

# What's behind a name: The taxonomic status of *Helicancylus* Gabb, 1869 and *Hamiticeras* Anderson, 1938 (Ammonoidea, Lower Cretaceous)

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**Abstract.**—The present contribution illustrates the type material of the Lower Cretaceous ammonoids *Ptychoceras aequicostatus* Gabb, 1864 (type species of *Helicancylus* Gabb, 1869) and *Hamiticeras pilsbryi* Anderson, 1938 (type species of *Hamiticeras* Anderson, 1938). The typification and taxonomic validity of both genera are clarified, and the affinities with coeval Acrioceratidae are discussed. Their stratigraphic range is investigated with implications for correlation between northern Pacific and European ammonoid scales.

## Introduction

The Lower Cretaceous small-sized heteromorph ammonoids with simplified ornamentation on the hook were commonly assigned to the Helicancylidae Hyatt, 1894, the genotype of which is *Helicancylus* Gabb, 1869 and type species is *Ptychoceras aequicostatus* Gabb, 1864 (p. 74, pl. 13, fig. 20). He described *Ptychoceras aequicostatus* on the basis of a small fragment of a retroversum from the Horsetown Beds of California housed at the University of California Museum of Paleontology (specimen UCMP.12090). Five years later, the same author included two other fragments (i.e., the helix UCMP. 4799 and a lost fragment of a proversum plus retroversum) in the type material of *Ptychoceras aequicostatus* for which he introduced the genus *Helicancylus*.

According to Anderson (1938), the three specimens that compose the type material of *Ptychoceras aequicostatus* are not conspecific and should be subdivided into different taxa. He introduced the new genus *Hamiticeras* Anderson, 1938 and selected the new species *Hamiticeras pilsbryi* Anderson, 1938 as the type species, typified by the lost fragment of *Ptychoceras aequicostatus* illustrated by Gabb (1869, pl. 25, fig. 20b–f). He considered the species *Ptychoceras aequicostatus* as a member of *Hamiticeras*, and he selected the original material published in 1864 as the holotype of that species (Gabb, 1864, pl. 13, fig. 20). He, finally, confined *Helicancylus* to his new species *Helicancylus gabbi* Anderson, 1938 based on the helix of *Ptychoceras aequicostatus* illustrated by Gabb (1869, pl. 25, fig. 20, 20a).

The specimen UCMP.12090 was conservatively retained as the holotype of *Ptychoceras aequicostatus* by Frau et al. (2017), because the subsequent fragments (i.e., the helix UCMP. 4799,

and the lost fragment) reported to further typify that species by Gabb (1869) were considered as an abusive emendation in the sense of ICZN Art. 74.6 (ICZN, 1999). Re-examination of specimen UCMP.12090 has shown that it is based on a worn fragment of a flexus that lacks any diagnostic features (Frau et al., 2017). *Ptychoceras aequicostatus* was thus considered as a nomen dubium, and, therefore, that *Helicancylus* is a nomen nudum (Frau et al., 2017). As a consequence, these authors retained the Acrioceratidae Vermeulen, 2004 as a substitute for Helicancylidae because there is agreement that the two families share the same specific content (Bert, 2009; Vermeulen, 2010; Vincent et al., 2010; Bulot et al., 2018; Bersac and Bert, 2021). As to the difference, Klein et al. (2007) considered the Helicancylidae as a collection of small forms and microconchs of various Lower Cretaceous heteromorphic ammonoids, and the family was synonymized with the Ancyloceratidae Gill, 1871. However, the issue of sexual dimorphism between the Acrioceratidae and the Ancyloceratidae has not yet been proven and remains largely speculative throughout their range (e.g., Vermeulen, 2010, p. 64).

The lack of consensus on the validity of the Helicancylidae has long depended on the taxonomic emendation of *Helicancylus* made by Anderson (1938). A comprehensive revision of Gabb's (1869) type material is, however, lacking. The aim of his paper is to re-evaluate the original material and to clarify the taxonomic status of *Helicancylus* and *Hamiticeras*, and their stratigraphic ranges.

## Stratigraphic range

**Background.**—The studied material was collected from Shasta County, northwestern California, but the exact locality and horizon were not defined by Gabb's (1864, 1869) contributions. In his monograph on the Lower Cretaceous of California, Anderson (1938) reported *Hamiticeras* and *Helicancylus* from the middle part of the Horsetown Group of

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Shasta County. The stratigraphic framework of the Horsetown Group was revised by Murphy (1956) who introduced a formal lithostratigraphic unit, the Ono Formation, for sediments previously included in the Horsetown Group. He also outlined that Anderson's (1938) zonal scheme for the Horsetown Group is of limited value, noted contradictions regarding the ranges and stratigraphic positions of several species, and established a new zonal classification based entirely on his collections. A new *Gabbioceras wintunium* (now *Eotetragonites wintunius*; see Murphy, 1967) Biozone was introduced to accommodate parts of the Horsetown Group of Anderson (1938). The faunal content of the *Eotetragonites wintunius* Biozone was discussed by Popenoe et al. (1960, p. 1508), who subdivided it into three informal subzones:

- (1) a lower subzone lacking diagnostic ammonoids;
- (2) a middle subzone that is characterized by an undescribed species originally assigned to *Gabbioceras* Hyatt, 1900, which was more recently assigned to *Eotetragonites shoupi* Murphy, 1967 = *Gabbioceras angulatum* (Anderson, 1902) in Anderson (1938, pl. 35, fig. 2), '*Australiceras*' *argus* Anderson, 1938, *Parahoplites shoupi* (Anderson, 1938), *Parahoplites dallasi* Anderson, 1938, and *Shastoceras shastense* Anderson, 1938; and
- (3) an upper subzone that is characterized by the presence of *Gabbioceras angulatum*, *Lytoceras batesii* (Trask, 1855), *Neocalliphylloceras aldersoni* (Anderson, 1938), *Parahoplites cerrosensis* (Anderson, 1938), *Hulenites reesidei* (Anderson, 1938), and *Hamulina aldersoni* Anderson, 1938. According to Popenoe et al. (1960), *Hamiticeras* occurs in the middle and upper parts of this subzone.

The lithostratigraphic framework of the Lower Cretaceous of the Ono Quadrangle was finally improved by Murphy et al. (1969) and Murphy (1975). The Ono Formation was abandoned and the Budden Canyon Formation formally defined and divided into seven members, namely the Rector Conglomerate, the Ogo Member, the Roaring River Member, the Chickabally Member, the Huling Sandstone, the Bald Hills Member, and the Gas Point Member. The *Eotetragonites wintunius* Zone covers the lower part of the upper Chickabally Member, but the zone was extended to the base of the Huling Sandstone Member by Fernando et al. (2011). No further *Hamiticeras* occurrence was mentioned in the contributions of Fernando and his collaborators (Fernando et al., 2011), and it seems that no new material was collected during the mapping of the Ono quadrangle by Murphy et al. (1969).

*Range and calibration of the Eotetragonites wintunius Zone.*—The correlation of the *Eotetragonites wintunius* Zone with the Standard Mediterranean Ammonite Zonation (SMAS of Reboulet et al., 2018) remains largely unclear. A complete revision of the faunal content of the zone is well beyond the scope of the present contribution but a few points should be outlined to clarify the range of the taxa discussed in the present contribution (Fig. 1).

First, the lower boundary of the *Eotetragonites wintunius* Zone lies on the Huling Sandstone Member, consisting of poorly

sorted, conglomeratic, relatively massive sandstones (Fernando et al., 2011). According to these authors, the deposits reflect an episode of marine erosion coinciding with a major sea-level drop, also associated with a hiatus of a major portion of the Barremian/Aptian boundary interval because there is no record of the magnetic reversal CM0r at this level (Fernando et al., 2011, p. 362), the latter being presumably latest Barremian in age (Frau et al., 2018; Gale et al., 2020). This hiatus conforms with the high-amplitude relative sea-level fall recorded at that time in many platform environments of the Tethys (Frau et al., 2020).

Secondly, Murphy and Rodda (2006) suggested that the *Eotetragonites wintunius* Zone, the '*Acanthoplites*' *gardneri* Biozone, and the '*Acanthoplites*' *reesidei* Biozone of the upper Chickabally Member correlate with the upper Aptian of Europe. This is partly based on the reinterpretation of faunal association of the '*Acanthoplites*' *gardneri* and '*Acanthoplites*' *reesidei* zones by Amédéo and Robaszynski (2005, p. 590) as equivalent to the *Nolaniceras nolani* Biozone of the SMAS. However, all of the Californian index species are endemic to the northern Pacific, and their affinities and ranges remain unclear with respect to the European relatives.

In fact, the correlation between the northern Pacific and the European ammonoid scales can only be indirectly constrained by the integrated calcareous nannofossil biostratigraphy and magnetostratigraphic framework established by Fernando et al. (2011). It has been suggested that the *Eotetragonites wintunius* Zone correlates with the BC18 to lower BC21 nannofossil zones, indicative of a middle-lower to lower-upper Aptian range according to the Cretaceous Geological Time Scale of Gale et al. (2020). As further evidence, Fernando et al. (2011) documented a short-lived magnetic reversal M1r at the boundary between the *Eotetragonites wintunius* Zone and the '*Acanthoplites*' *gardneri* Zone. This magnetic reversal, otherwise known as ISEA, is well constrained in the Tethys, and occurs just above the first occurrence of the planktonic foraminiferan index species *Globigerinelloides algerianus* Cushman and ten Dam, 1948 (see Tarduno et al., 1989). Correlations between Tethyan planktonic foraminiferan and ammonoid scales suggest, de facto, that the upper boundary of the *Eotetragonites wintunius* Zone falls in levels correlating to the upper *Epicheloniceras martini* Biozone and/or lower *Parahoplites melchioris* Biozone depending the definitions of these zones (e.g., Dauphin, 2002; Herrle and Mutterlose, 2003; Guzhikov et al., 2003; Dutour, 2005; Luber et al., 2017, 2019; Gale et al., 2020). As a consequence, we should consider a lower upper Aptian range for the Californian *Hamiticeras*.

## Material

*Repositories and institutional abbreviations.*—Examination of the Gabb and Anderson collections was made possible through the courtesy of Erica Clites and Dave Strauss at the University of California Museum of Paleontology (UCMP), Sara Mansfield and Peter Roopnarine at the California Academy of Sciences (CAS), and Lindsay Walker at the Natural History Museum of Los Angeles County (LACMIP). These include the holotype of *Helicancylus aequicostatus* (Gabb, 1864, pl. 13, fig. 20), the holotype of

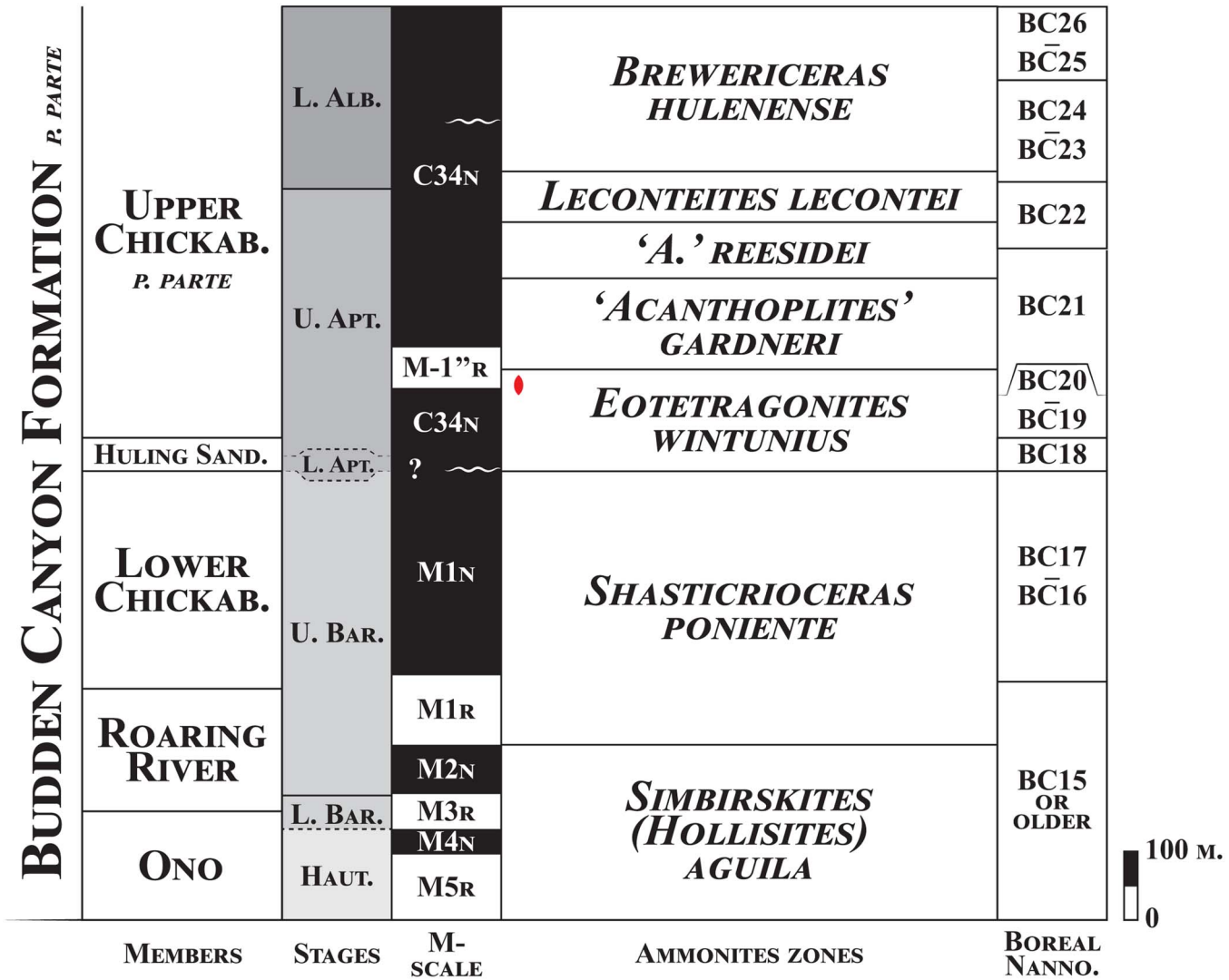


Figure 1. Integrated magnetostratigraphy and northern Pacific ammonoid and nannofossil biostratigraphy of the Budden Canyon Formation in the North Fork Cottonwood Creek section (modified from Fernando et al., 2011). The red dot indicates the putative occurrence of *Hamiticeras* according to Popenoe et al. (1960).

*Helicancylus gabbi* (see Gabb, 1869, pl. 25, fig. 20, 20a), and the holotype of *Hamiticeras philadelphium* Anderson, 1938 (p. 216, pl. 79, figs. 2, 3), respectively labelled UCMP.12090 (Fig. 2.1, 2.2), UCMP.4799 (Fig. 2.3–2.6), and UCMP.4797 (Fig. 2.7–2.10).

Despite an extensive search in the Californian paleontological collections, the specimen of *Helicancylus aequicostatum* illustrated by Anderson (1938, pl. 37, figs. 2, 2a, 3) and the holotype of *Hamiticeras pilsbryi* (see Gabb, 1869, pl. 25, fig. 20a–f) could not be located. A cast of *Hamiticeras pilsbryi* resides in the collections of the California Academy of Sciences (CAS.5876) and is herein designed as *plastoholotype* (Fig. 3.1–3.3).

The specimen of *Hamiticeras pilsbryi* found by W.P. Popenoe and D.W. Scharf mentioned by Anderson (1938, p. 216) is repositied in the Natural History Museum of Los Angeles County (LACMIP.9951-3). It is here illustrated for the first time (Fig. 3.4–3.9); a 3D, digital-model has been uploaded to: <https://www.morphosource.org/Detail/>

[MediaDetail/Show/media\\_id/40009](#). Note that a plastic mold of this specimen is included in the UCMP collection (UCMP.006402F).

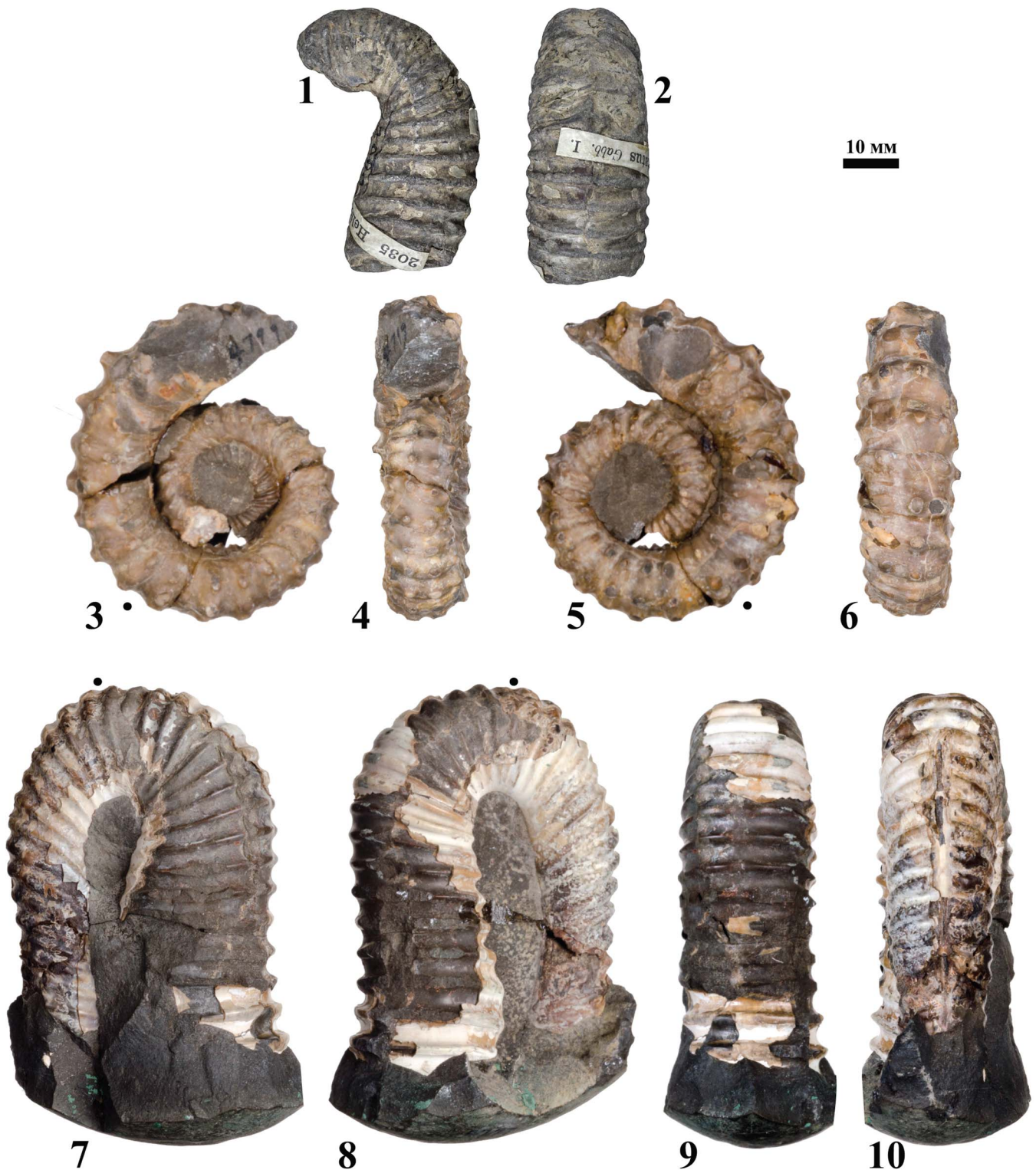
**Systematic paleontology**

- Order Ammonitida Haeckel, 1866
- Family Acrioceratidae Vermeulen, 2004 (= Helicancylidae Hyatt, 1894)
- Genus *Helicancylus* Gabb, 1869 (nomen nudum)

*Type species.*—*Ptychoceras aequicostatus* Gabb, 1864 by monotypy.

*Helicancylus aequicostatus* Gabb, 1864 (nomen dubium)  
Figure 2.1, 2.2

1864 *Ptychoceras aequicostatus* Gabb, p. 74, pl. 13, fig. 20.



**Figure 2.** Holotypes, Budden Canyon Formation, Shasta County, northwestern California: (1, 2) UCMP.12090, *Ptychoceras aequicostatus* Gabb, 1864, 2 views; (3–6) UCMP.4799, *Helicancylus gabbi* Anderson, 1938, 4 views; (7–10) UCMP.4797, *Hamiticeras philadelphium* Anderson, 1938, 4 views. Black dots indicate the ends of phragmocones.

non 1869 *Helicancylus aequicostatus*; Gabb, p. 141, pl. 25, fig. 20, 20a (= *Pseudoaustralicerias gabbi*), fig. 20b–f, ?g (= *Hamiticeras pilsbryi*).

non 1938 *Hamiticeras aequicostatum*; Anderson, p. 216, pl. 37, figs. 2, 2a. 3, pl. 79, fig. 6 (= *Hamiticeras* aff. *H. philadelphium*).



**Figure 3.** Specimens from the Budden Canyon Formation of Shasta County, northwestern California: (1–3) plastoholotype CAS.5876, *Hamiticerus pilsbryi* Anderson, 1938, 3 views; (4–9) LACMIP.9951-3, *Hamiticerus pilsbryi* (mentioned by Anderson, 1938, p. 216), 6 views. Black dots indicate the ends of phragmocones.

non 1943 *Hamiticerus aequicostatus*; Hanna and Hertlein, fig. 61-18 (= Anderson, 1938, pl. 37, figs. 2, 3).

non 1996 *Helicancylus aequicostatus*; Wright et al., p. 225, fig. 174, 2a, 2b (= Anderson, 1938, pl. 37, figs. 2, 3).

non 2001 *Helicancylus aequicostatus*; Avram et al., p. 17, pl. 1, figs. 12 (?), 13 = '*Hamiticerus*' *carcitanense* (Matheron, 1880).

*Holotype*.—UCMP.12090 (Frau et al., 2017).

*Description.*—Specimen UCMP.12090 consists of a worn fragment of a flexus bearing the simple ornament typical of the Acrioceratidae.

*Synonymy list.*—The doubtful species *Helicancylus aequicostatus* was reported by Anderson (1938, pl. 37, figs. 2, 2a, 3, pl. 79, fig. 6) from California, but the figured specimens should be reassigned to *Hamiticerias* aff. *H. philadelphium* as defined below. The report from the northern Apuseni Mountains of Romania (Avram et al., 2001, pl. 1, figs. 12, 13) was confused with ‘*Hamiticerias*’ *carcitanense* (see discussion below).

*Remarks.*—The holotype UCMP.12090 lacks valuable diagnostic features and prevents clear typification of *Helicancylus*, as well as the Helicancylidae. In line with Frau et al. (2017), both *Helicancylus* and the family Helicancylidae are nomina nuda.

Genus *Hamiticerias* Anderson, 1938

*Type species.*—*Hamiticerias pilsbryi* Anderson, 1938 by original designation.

*Hamiticerias pilsbryi* Anderson, 1938  
Figure 3.1–3.3

- 1869 *Helicancylus aequicostatus* (Gabb); Gabb, p. 141, pl. 25, fig. 20b–f, ?g.  
1938 *Hamiticerias pilsbryi* Anderson, p. 216, pl. 79, fig. 1 (= Gabb, 1869, pl. 25, fig. 20b–f).  
1957 *Hamiticerias pilsbryi*; Arkell et al., p. L212, fig. 240.3 (= Anderson, 1938, pl. 79, fig. 1).  
non 1960 *Hamiticerias pilsbryi*; Drushchits, p. 295, pl. 11, fig. 6a–6 (= ?Acrioceratidae gen. indet. sp. indet.), fig. 7a–6 (= ? ‘*Hamiticerias*’ *carcitanense*).  
1996 *Hamiticerias pilsburyi* (sic); Wright et al., p. 224, fig. 174, 2c (= Anderson, 1938, pl. 79, fig. 1).  
? 1997 *Hamiticerias pilsbryi*; Kakabadze and Hoedemaeker, p. 75, pl. 13, fig. 1a, b, text-fig. 10a–d.  
non 2001 *Hamiticerias* cf. *H. pilsbryi*; Avram et al., p. 17, pl. 1, fig. 11 (= Acrioceratidae gen. indet. sp. indet.).  
non 2004 *Hamiticerias pilsbryi*; Kakabadze and Hoedemaeker, pl. 54, fig. 2 (= *Toxoceratoides* sp. indet.).

*Type specimens.*—The species *Hamiticerias pilsbryi* is based on the proversum and retroversum fragment illustrated by Gabb (1869, pl. 25, fig. 20b–f) and considered to be lost in the UCMP collections. The plastic mold CAS.5876 is here designated as plastoholotype of that species. The specimen LACMIP.9951-3 of W.P. Popenoe and D.W. Scharf, and its plastic mold UCMP.006402F, conforms to the plastoholotype.

*Description.*—*Hamiticerias pilsbryi* has a toxoceratid-like shell whose inner ontogeny remains unknown. The proversum is long and slightly flexuous and followed by a gooseneck flexus and an elongated flexuous retroversum. Proversum and retroversum are almost contiguous at midheight. The proversum ornamentation develops alternating trituberculate

primaries and one atuberculate intercalatory that disappear as growth increases. All of the ribs are interrupted on the venter delimiting a narrow-flattened ventral band vanishing on the flexus. The lateral tubercles are rounded and discrete on the primary ribs, whereas the external ones form indistinct clavi on the periventral area. The ornamentation changes as flat-topped simple ribs on the flexus, becoming distant and sharper, almost annular on the retroversum, and continuous over the venter. The peristome is marked by a constriction followed by a distinctive bifurcate annular rib. Based on Gabb (1869, pl. 25, fig. 20g), the suture line has a subrectangular ventral lobe; a broad, rather symmetric external saddle; a deep, symmetrically trifold adventive lobe; and a narrow, bipartite lateral saddle (Fig. 4.1).

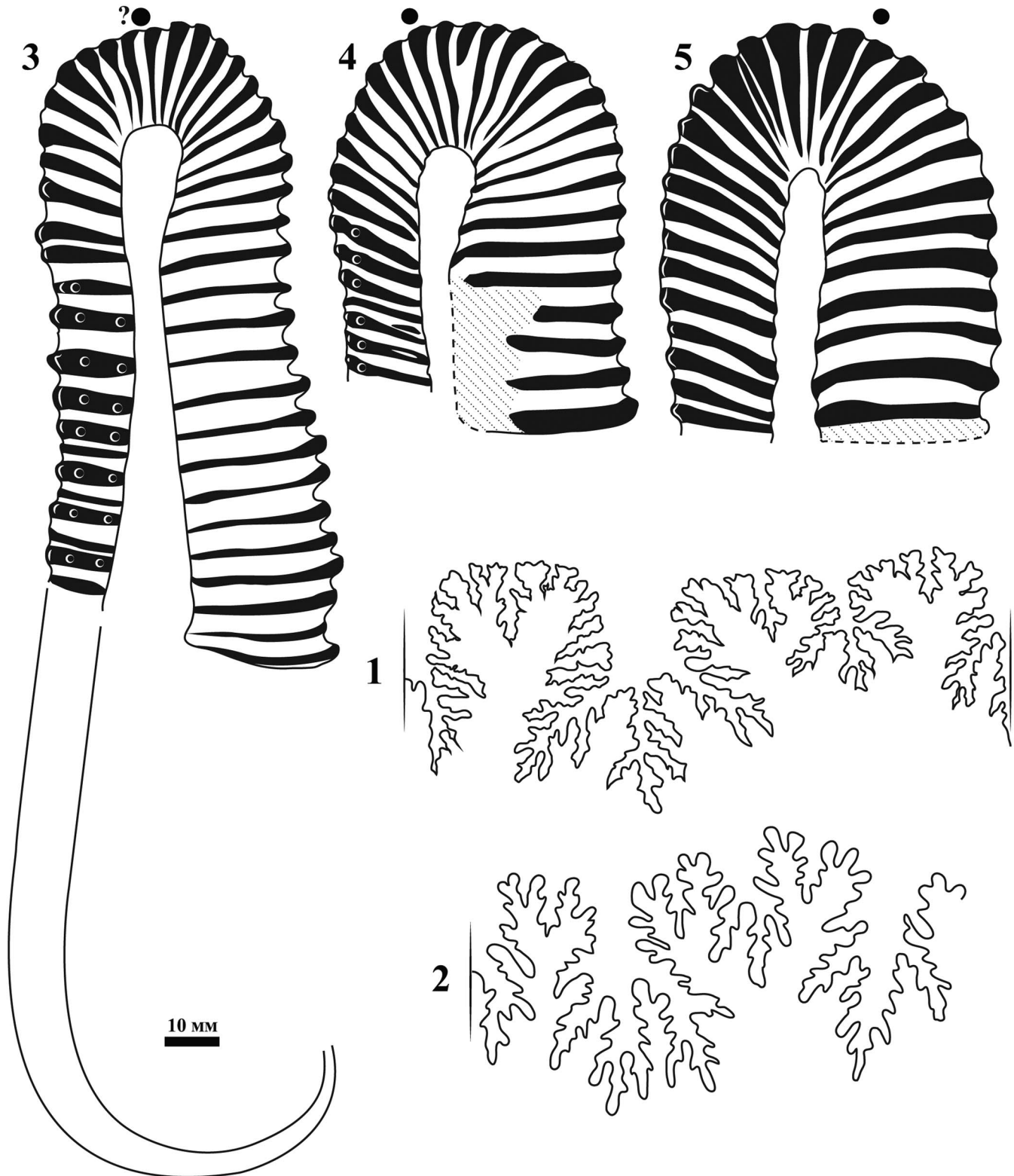
*Synonymy list.*—*Hamiticerias pilsbryi* has been reported outside of California: in the northwestern Caucasus (Drushchits, 1960), the northern Apuseni Mountains of Romania (Avram et al., 2001) and the Boyacá district of Colombia (Kakabadze and Hoedemaeker, 1997, 2004).

The specimen figured by Drushchits (1960, pl. 11, fig. 6a–6) is a rather complete acrioceratid lacking the spire. Its general coiling mimics that of *Hamiticerias pilsbryi*, but it can be easily differentiated by its rounded whorl section in the adult lacking ventral rib interruption. The other specimen of Drushchits (1960, pl. 11, fig. 7a–6) is a large retroversum fragment that has affinities with ‘*Hamiticerias*’ *carcitanense* (see discussion below).

The Romanian specimen consists of a poorly preserved flexus fragment of doubtful identification.

The Colombian form figured by Kakabadze and Hoedemaeker (1997, pl. 13, fig. 1a, b) is a large flexus and retroversum fragment that very closely matches *Hamiticerias pilsbryi*. The lack of proversum prevents further confirmation. The other specimens figured by Kakabadze and Hoedemaeker (2004, pl. 54, fig. 2) resemble the Colombian species *Hamiticerias chipatai* Kakabadze and Hoedemaeker, 1997, but its general coiling, regular alternation of trituberculate and atuberculate ribs on the proversum, becoming atuberculate, cuneiform then flat-topped over the venter through the retroversum better compare with the upper Aptian *Toxoceratoides* representatives (e.g., Frau et al., 2017; Bulot et al., 2018).

*Remarks.*—*Hamiticerias pilsbryi* retains the general features of the Acrioceratidae, viz. small heteromorphic shell with tripartite coiling and simplified ornamentation on the retroversum (e.g., Vermeulen, 2004; Bulot et al., 2018). The closest affinities are found with the genus *Toxoceratoides* Spath, 1924 (type species *Toxoceras royerianus* d’Orbigny, 1842). *Toxoceratoides* encompasses small to medium-sized taxa that differ from *Hamiticerias* by their toxoceratid coiling with a shorter retroversum; slightly depressed, subrounded to octagonal whorl section in the adult; and generally the following ornamental stages: (1) atuberculate annular simple ribs; (2) alternation of a variable number of thin, slightly prorsiradial, intercalate ribs and trituberculate primary ribs that interrupt on the venter; and (3) loss of lateral and ventral tubercles; and sharp, radial, narrow single ribs, sometimes originating by twos or threes from tubercles on the dorsal shoulder (Bulot et al., 2018). The *Toxoceratoides* suture line



**Figure 4.** Suture lines: (1) *Hamiticeras pilsbryi* Anderson, 1938 based on Gabb (1868, pl. 25, fig. 20g); (2) *Hamiticeras* aff. *H. philadelphium* Anderson, 1938 based on Anderson (1938, pl. 79, fig. 6). Suture lines not to scale. Diagrammatic reconstruction of Californian *Hamiticeras*: (3) *Hamiticeras pilsbryi* Anderson, 1938 and hypothetical general coiling; (4) *Hamiticeras philadelphium* Anderson, 1938; (5) *Hamiticeras* aff. *H. philadelphium* Anderson, 1938. Black dots indicate the ends of the phragmocones.

differs from that of *Hamiticerias pilsbryi* by its narrow, asymmetric external saddle and broader bipartite lateral saddle (compare Bulot et al., 2018, fig. 2F).

Of major interest is the end of the phragmocone at the transition between the proversum and the flexus in *Hamiticerias pilsbryi* and other *Hamiticerias* taxa described below. This long phragmocone is rather unique for the Acrioceratidae. In comparison, the end of phragmocone most commonly occurs in the upper proversum in *Toxoceratoides* (e.g., Bulot et al., 2018). For the above-mentioned reasons, *Hamiticerias* should be retained as a separate Acrioceratidae genus.

*Hamiticerias philadelphium* Anderson, 1938

Figure 2.7–2.10

- 1938 *Hamiticerias philadelphium* Anderson, p. 216, pl. 79, figs. 2, 3.  
 non 1989 *Hamiticerias philadelphium*; Föllmi, p. 122, pl. 4, figs. 2, 3 (= Acrioceratidae gen. indet. sp. indet.).  
 ? 2004 *Helicancylus* cf. *H. philadelphium*; Kakabadze and Hoedemaeker, p. 77, pl. 64, fig. 2a–c.

*Holotype*.—UCMP.4797 (Anderson, 1938).

*Description*.—The holotype UCMP. 4797 develops a moderately straight upper proversum, a gooseneck flexus, and an elongated retroversum. Its general adult coiling thus rather compares to that of *Hamiticerias pilsbryi*, but the species differs by its ribbing style because it develops prorsiradiate ribs with discrete thickenings in the upper lateral and periventral margins along part of the proversum. The specimen referred to as *Hamiticerias aequicostatum* by Anderson (1938, pl. 37, figs. 2, 2a, 3) closely resembles *Hamiticerias philadelphium*, by its coiling and long phragmocone, but it differs in its proversum ornament lacking upper lateral tubercles. This specimen is here referred to as *Hamiticerias* aff. *H. philadelphium*. Both species have a long phragmocone ending at the transition between the proversum and the flexus. The suture line of *Hamiticerias* aff. *H. philadelphium* illustrated by Anderson (1938, pl. 79, fig. 6) is similar to that of *Hamiticerias pilsbryi* drawn by Gabb (1869, pl. 25, fig. 20g), although marked by a simpler external saddle and a narrower, less symmetrical bipartite lateral saddle (Fig. 4.2).

*Synonymy list*.—*Hamiticerias philadelphium* has been reported outside of California: the Helvetic nappes (Föllmi, 1989, pl. 4, figs. 2, 3), and the Boyacá district of Colombia (Kakabadze and Hoedemaeker, 2004, pl. 64, fig. 2a–c). The specimens from the Helvetic nappes are based on a poorly preserved acrioceratid fragment of doubtful identification whereas the Colombian specimen is rather convincing.

*Remarks*.—The Californian *Hamiticerias* taxa differ in ornamental style on the proversum either marked by trituberculate (*Hamiticerias pilsbryi*, Fig. 4.3), bituberculate (*Hamiticerias philadelphium*, Fig. 4.4), or unituberculate ribs (*Hamiticerias* aff. *H. philadelphium*, Fig. 4.5). Those ornamental styles can be used for specific identification.

However, this can also illustrate intraspecific variabilities but the low number of specimens and poorly resolved stratigraphy prevent further confirmation.

Family Ancyloceratidae Gill, 1871

Genus *Pseudoaustralicerias* Kakabadze, 1981

*Type species*.—*Crioceras ramososeptatum* Anthula, 1900 by original designation.

*Pseudoaustralicerias gabbi* Anderson, 1938

Figure 2.3–2.6

- 1869 *Helicancylus aequicostatus* (Gabb); Gabb, p. 141, pl. 25, fig. 20, 20a.  
 1938 *Helicancylus gabbi* Anderson, p. 222, pl. 79, figs. 4, 5 (= Gabb, 1869, pl. 25, fig. 20, 20a).

*Holotype*.—UCMP.4799 (Anderson, 1938).

*Description*.—The holotype corresponds to a moderately-sized, dextral, open, descending spiral. The end of the calcified phragmocone is in the outer whorl. The ornamentation is composed of two distinct stages: (1) strong, rectiradiate single ribs that progressively change into (2) distant, robust trituberculate ribs with strong spiny tubercles.

*Synonymy list*.—There are no other citations of *Pseudoaustralicerias gabbi* in the literature.

*Remarks*.—Specimen UCMP.4799 cannot be the spire of a U-shaped acrioceratid ammonoid because it is almost complete. Aguirre-Urreta (1986) compared *Helicancylus gabbi* to the ancyloceratid *Kutatissites* Kakabadze, 1970, the helicoidally coiled inner whorls of which resemble the species (e.g., Kakabadze, 1970; Stoykova, 1992; Delanoy et al., 2000). The genus flourished within the Barremian/Aptian boundary interval in the Mediterranean Tethys, and extends into the upper lower Aptian in Colombia (= *Dufrenoyia sanctorum-Stoyanowiceras treffryanus* Biozone of Etayo-Serna, 1979, 1983). In this zone, Etayo-Serna (1983) reported *Pseudoaustralicerias columbiae* (Basse, 1928), the inner whorls of which have a “coiling elliptical in one more or less inclined plane” (Etayo-Serna, 1983, p. 7) and bear the two similar ornamental stages of *Helicancylus gabbi* described above. The presence of a helicoidally spiral in the inner whorls of *Pseudoaustralicerias* is observed in many upper Aptian taxa from the Tethys and the Pacific Coast, notably in the widespread species group *Pseudoaustralicerias ramososeptatum* (Anthula, 1900) – *Pseudoaustralicerias pavlowi* Wassiliewsky, 1909 (see, e.g., Kakabadze and Hoedemaeker, 2004, pl. 66, fig. 1). For these reasons, specimen UCMP.4799 could correspond to the helicoidally coiled inner whorls of a *Pseudoaustralicerias* species. *Helicancylus gabbi* is, therefore, transferred to the Ancyloceratidae and referred to *Pseudoaustralicerias gabbi*. The presence of *Pseudoaustralicerias* in the Aptian of California remains unknown to date. However, the taxonomy of two ancyloceratids from Shasta County, e.g., *Tropaeum percostatum* (Gabb, 1864) and *Australicerias argus*, are indeed in need of revision because both taxa better conform



to the original understanding of *Pseudoaustraliceras* given by Kakabadze (1981).

## Discussion

*Specific content of Hamiticeras.*—In the Fossilium Catalogus, Klein et al. (2007) listed seven species of *Hamiticeras*. Their validity and taxonomic assignment are discussed below:

*Hamiticeras aliensis* Lobjanidze, 1972 is a nomen nudum according to ICZN Art. 13.1 (ICZN, 1999) because it does not meet the requirements for a species designation for material published after 1930 (Klein et al., 2007).

*Anisoceras carcitanense* Matheron, 1880 was introduced on the basis of a large retroversum fragment from the Aptian of Cassis, southern France (Matheron, 1880, pl. D-25, fig. 2). The species was transferred to *Hamiticeras* by Conte (1995) and Vermeulen et al. (1999), but many individuals of that species were commonly confused with Californian taxa in the literature (see synonymy lists above). The species is under revision thanks to the collection of new topotypes, and it seems that the species can hardly be accommodated into *Hamiticeras* due to its larger size; simple, uniform, denser ribbing crossing the venter through most of the proversum; and smooth ribs in the flexus and retroversum. It is herein referred to ‘*Hamiticeras*’ *carcitanense* pending revision.

The Hauterivian species *Hamiticeras crevolai* Vermeulen, Thieuloy and Lapeyre, 1999 was selected as the type species of *Monodites* Bert, 2009, the latter typifying the monogeneric family Monoditidae Bert, 2009 from the upper Hauterivian of southeastern France.

Finally, the taxa *Hamiticeras chipatai*, *Hamiticeras longus* Kakabadze and Hoedemaeker, 2004, and *Hamiticeras ventrotuberculatum* Kakabadze and Hoedemaeker, 2004 form a closely allied group of species from the ‘middle’ Aptian of Colombia. Those species compare well to *Hamiticeras* and can be distinguished from one another by varying lengths of the proversum and ornaments. After a juvenile stage made of simple ribs, the Colombian species either develop alternating thin atuberculate intercalatories and strong trituberculate (*Hamiticeras chipatai*), bituberculate (*Hamiticeras longum*), or unituberculate primaries (*Hamiticeras ventrotuberculatum*) along the proversum. Such variability mimics that observed in Californian *Hamiticeras*. However, differences are seen in the extension of intercalatories up to the upper proversum, and an early termination of the phragmocone at this stage (see e.g., Kakabadze and Hoedemaeker, 1997, pl. 13, fig. 2a–d; 2004, pl. 54, fig. 2a, b).

*Origin of Hamiticeras.*—The plexus of Colombian *Hamiticeras*—namely *Hamiticeras chipatai*, *Hamiticeras longus*, and *Hamiticeras ventrotuberculatum*—have a mixture of features of *Toxoceratoides* and *Hamiticeras*. It is tempting to consider that Mediterranean *Toxoceratoides* and northern Pacific *Hamiticeras* could be phylogenetically linked through this plexus of Colombian species. Note that some fragmented *Hamiticeras* individuals are known in the lower upper Aptian of the Caribbean domain (e.g., Moreno-Bedmar et al., 2018), which could indeed correspond to the area of inception of *Hamiticeras*.

## Conclusions

Revision of the types of *Ptychoceras aequicostatus* invalidates the genus *Helicancylus* and thus the family Helicancylidae. Anderson’s (1938) taxon *Helicancylus gabbi* is transferred to *Pseudoaustraliceras*. The Acrioceratidae should be used as a valid substitute. Designation of a plastoholotype of *Hamiticeras pilsbryi* supports the separate use of *Hamiticeras* for grouping the plexus *Hamiticeras pilsbryi*, *Hamiticeras philadelphium*, and *Hamiticeras* aff. *H. philadelphium* from California, and *Hamiticeras chipatai*, *Hamiticeras longus*, and *Hamiticeras ventrotuberculatum* from of Colombia. *Hamiticeras* has the closest affinities with *Toxoceratoides*, but its toxoceratid-like coiling with a gooseneck flexus and an elongated flexuous retroversum, a long phragmocone extending up to the lower flexus, and a suture line with a rather symmetric external saddle and a narrow, bipartite lateral saddle are diagnostic features to be used to identify that genus. The presence/absence of intercalatories on the proversum is variable in both genera, and this cannot be used as a reliable diagnostic parameter. A phyletic link between *Toxoceratoides* and *Hamiticeras* is hypothesised but is in need of further investigation.

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## Declaration of competing interests

The authors declare that they have no conflicts of interest to disclose.

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