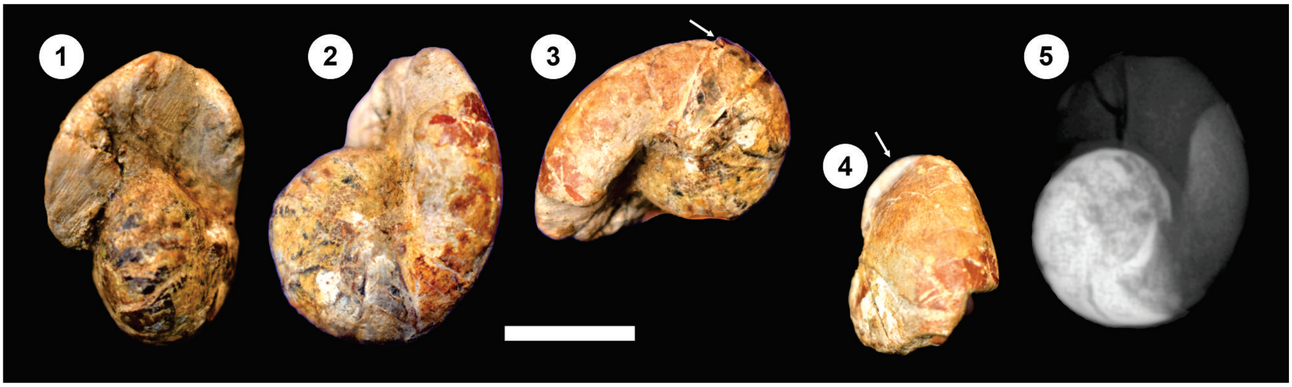

Figure 4. ***Eutrephoceras hannai*****, MHN-UABCS Te9/49/27; 1,** apertural view; **2,** right lateral view; **3,** right lateral view with arrow showing the body chamber slightly displaced from the rest of the shell (post-mortem displacement); **4,** ventral view with arrow showing the body chamber slightly displaced from the rest of the shell (post-mortem displacement); **5,** X-Ray image. Scale bar= 10 mm.

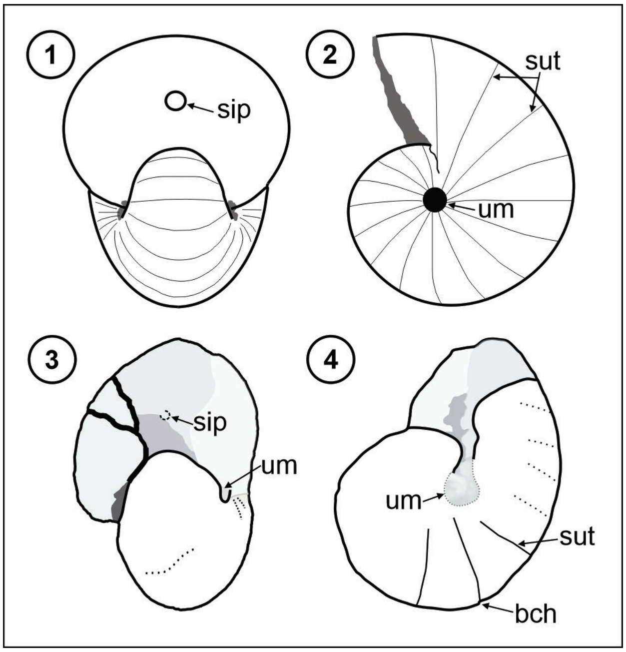

Figure 5. ***Eutrephoceras hannai***; **1,** apertural view reference image of the genus *Eutrephoceras* (LeBlanc, 2019); **2,** right lateral view reference image of the genus *Eutrephoceras* (LeBlanc, 2019); **3,** apertural view, digitized version of specimen **MHN-UABCS Te9/49/27** (***E. hannai***); **4,** right lateral view, digitized version of specimen **MHN-UABCS Te9/49/27** (***E. hannai***). Abbreviations: **bch**, body chamber (slightly displaced from the rest of the shell); **sip**, siphuncle; **sut**, suture; **um**, umbilicus.

noticeable as a result of mold fracture (Figs. 6.2, 7.2). In ventral view two incomplete inclined sutures are observable (Figs. 6.3, 7.3). Inclination is probably due to the burial or relocation of the specimen at time of death or during the fossilization process.

Remarks. The genus *Nautilus* is among the best represented cephalopod taxa in the fossil record (≈ 340 Ma), although for nautiloids in general, taxon determination is still in the process of debate (PBDB, 2023). Regardless of this taxonomic issue, some taxa are recognizable with a greater degree of certainty than others. In this sense, for genus level determination, we revised the original description provided by Linnaeus (1758) and the two great paleontological encyclopedias: the Treatise on Invertebrate Paleontology and the Osnovy Paleontologii, which mention that *Nautilus* shells are simple, without ornaments, involute and with simple or almost straight sutures (Fig. 7).

Moreover, despite the vast fossil record of *Nautilus*, before this study, only two species were described for the Eocene: *N. praepompilius* Shimansky, 1957 from Kazakhstan (Priabonian, 37.71 to 33.9 Ma) and *N. cookana* Whitfield, 1892 from New Jersey, USA (Lutetian to Priabonian 47.8 to 33.9 Ma), with a tentative record (*Nautilus* sp., aff. *N. cookana*, Priabonian, 37.71 to 33.9 Ma) in Washington, USA (Squires, 1988; Tab. 3). Thus, *Nautilus sudcalifornianus* sp. nov. is the most ancient record of *Nautilus* in the Eocene (Ypresian, 51±2 Ma) and in the Pacific coast of North America.

In the planispiral shell of *Nautilus sudcalifornianus* sp. nov., the suture shape greatly differs from that of its congeners, except for *N.* sp. aff. *N. cookana*, with which it shares a certain degree of similarity (Fig. 8.4). However, based on the descriptions and illustrations provided by Miller (1947, p. 30–31, plates 10–13) and Squires (1988, p. 76–78, figs. 2.1, 3.1–3.4), the sinuosity of the suture is more conspicuous in *Nautilus sudcalifornianus* sp. nov. For *N. cookana*, both authors (Miller formerly regarding *Eutrephoceras cookanum*, and Squires referring to *Nautilus* sp. aff. *N. cookana*) describe the suture shape as having a "broad lateral lobe", slightly deeper than in *Nautilus sudcalifornianus* sp. nov., which in

TABLE 3 – Species of genus *Nautilus* reported in the Eocene epoch

Species	Age	Location(s)	Author(s)
Nautilus praepompilius Shimansky, 1957	Priabonian (37.71 to 33.9 Ma)	North coast of the Aral Sea & Ustjurt Plateau, Kazakhstan	Saunders *et al.* (1996)
Nautilus sp. aff. *N. cookana* Whitfield, 1892	Priabonian (37.71 to 33.9 Ma)	Washington, USA	Squires (1988)
Nautilus cookana Whitfield, 1892	Middle Eocene (47.8 to 37.71 Ma)	New Jersey, USA	Miller (1947); Palmer & Brann (1965)
Nautilus sudcalifornianus sp. nov.	Ypresian (51±2 Ma)	Baja California Sur, Mexico	This study

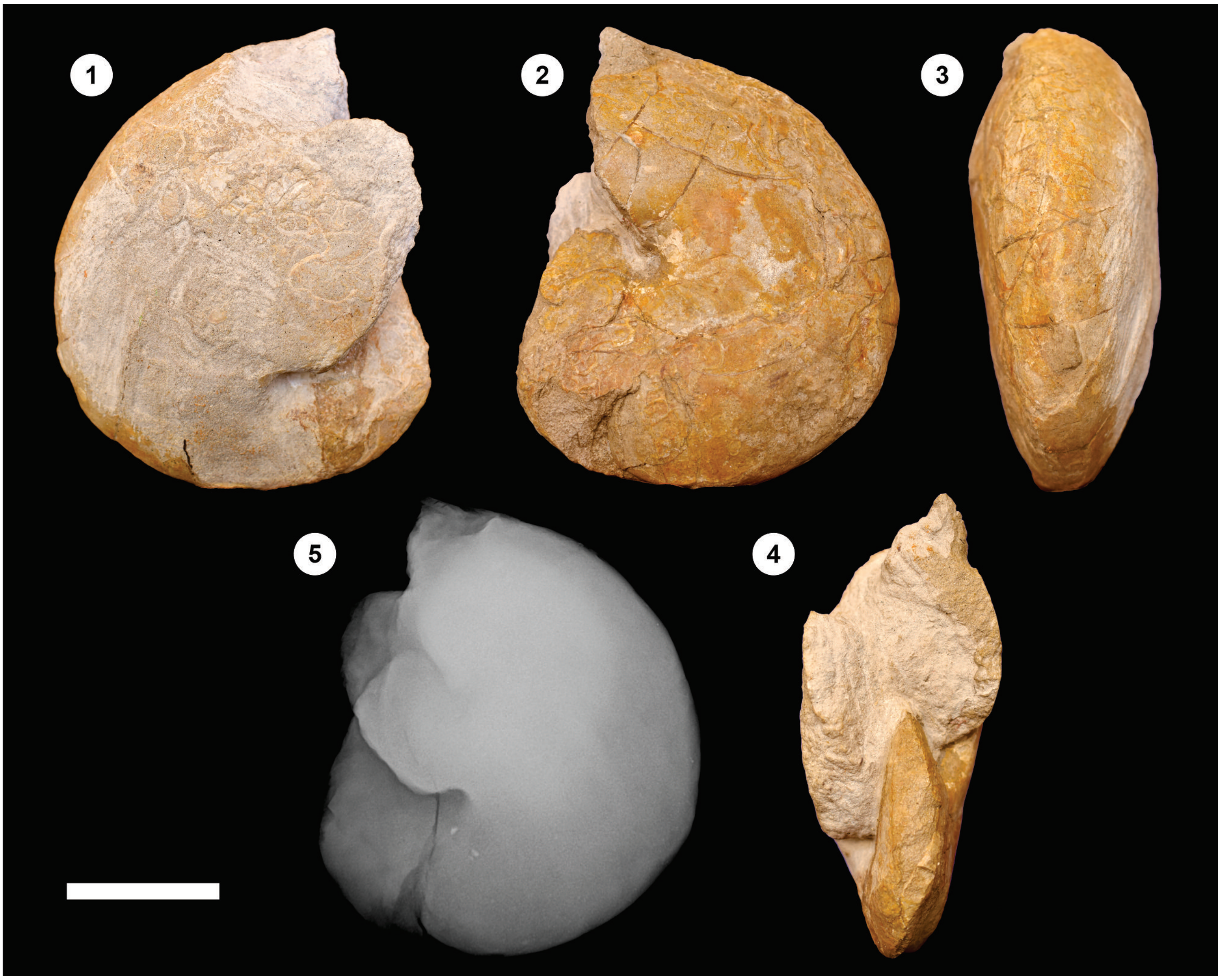

Figure 6. ***Nautilus sudcalifornianus*** sp. nov., **MHN-UABCS Te14/66/65**; **1,** left lateral view; **2,** right lateral view; **3,** ventral view; **4,** apertural view; **5,** X-Ray image. Scale bar= 50 mm.

contrast exhibits a more subtle concavity (Fig. 8.5). Furthermore, coinciding with our observations for the *species nova* described herein, *Nautilus* descriptions mention that the dorsal lobe is broad and in "V" shape (Fig. 8.5).

Finally, given its ancestry and distinct shape, we suggest that the suture of *Nautilus sudcalifornianus* sp. nov. is the basal shape for the genus *Nautilus* from the Eocene.

Type Locality. Arroyo El Conejo, at kilometre 76 of the Mexican Federal Highway 1. Station Te14, northeast side (24°10.1' N, 110°55.1' W; Figs. 1.4, 3).

Age. Early Eocene, Ypresian (51±2 Ma).

DISCUSSION

In this study, we found two fossil nautiloid specimens from Eocene strata in the Baja California Peninsula. Nautiloids exhibit an ancient origin, which is estimated to have been in the Early Cretaceous; and while their maximum diversity is estimated to have been reached by the Late Cretaceous, these cephalopods also seem to have had a wide geographic distribution and high species diversity during the Cenozoic (Halder, 2012; Ward *et al.*, 2016a). However, as with any cephalopod, the exact number of extant and extinct species is unknown. Therefore, new records are of relevance to better understand the evolutionary history of nautiloids, especially for the Cenozoic, given their distribution ranges and diversity in this Era. In this sense, in this work we provide the most ancient records of Nautilidae for the Eocene epoch,

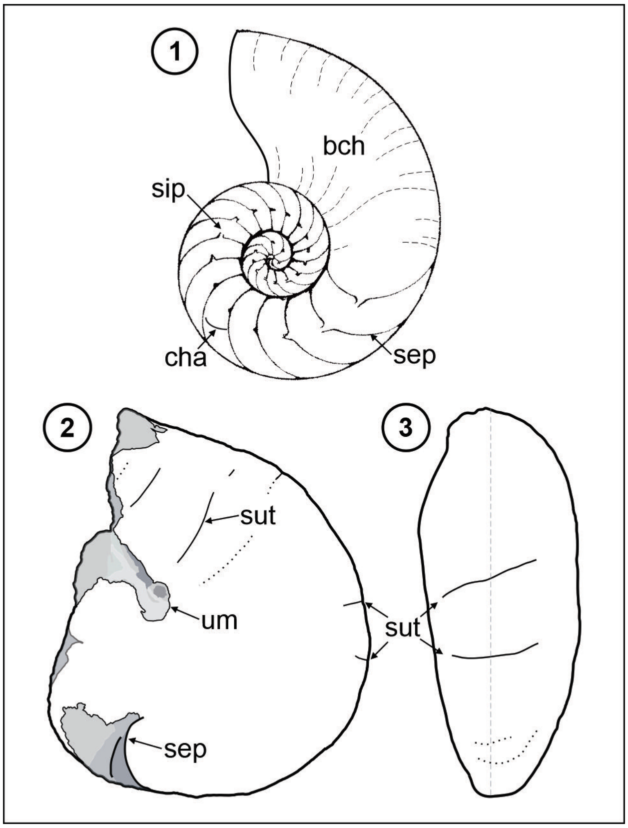

Figure 7. ***Nautilus sudcalifornianus*** sp. nov.; **1,** a transversal section of the modern *Nautilus*; **2,** right lateral view, digitized version of specimen **MHN-UABCS Te14/66/65**; **3,** ventral view, digitized version of specimen **MHN-UABCS Te14/66/65**. Abbreviations: **bch**, body chamber; **cha**, chamber; **sep**, septum; **sip**, siphuncle; **sut**, suture; **um**, umbilicus.

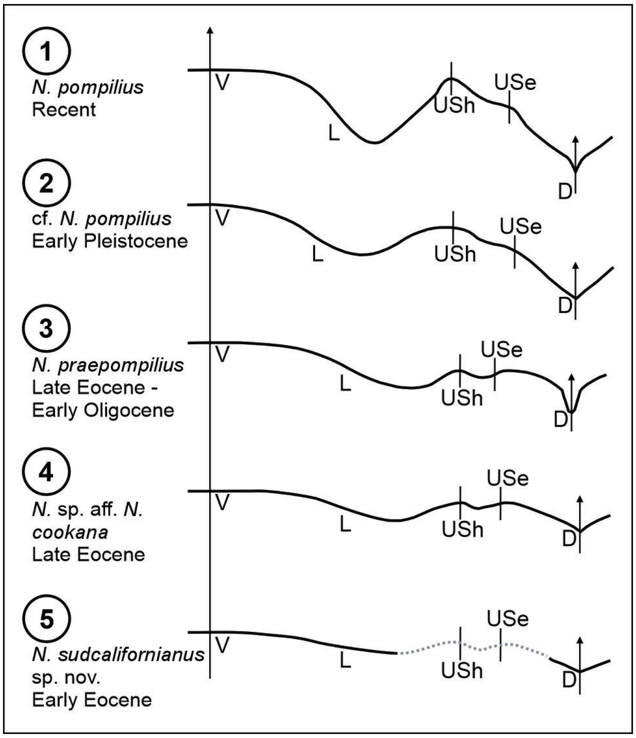

Figure 8. Sutures of extant and extinct *Nautilus*; **1,** ***Nautilus pompilius*** (modern); **2,** a specimen of cf. ***Nautilus pompilius*** (Early Pleistocene); **3,** ***Nautilus praepompilius*** Shimansky, 1957 (Late Eocene–Early Oligocene); **4,** ***Nautilus*** sp. aff. ***N. cookana*** Whitfield, 1892 (Late Eocene); **5,** ***Nautilus sudcalifornianus*** sp. nov. (Early Eocene, hypothetic proposal). Abbreviations: **D**, dorsal lobe; **L**, lateral lobe; **USe**, saddle near umbilical seam; **USh**, saddle in umbilical shoulder; **V**, ventral saddle (modified from Wani *et al.*, 2008).

specifically *Eutrephoceras hannai* and the *species nova*, *Nautilus sudcalifornianus*.

Assigning a genus and/or species to a fossil is a complex endeavor, especially for poorly preserved specimens (Goedert *et al.*, 2022). From this perspective, it is worth noting that we conducted our species identifications and new description, respectively, based on internal molds, which is a valid procedure in cephalopod paleontological taxonomy (*e.g.*, Vokes, 1937; Miller, 1947; Squires, 1988; Squires & Demetrion, 1992; Araújo-Tavora *et al.*, 2019; Goedert *et al.*, 2022). Furthermore, it has been argued that for fossil nautiloids, the taxonomy of genera and species is supported by a small number of morphological characters (*e.g.*, shell sculpture, planispiral shell forms, suture, umbilicus, among others), which due to their scarcity, make identification and classification difficult (Kummel, 1956; Ward *et al.*, 2016b). However, these are also the diagnostic morphological characters accepted and used for the taxonomy of extant nautiloids at present (*e.g.*, Barord *et al.*, 2023). Indeed, current nautiloid paleontological taxonomy is primarily based on the lateral lobe (Teichert & Matsumoto, 2010). Considering this, we are confident that the specimens evaluated here accounted with sufficient quality and quantity of characters to guarantee a high degree of certainty in the species designations.

Palaeobiological implications

After the sudden disappearance of the Mesozoic cephalopod fauna during the Cretaceous/Paleogene mass extinction (K/Pg), nautiloids were still widespread in the Pacific Ocean during the Paleogene (Halder, 2012; Ward *et al.*, 2016a; Goedert *et al.*, 2022). This can be attributed to two main aspects: a) the lack of predators influencing their geographic distribution, which in the Neogene shaped the present-day geographic distribution of the Nautilidae (Kiel *et al.*, 2022); and b) their life history strategy in terms of reproduction, as extant nautilids exhibit polycyclic spawning (Nesis, 1996). Indeed, according to estimations for their coleoid relatives (subclass Coleoidea Bather, 1888), asynchronous ovulation as a life history strategy is correlated with unstable environments (Ibáñez *et al.*, 2021). In this sense, environmental instability was markedly present during the Early Eocene, as will be further discussed here.

As mentioned earlier, the two nautiloid species found in the Tepetate Formation constitute both the southernmost geographic distribution and the most ancient record of Nautilidae for the Eocene epoch. We hypothesize that their presence in this area could be attributed to two scenarios: in scenario 1, the shells of both species were deposited in the Tepetate Formation due to post-mortem transport. The rationale of this scenario is that extant nautiloids remain buoyant after death and may be carried considerably outside the distribution area of their main populations (Boyle & Rodhouse, 2005; Ward *et al.*, 2016a). However, this assumption is remote for our specimens given that it has been detected that post-mortem drift is not significant in disturbing the fossil record (Chirat, 2000) and that nautiloids during the Eocene were parautochthonous (organisms were transported over a relatively short distance) (Halder, 2012). Another aspect to consider is that it has been noted that living nautiloids migrate passively by drifting for thousands of kilometers (Ward, 1987). However, biogeographic considerations for marine species that spend long periods at young stages (5–6 years in extant nautiloids; Boyle & Rodhouse, 2005), indicate that drifting is a strategy used to remain in small to middle-sized geographic distribution ranges in order to ensure survival, rather than to cover large geographic areas by dispersion (Cox *et al.*, 2020). We concur with the latter suggestion, discarding scenario 1.

Scenario 2 poses the following: the two species identified in this study used the geographic area of the Tepetate Formation (24° N) as a transitory zone for spawning and growth of young stages during the Eocene. For present-day nautiloids, no spawning and/or hatching events have been observed in nature (Jereb & Roper, 2006). However, according to optimal temperatures exhibited in reared individuals (21° to 24 °C), specialists hypothesize that nautiloids migrate towards warm shallow water (80 to 100 m deep) areas for spawning and hatching, and that the young move to colder waters as they grow (Jereb & Roper, 2006). In this sense, some authors have mentioned that current environmental conditions might not have differed conspicuously from the sites preferred by ancient nautiloids (Dzik & Gaździcki, 2001; Ward *et al.*, 2016a,b). The species identified in our study (or their ancestors) could have arrived in the Pacific Ocean by the global transport of the Tethys current since the origin of nautiloids (Early Cretaceous; Halder, 2012; Ward *et al.*, 2016a). The Tethys circulation pattern (from east to west) remained influencing the distribution of nautiloids up to the Late Eocene, linking the Atlantic and Pacific oceans (*e.g.*, presence of *Nautilus cookana* in New Jersey and in Washington State during the Eocene; Miller, 1947; Palmer & Brann, 1965; Squires, 1988). Moreover, the Paleogene underwent large climatic fluctuations with three thermal maximum events, probably triggered by Milankovitch cycles, which caused a redistribution of the marine fauna (Lunt *et al.*, 2011; Rosengard, 2011; Payros *et al.*, 2015). In this sense, during the Eocene, marine species thrived towards higher latitudes (30–50°) in temperate waters, away from the hot equator (Dzik & Gaździcki, 2001; Das & Halder, 2018). The Ypresian (the age estimated in this study) was characterized by 27–33 °C mean planetary temperatures and 10–16 °C mean sea surface temperatures (Inglis *et al.*, 2020; Crichton *et al.*, 2023). Thus, considering this and the fact that extant nautiloids can migrate ≈ 4 km per day (O'Dor *et al.*, 1993), we hypothesize that *N. sudcalifornianus* sp. nov. and *E. hannai* migrated towards latitudes with warm shallow water areas for spawning and hatching, which agrees with the shell diameter (150 mm) of specimen MHN-UABCS Te14/66/65 (*Nautilus sudcalifornianus* sp. nov.), representing an adult (mature) individual, and also with the shell diameter (23 mm) and the presence of longitudinal ridges in specimen MHN-UABCS Te9/49/27 (*Eutrephoceras hannai*), typical of juveniles of this species (Morton, 1834). Additionally, the other faunal groups found in the study area are foraminifera (*Pseudophragmina*), solitary corals, calcareous sponges (*Elasmostoma bajaensis* Squires & Demetrion, 1989), bivalves (*Phygraea pacifica* Squires & Demetrion, 1990, *Cubitostrea mezquitalensis* Squires & Demetrion, 1990, *Spondylus batequensis* Squires &

Demetrion, 1990), gastropods (*Gyrodes* sp., *Velates perversus* Gmelin, 1791), crabs (see listings in Schweitzer *et al.*, 2002, 2005, 2006), and echinoderms (*Eupatagus batequensis* Squires & Demetrion, 1992, *Haimea bajasurensis* Squires & Demetrion, 1994) (Vázquez-García, 1996; Morales-Ortega, 2010, 2012). This faunistic diversity characterizes a well-established shallow water and warm ecosystem typical of the Early Eocene, which could have been an idoneous location for spawning/hatching and growth of the species identified in our study. Therefore, we propose this migratory behavior as an ancestral feature for nautiloids. However, further findings could better support or discard this hypothesis.

CONCLUSIONS

According to this study, the suture shape, especially at the lateral lobe, is the most conspicuous diagnostic feature to discriminate nautiloids. In *Eutrephoceras hannai*, the suture is straighter than the rest of its congeners, and similarly, in *Nautilus sudcalifornianus* sp. nov., the suture in the lateral lobe is less sinuous than the rest of its congeners, including taxa from the Eocene. Moreover, based on our records, we infer that the origin of *E. hannai* and *N. sudcalifornianus* sp. nov. occurred at least during the Ypresian. In addition, the Tepetate Formation is the southernmost location in the geographic distribution ranges of both species. Due to the characteristics detected in the specimens evaluated here, this area was probably an idoneous site for spawning/hatching and growth of young stages of both species during the Eocene. In this sense, for nautiloids, we suggest that the environmental conditions of suitable areas for spawning/hatching and growth of young stages during the Early Eocene were similar to those preferred by the present-day species. Thus, we support the hypothesis that extant nautiloids migrate towards warm shallow water areas for spawning, hatching and growth of young stages, and propose that this migratory behavior is ancient within the subclass. Lastly, our records provide new insights into the taxonomy, biology, ecology, and biogeography of nautiloids from the Eocene and increase the malacological record for the Western North American Province, highlighting the geological and palaeontological importance of the Tepetate Formation, Baja California Sur, Mexico.

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