



This work is licensed under a Creative Commons Attribution License (CC BY 4.0).

## Research article

[urn:lsid:zoobank.org:pub:56507FD3-29FE-4CF7-B205-A339EC9D471A](https://zoobank.org/pub:56507FD3-29FE-4CF7-B205-A339EC9D471A)

# The systematic affinities between the Lower Cretaceous Ammonoidea *Protacanthoplites abichi* (Anthula, 1900) and *Acanthohoplites aschiltaensis* (Anthula, 1900)

Camille FRAU

Groupement d'Intérêt Paléontologique, Science et Exposition, 60 bd Georges Richard,  
83000 Toulon, France.

Email: [camille\\_frau@hotmail.fr](mailto:camille_frau@hotmail.fr)

[urn:lsid:zoobank.org:author:4F202BE7-922D-4CE0-B961-311B29DEEB80](https://zoobank.org/author:4F202BE7-922D-4CE0-B961-311B29DEEB80)

**Abstract.** This work provides the first revision and illustration of the type material of the ammonite species *Parahoplites abichi* Anthula [Type species of *Protacanthoplites* Tovbina] and *Parahoplites aschiltaensis* Anthula [Type species of *Acanthohoplites* Sinzow] from the upper Aptian (Lower Cretaceous) of Dagestan, Russia. The close affinities and synonymy between these two species are confirmed, and *Acanthohoplites aschiltaensis* is here retained as the senior valid name by its long quoting history and its historical use as a zonal index of the upper Aptian. The genus *Protacanthoplites* should be thus synonymised with *Acanthohoplites* by priority in the date of publication. Comparison with, and distinction from, closely allied Acanthohoplitidae is provided.

**Keywords.** Acanthohoplitidae, Ammonoidea, Aptian, Dagestan, taxonomy.

Frau C. 2023. The systematic affinities between the Lower Cretaceous Ammonoidea *Protacanthoplites abichi* (Anthula, 1900) and *Acanthohoplites aschiltaensis* (Anthula, 1900). *European Journal of Taxonomy* 888: 137–158. <https://doi.org/10.5852/ejt.2023.888.2237>

## Introduction

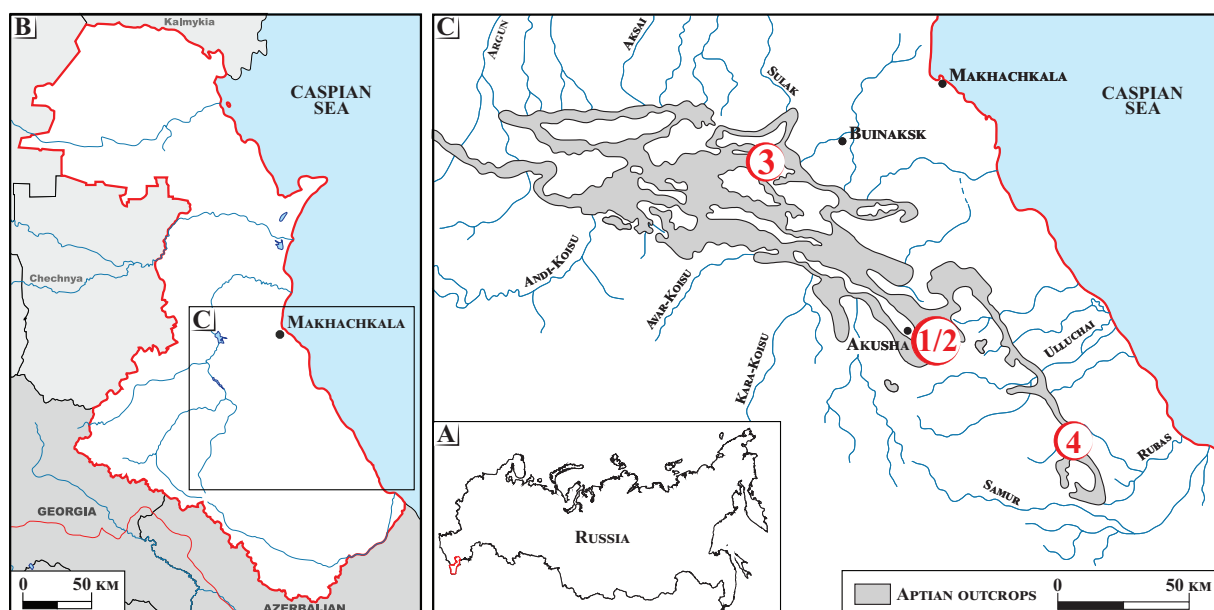
This paper continues the taxonomic revision of the most iconic taxa of the family Acanthohoplitidae Stoyanow, 1949 (Cephalopoda, Ammonoidea) initiated with the re-examination of the type species *Hypacanthoplites plesiotypicus* (Fritel, 1906) (Kennedy *et al.* 2000), *Nolaniceras nolani* (Seunes, 1887) (Bulot *et al.* 2014), *Colombiceras crassicostatum* (d'Orbigny, 1841) and *Gargasicerias gargasense* (d'Orbigny, 1841) (Frau *et al.* 2020). We here provide the first revision and illustration of the type material of *Parahoplites abichi* Anthula, 1900 [Type species of *Protacanthoplites* Tovbina, 1970] and *Parahoplites aschiltaensis* Anthula, 1900 [Type species of *Acanthohoplites* Sinzow, 1908] from the upper Aptian of Dagestan (Fig. 1A–C). The close affinities between the two taxa are clarified, and comparison with, and distinction from, other known Acanthohoplitidae is provided.

## Material and methods

The type series of *Parahoplites abichi* includes the two syntypes IPUW 1900-3a (Fig. 2A–G), and IPUW 1900-3b (Fig. 2H–K) belonging to the Anthula collection deposited at the Institut für Paläontologie, Universität Wien, Austria. Label indicates an origin from the upper Aptian of Akusha, Dagestan (Fig. 1A–C). Specimen IPUW 1900-3a was first designated holotype of *Protacanthoplites abichi* by Dimitrova (1967: 187). It was then re-considered as lectotype by Sharikadze *et al.* (2004) since the original description of Anthula (1900) was based on the amalgamation of two different syntypes.

The type series of *Parahoplites aschiltaensis* includes the four syntypes PMU.24105 (Fig. 2L–R), PMU.24106 (Fig. 3A–C), PMU.24107 (Figs 4A–B, 5A–C) and PMU.24108 (Fig. 5G–H) belonging to the Sjögren collection deposited at the Palaeontological Museum of Uppsala, Sweden. All specimens originate from the upper Aptian of Ashil'ta, Dagestan (Fig. 1A–C). The specimen of Anthula (1900: pl. X(IX) fig. 3a–b) from Akusha, that was designated lectotype of *Acanthohoplites aschiltaensis* by Stoyanow (1949: 107), is considered lost. The specimen PMU.24105 (= Anthula 1900: pl. X(IX) fig. 2a–b) was subsequently designated holotype by Kvantaliani (1971: 55). It was then considered as lectotype by Bogdanova & Mikhailova (2016) since the original description of Anthula was based on the amalgamation of four different syntypes.

In the palaeontological study, the description of the conch shape follows the guidelines of Klug *et al.* (2015). We quantified by standard measurements  $D$  (larger measurable diameter taken between the ribs),  $U$  (umbilical width),  $Wh$  (whorl height),  $Ww$  (whorl thickness). All dimensions are given in millimetres. The associated ratios of the conch shape ( $Ww/D$ ), the whorl width index ( $Ww/Wh$ ), the umbilical width index ( $U/Wh$ ) were investigated to compare conch parameters. This study is combined with a qualitative analysis of the ontogeny of the material at our disposal, including the definition of succeeding stages. Unless otherwise mentioned, this work follows the Standard Mediterranean Ammonite Zonation (SMAZ) of the Aptian Stage (Reboulet *et al.* 2018).



**Fig. 1.** A–B. Locality map of Dagestan, Russia. C. The main localities cited in the text located southwest of the Makhachkala town (after Bogdanova & Mikhailova 2016).

## Results

Class Cephalopoda Cuvier, 1797  
 Subclass Coleoidea Bather, 1888  
 Superorder Ammonoida Haeckel, 1866  
 Order Ammonitida Haeckel, 1866  
 Superfamily Acanthohoplitoidea Stoyanow, 1949  
 Family **Acanthohoplitidae** Stoyanow, 1949

## Remarks

The supraorder classification follows the account of Hoffmann *et al.* (2022), grouping all Devonian to Cretaceous ammonoids in the monophylum Ammonoida. The understanding of the superfamily Acanthohoplitoidea follows Sharikadze (2015), and Frau *et al.* (2020).

Genus ***Protacanthoplites*** Tovbina, 1970

## Type species

*Parahoplites abichi* Anthula, 1900; by original designation.

***Protacanthoplites abichi*** (Anthula, 1900)  
 Figs 2A–K, 3A, F

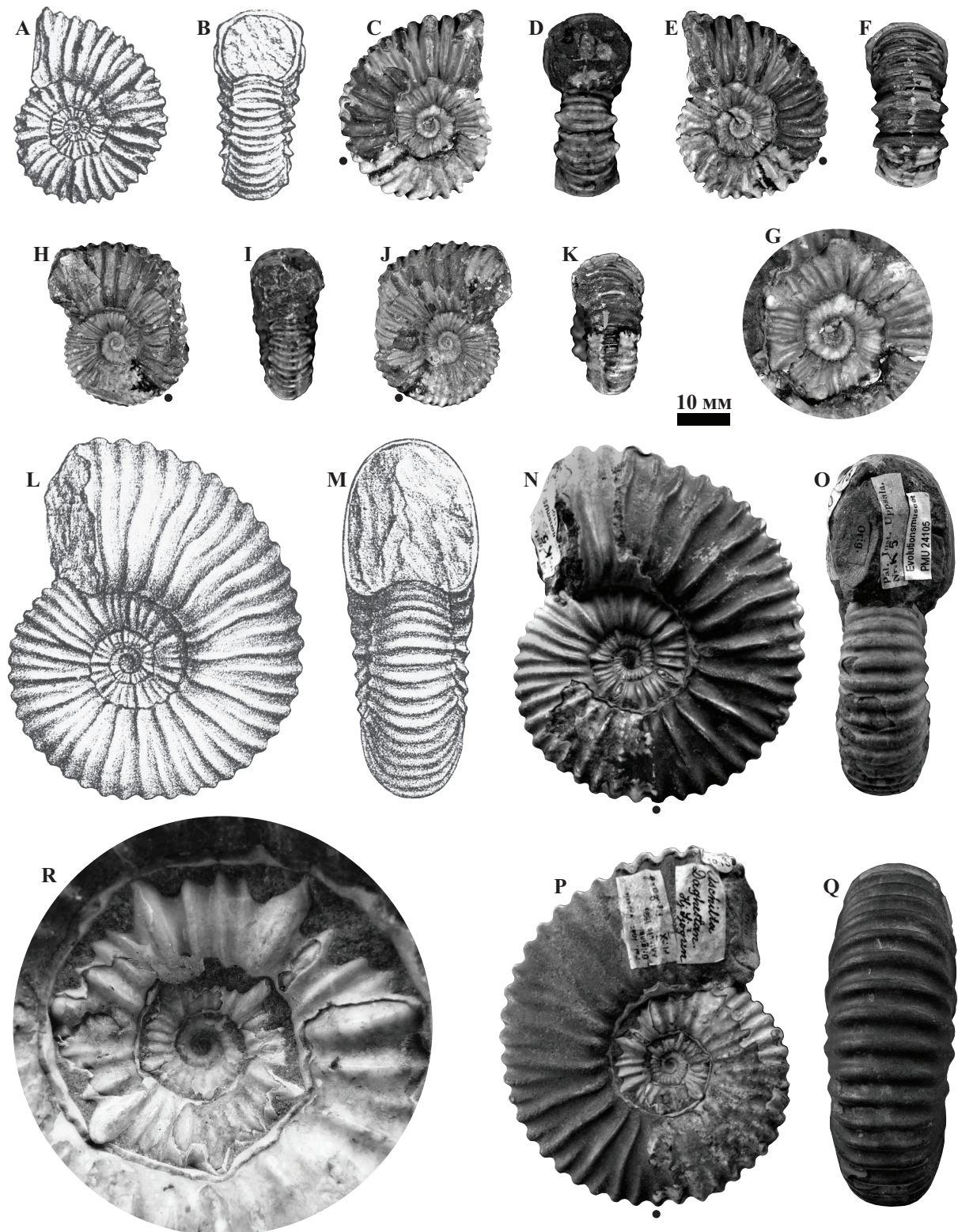
## Conch shape and ontogeny

### Lectotype IPUW 1900-3a

Understanding of the lectotype was so far based on the hand-drawing of Anthula (1900: pl. IX(VIII) fig. 2a–c) (see Fig. 2A–B). It is here properly illustrated for the first time (Fig. 2C–G). The specimen corresponds to a small-sized, 3D-preserved internal mould with a calcitic phragmocone and calcareous body chamber with trace of aragonitic shell. The body chamber occupies half of the last whorl, but the peristome is not preserved. Measurements are given in Table 1. Shell shape of the lectotype is characterised by a discoidal ( $Ww/D \sim 0.41$ ), weakly depressed ( $Ww/Wh \sim 1.08$ ), very evolute ( $U/Wh \sim 1.18$ ) subophiocone coiling ( $U/D \sim 0.45$ ).

The embryonic (Ammonitella) stage is poorly preserved, and remains poorly characterised. The first visible whorls of the shell develop a reniform whorl section, crateriform umbilicus, spaced and flat-topped ribs angulate at shoulders followed by smooth interspaces. This corresponds to the Royerianum stage that is typical of the early ontogeny of the basal Acanthohoplitidae (Frau *et al.* 2020).

Then, the whorl section progressively becomes depressed, sub-rounded with convex flanks. The umbilical wall is rounded. The ornamentation consists of an alternation of straight to convex, strong primary ribs and variable number, two to four, of sharp atuberculate secondaries, irregular in thickness and irregularly arranged. Primary ribs are gradually thickened on the flank. They develop strong, elongated tubercles, sometimes clavate, located high on the flank, in tight contact with the succeeding whorl. The tuberculate ribs get a distinct hexagonal cross section. The tubercles divide into two, rarely three, branches over the venter. They strengthen as fold-like ribs, notably the posterior branch, and generally join on the tubercles of the other side. A third discrete rib sometimes appears between two ventral ribs. The secondary ribs are simple, rarely bifurcate, and can be coalescent on the primaries forming a polygyrate pattern. Primary ribs can be followed by an approximated and enlarged secondary rib so that they mimic constrictions. By these features, the ontogeny closely resembles the Gargasense stage *sensu* Frau *et al.* (2020) of the Acanthohoplitidae *Colombiceras crasscostatum* but differences are seen in the quadratic whorl section with rounded venter, and distinctive strengthened ribbing and tubercles. This stage is here referred to as the Abichi stage.



**Fig. 2.** A–K. *Parahoplites abichi* Anthula, 1900. A–B. Reproduction of the original hand-drawing. C–G. Lectotype (IPUW 1900-3a). G. Focus on its inner whorls. H–K. Syntype (IPUW 1900-3b), which is here excluded from the species. – L–R. *Parahoplites aschiltaensis* Anthula, 1900. L–M. Reproduction of the original hand-drawing. N–R. Lectotype (PMU.24105). R. Focus on its inner whorls. Scale bar = 10 mm.

**Table 1.** Dimensions of *Protacanthoplites abichi* (Anthula, 1900), lectotype (IPUW 1900-3a). \*measurements taken between ventral ribs. Abbreviations: see Material and methods.

Specimen	D	U	Wh*	Ww*
IPUW 1900-3a	33.9	15.2	c.12.9	c.14.0

As growth proceeds, the number of intercalatories decreases, being mostly one to two, and coalescent ribs become sporadic. Primary ribs are dominantly bifurcate, then simple. They thicken along the flank, especially at the umbilical margin, while the tubercles tend to disappear. Ribs distinctly bend forward on the venter. All ribs are flat-topped or cuneiform over the venter. This stage mimics the *Crassicostatum* stage sensu Frau *et al.* (2020) of *Colombiceras crassicostatum*, but differences are seen in the whorl section that is broadly rounded, with subhexagonal rib section with a convex venter lacking ventral attenuation. This sequence is here referred to as the *Crassicostatum*-like stage.

The ontogenetic sequence of *Protacanthoplites abichi* is illustrated on Fig. 3A.

#### Specimen IPUW 1900-3b

The second syntype of Anthula (1900) is here properly illustrated for the first time (Fig. 2H–K). It is a small, 3D-preserved internal mould with a calcitic phragmocone and calcareous body chamber with remains of aragonitic shell. It shows a slight distortion of the shell at the beginning of the body chamber. The latter occupies half of the last whorl. The peristome is not preserved. Measurements are given in Table 2. Shell shape is characterised by a discoidal ( $Ww/D \sim 0.39$ ), weakly depressed ( $Ww/Wh \sim 1.02$ ), very evolute ( $U/Wh \sim 0.91$ ) subvirgacone coiling ( $U/D \sim 0.35$ ).

The first visible whorl of the shell develops the Royerianum stage, changing into the Abichi stage of the lectotype *Protacanthoplites abichi*. To the difference, the ribbing is more gracile, with discrete spiny tubercles. The venter is narrower. As growth proceeds, the *Crassicostatum*-like stage initiates on the body chamber, but it is also much more gracile and regular than the lectotype of *Protacanthoplites abichi*, and develops flexuous primary ribs. By these features, specimen IPUW 1900-3b poorly matches the lectotype.

#### Suture line

Anthula (1900: pl. IX (VIII) fig. 2c) provided a partial suture line drawing for *Protacanthoplites abichi* showing a quinquelobate pattern. The lectotype seems to be immature as it does not show any sign of suture approximation at the end of the phragmocone. The suture morphogenesis of that species has subsequently been examined by Mikhailova (1957: fig. 5; 1958: fig. 1) and Tovbina (1970: fig. 4). According to these authors, the umbilical lobe is tripartite and rather symmetrical. A wide umbilical saddle is divided into two parts, the outer of which in turn becomes bifid. The ventral and dorsal lobes are bifid and complicated by lateral teeth. The ventral lobe has a low median saddle.

#### Age

The litho- and biostratigraphy of the Akusha locality was documented by Mordvilko (1962) and Bogdanova & Mikhailova (2016), but none of these authors have reported the type stratum of *Protacanthoplites abichi*. The species is, however, known to occur in the '*Acanthoplites* (sic) *aschiltaensis*–*Acanthoplites uhligi* Zone' sensu Mordviko (1962) of Dagestan (Bogdanova & Mikhailova 2016). Correlation of this zone with the SMAZ is still not obtained with certainty, but it may cover part of the *Epicheloniceras martini* and *Parahoplites melchioris* standard zones (Luber *et al.* 2017; Frau, 2020a, 2020b).

**Table 2.** Dimensions of *Protacanthoplites abichi* (Anthula, 1900), specimen IPUW 1900-3b. \*measurements taken between ventral ribs. Abbreviations: see Material and methods.

Specimen	D	U	Wh*	Ww*
IPUW 1900-3b	29	10,3	11,3	11,5

Genus *Acanthohoplites* Tovbina, 1970

**Type species**

*Parahoplites aschiltaensis* Anthula, 1900; by subsequent designation of Roman (1938).

*Acanthohoplites aschiltaensis* (Anthula, 1900)

Figs 2L–R, 3B–C, F–J, 4–6

**Conch shape and ontogeny**

**Lectotype PMU.24105**

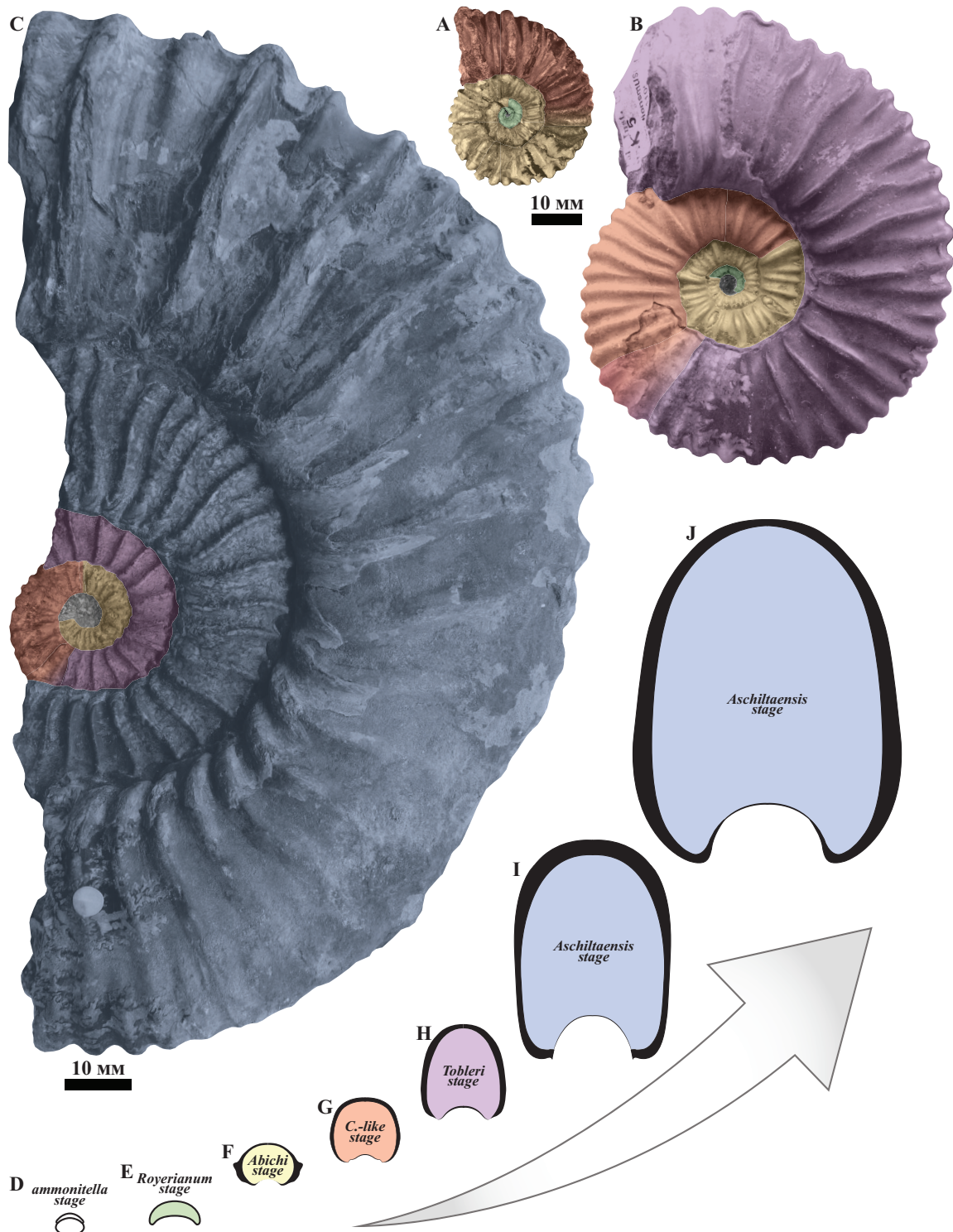
Understanding of the lectotype was so far based on the hand-drawing of Anthula (1900: pl. X(IX) fig. 2a–b) (see Fig. 2L–M). It is here properly illustrated (Fig. 2N–R). The lectotype shows the same state of preservation as that of *Protacanthoplites abichi* described above. Peristome is not preserved. The body chamber occupies half of the outer whorl. Measurements are given in Table 3. Its shell shape is characterised by a moderate size, discoidal ( $Ww/D \sim 0.35$ ), weakly compressed ( $Ww/Wh \sim 0.82$ ), subevolute ( $U/Wh \sim 0.76$ ) and subvirgacone coiling ( $U/D \sim 0.33$ ).

The ontogenetic sequence develops four stages following the worn embryonic whorls (Fig. 3B) that closely match those of *Protacanthoplites abichi* described above. The first visible whorls bear the latest part of a typical Royerianum stage that is well visible on the left face. It changes to an Abichi stage almost identical to that of *Protacanthoplites abichi*, except its more regular pattern of secondary ribs at the beginning. The Abichi stage occupies one whorl and a half. As growth proceeds, the primary ribs lose their tubercles, while secondaries become irregular, and start decreasing. Ribbing changes progressively on the late phragmocone into an alternation of simple, primary ribs, and generally one secondary, irregular, both in length and strength on the flank. The secondaries can be indistinctly branched on the primary ribs in the lower third of the flank or at mid-flank. All ribs are flat-topped or cuneiform over the venter. This is almost similar to the Crassicostatum-like stage of *Protacanthoplites abichi*, but differences are seen in the progressive change of the whorl section becoming weakly compressed, subrectangular, higher than wide.

The Crassicostatum-like stage changes again in the late phragmocone into a regular alternation of strong, slightly flexuous, primary ribs, with a slight retrocurvature at the umbilical margin, and a single secondary starting high on the flank. The maximum whorl width is reached in the lower third of the flank. Twenty-five ventral ribs are observed on the last half whorl. They are distinctly flat-topped over the venter. These features conform to the adult ontogeny of *Colombiceras crassicostatum* referred to as the Tobleri stage (Frau *et al.* 2020). The Tobleri stage starts around  $D \sim 40$  mm (estimation) and occupies the rest of the outer whorl.

**Paralectotype PMU.24106**

This paralectotype was not figured by Anthula (1900). It corresponds to a fragment of a large-sized phragmocone displaying the features of the Tobleri stage, including a rather regular alternation of strong, moderately flexuous primary ribs, with a slight retrocurvature at the umbilical margin, and a single secondary of variable height (Fig. 4).

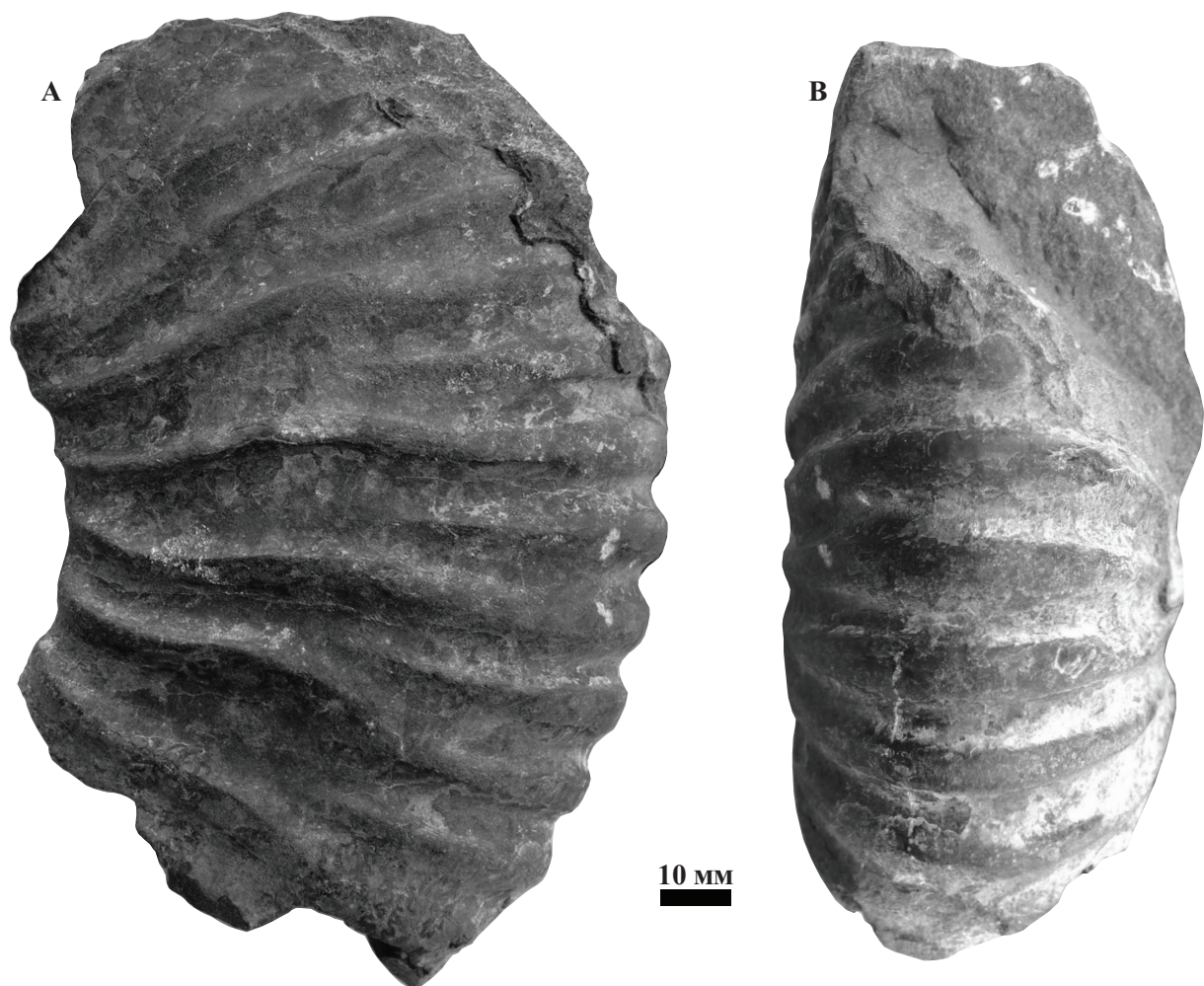


**Fig. 3.** Illustration of the ontogenetic stages observed after the ammonitella (not seen), including Royerianum (green), Abichi (yellow), Crassicostatum-like (orange), Tobleri (violet), and Aschiltaensis (blue). **A.** *Protacanthoplites abichi* (Anthula, 1900), lectotype (IPUW 1900-3a). **B.** *Acanthohoplites aschiltaensis* (Anthula, 1900), lectotype (PMU.24105). **C.** *A. aschiltaensis*, paralectotype (PMU.24107). **D–J.** Schematic evolution of the whorl section of the plexus *P. abichi* – *A. aschiltaensis*. **D–E.** After Bogdanova & Mikhailova (2016: fig. 57), not to scale. **F.** After IPUW 1900-3a, not to scale. **G.** After paralectotype (PMU.24108), at scale. **H–J.** After paralectotype (PMU.24107), at scale.

**Paralectotype PMU.24107**

Anthula (1900: pl. XI(X) fig. 1) provided a hand-drawing of this paralectotype. It is here properly illustrated for the first time (Figs 5A–B, 6A–C). It corresponds to a 3D-preserved internal mould but of larger size compared to the lectotype. Measurements are given in Table 3. Estimated diameter is about 297 mm. Its phragmocone is broken, but the general shell shape is virgacone ( $U/D \sim 0.39$ ) with extremely discoidal ( $Ww/D \sim 0.25$ ), very evolute ( $U/Wh \sim 1.19$ ) and weakly compressed coiling ( $Ww/Wh \sim 0.77$ ). Its last preserved sutures are approximated suggesting its maturity.

The first preserved whorls bear a late Abichi stage, consisting in strong primaries, simple or bifurcate, bearing tubercle-like thickenings at the point of furcation, and a variable number of strong secondaries. It gives way to a short Crassicostatum-like stage (estimation:  $D \sim 35$  mm), made of strong primaries, simple or bifurcate, with decreasing thickenings on the flank, and generally one strong secondary. All ribs are flat-topped or cuneiform over the venter. Then, a Tobleri stage develops at  $D \sim 50$  mm (estimation) bearing spaced, sharper primary ribs, being slightly flexuous with a slight retrocurvature at the umbilical margin. Secondary ribs are unique, high on the flank, so that they are almost covered by the succeeding whorl. Ribbing changes in the last two whorls into more spaced and enlarged, more flexuous, primaries with a maximum on the body chamber. Primary ribs start with a distinctive retrocurvature at the umbilical margin except approaching the aperture, and are simple, rarely bifurcate, over the flank.



**Fig. 4.** *Acanthohoplites aschiltaensis* (Anthula, 1900), paralectotype (PMU.24106). Scale bar = 10 mm.



**Table 3.** Dimensions for specimens of *Acanthohoplites aschiltaensis* (Anthula, 1900), lectotype (PMU.24105) and paralectotypes (PMU.24107 and PMU.24108). \*measurements taken between ventral ribs. Abbreviations: see Material and methods.

Specimen	D	U	Wh*	Ww*
PMU 24105	68.6	22.6	29.6	24.3
PMU 24107	297	117	98	75.6
PMU 24108	93	39	32.8	30.8

The secondaries are unique, and generally start in the middle, or upper flank. This last ontogenetic stage is here referred to as the *Aschiltaensis* stage (Fig. 3C). Number of ventral ribs cannot be estimated but it seems denser than during the *Tobleri* stage.

#### Paralectotype PMU.24108

Anthula (1900: pl. X(IX) fig. 1) only gave an idealised hand-drawing of the cross section of this paralectotype. A proper illustration is given here (Fig. 6D–H). It corresponds to a half of a moderately large phragmocone. Measurements are given in Table 3. The broken part allows to observe the *Abichi* stage extending up to  $D \sim 18$  mm (estimation), and then, a part of the *Crassicostatum*-like stage. Beyond, the ontogeny is rather similar to the lectotype although the *Tobleri* stage is more robust and shows great affinity with specimen PMU.24107. Indeed, the shell shape differs from the lectotype by a more discoidal ( $Ww/D \sim 0.33$ ) and weakly compressed ( $Ww/Wh \sim 0.94$ ) coiling, while the umbilicus is more open ( $U/Wh \sim 1.19$ ). Specimen PMU.24108 further displays a lower number of ventral ribs (estimated at  $\sim 21$ ) on the last half whorl.

#### Suture line

A partial suture line of *Acanthohoplites aschiltaensis* was drawn by Anthula (1900: pl. X(IX) fig. 3b) based on the lost syntype. It is of quinquelobate type and shows a deep inner lateral lobe with distinctive central and inner branches. This drawing was commented on by Stoyanow (1949, 1958), and his re-examination of the lectotype PMU.24105 highlighted a distinctive symmetrically trifid first lateral lobe, with some asymmetry in its inner branch, and bifid saddles. The lectotype seems to be mature as it shows suture approximation at the end of the phragmocone. The suture morphogenesis of that species has then been examined by Drushchits (1956), and Bogdanova & Mikhailova (2016) based on individuals from Dagestan. The suture line consists of a bifid ventral lobe with a low bifid median saddle; rather symmetrical umbilical lobe with distinctive lateral branches; symmetrical, short and trifid first umbilical lobe; deep inner lateral lobe with distinctive central and inner branches; bifid dorsal lobe with variable digits; broad and high, asymmetrically bifid external and umbilical saddles. The first umbilical saddle (U1/I) is indistinctly asymmetrically trifid. There is no difference between the suture lines of *Protacanthoplites abichi* and *Acanthohoplites aschiltaensis*.

#### Age

There is no comprehensive description of the Ashil'ta locality that yielded the type material of *Acanthohoplites aschiltaensis*. Nevertheless, the *Acanthohoplites*-bearing beds of Akusha consist of a  $\sim 25$  m-thick interval assigned to the '*Acanthoplites aschiltaensis*–*Acanthoplites uhligi* Zone' (Mordvilko 1962). This is the case in the reference Dargi River section (Bogdanova & Mikhailova 2016: figs 10–11). Most of the taxa from the '*Acanthoplites aschiltaensis*–*Acanthoplites uhligi* Zone' of the Dargi River section derive from a siltstone horizon including fossiliferous phosphatic nodules.

*Acanthohoplites aschiltaensis* co-occurs here with *Parahoplites sjogreni* Anthula, 1900, *Phylloceras* (*Hypophylloceras*) *velledae* Michelin, 1834, *Aconeceras* sp., and the problematic *Chelonicer* sp. (Bogdanova & Mikhailova 2016). This horizon is of regional significance since it also crops out in the Rubas-chai section, in the vicinity of Khuchni (Bogdanova & Mikhailova 2016: fig. 12). A younger *Acanthohoplites*-bearing horizon is documented in the upper part of the ‘*Acanthohoplites aschiltaensis*–*Acanthohoplites uhligi* Zone’ in the Dargi River and Rubas-chai sections. Representatives assigned to *Acanthohoplites* ex gr. *aschiltaensis* would be still present in the corresponding horizon but the fauna lacks illustration for further confirmation.

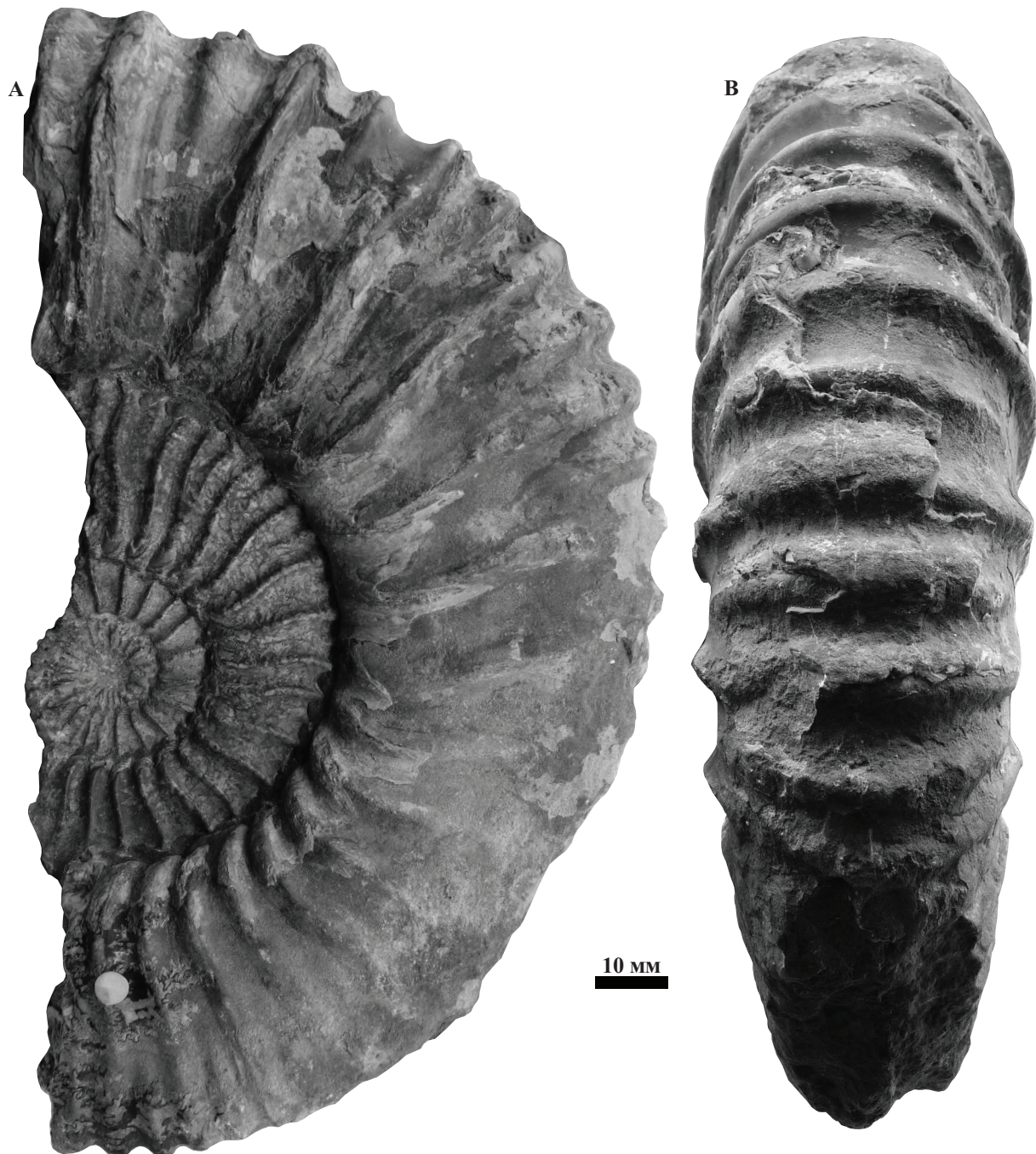
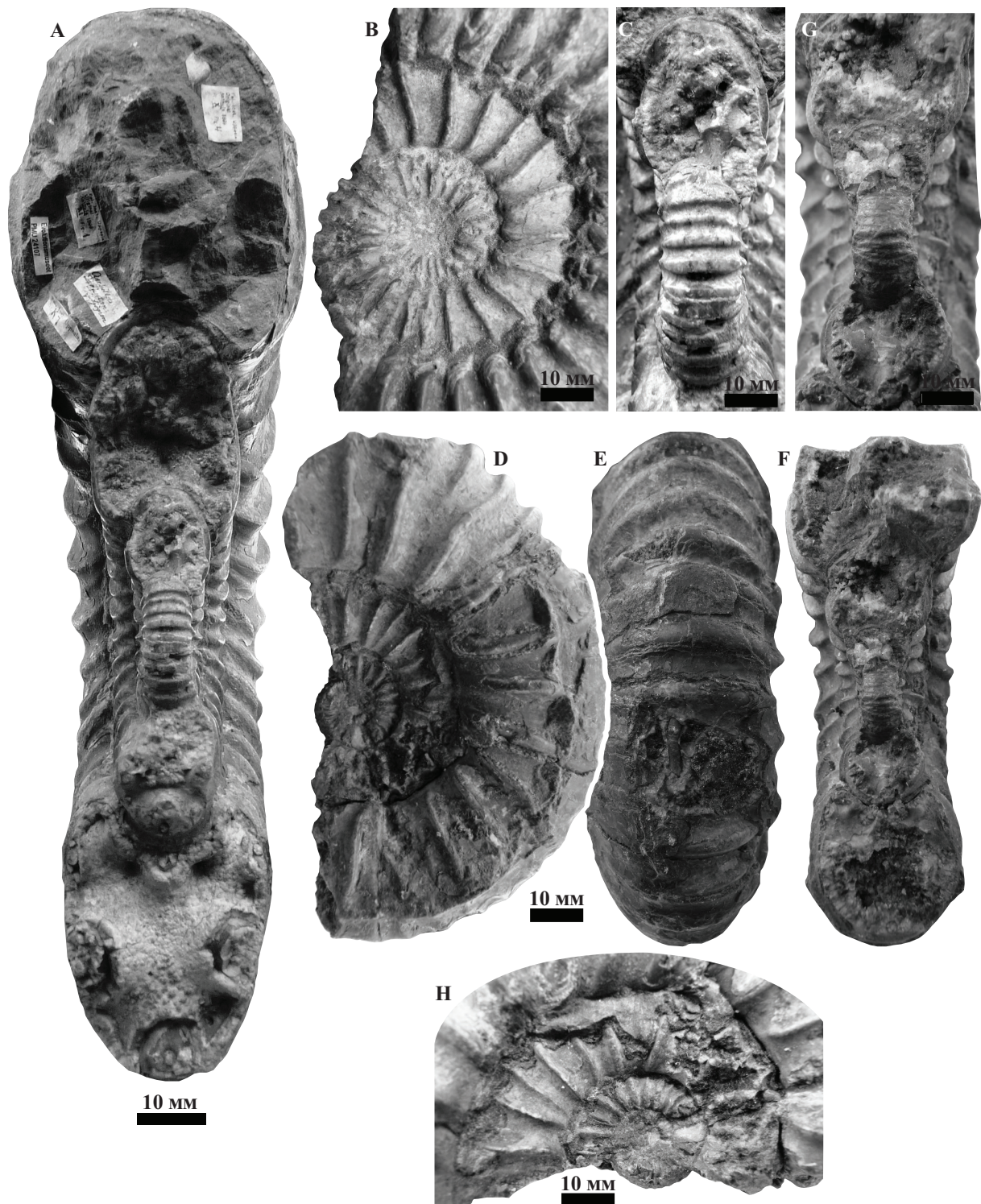


Fig. 5. *Acanthohoplites aschiltaensis* (Anthula, 1900), paralectotype (PMU.24107). Scale bar = 10 mm.

**Subspecies of *Acanthohoplites aschiltaensis***

Klein & Bogdanova (2013) listed three subspecies of *Acanthohoplites aschiltaensis* in the *Fossilium Catalogus*. Their validity is discussed below.



**Fig. 6.** *Acanthohoplites aschiltaensis* (Anthula, 1900). A–C. Paralectotype (PMU.24107). D–H. Paralectotype (PMU.24108). Scale bars = 10 mm.

*Acanthohoplites aschiltaensis* var. *rotundatus* Sinzow, 1908

The subspecies is based on a single, incomplete, moderate-sized phragmocone of an acanthohoplite from the Mangyshlak Peninsula (Sinzow 1908: pl. 5 figs 2–3). The specimen closely resembles the paralectotype PMU.24108 of *Acanthohoplites aschiltaensis* (compare with Fig. 6D–H). The rounded whorl section of *Acanthohoplites aschiltaensis* var. *rotundatus* cannot be retained as a distinctive conch parameter since its whorl width index ( $Ww/Wh \sim 1$ ) falls in the variability of the type material. Consequently, it seems unnecessary to separate the subspecies *rotundatus* from *Acanthohoplites aschiltaensis*. Other citations of the subspecies *rotundatus* in the literature differ from true *Acanthohoplites aschiltaensis* (see synonymy list in Appendix).

*Acanthohoplites aschiltaensis* var. *aplanatus* Sinzow, 1908

*Acanthohoplites aschiltaensis* var. *aplanatus* is based on two, well-preserved, moderate-sized acanthohoplites from the Mangyshlak Peninsula (Sinzow 1908: pl. V figs 4–7). The subspecies was subsequently considered as a valid species by Kazansky (1914), as it shows a distinctive morphology (moderately evolute coiling, compressed, quadratic then sub-rectangular whorl section, flattened venter in the juvenile and progressively rounded in the adult with convergent outer flanks on the body chamber, narrowly to broadly rounded umbilical wall) and ornamentation (complex rib and tubercle pattern of the inner whorls, early loss of the feeble lateral tubercles). These features better compare to the character and sculpture of *Hypacanthoplites* as revised by Kennedy *et al.* (2000). The species is here transferred to that genus pending further investigation. The individuals figured by Luppov & Drushchits (1958: pl. XLVII fig. 4a–b), Eristavi (1961: pl. II fig. 11) and doubtfully Kazansky (1914: pl. III fig. 48a–c) match *Hypacanthoplites aplanatus*. The specimen figured by Sinzow (1913: pl. 6 fig. 4) better compares to *Acanthohoplites lautum laxa* Glazunova (1953); the latter taxon having been tentatively transferred to *Egoianiceras* Avram, 1974 by Frau *et al.* (2020).

*Acanthohoplites aschiltaensis* var. *subangulata* Luppov, 1961

The subspecies is based on two, well-preserved, acanthohoplites from the southwest termination of the Gissar Range, Uzbekistan (Luppov 1961: pl. I figs 2a–b, 3a–b). The species is broadly similar to *Acanthohoplites aschiltaensis* but differs by feebly but distinctive bituberculate primary ribs in the juvenile, a compressed quadratic whorl section with a flattened venter during the growth, and fine ribs in the adult. As such, it better conforms to *Hypacanthoplites*. The individual figured by Kvantaliani (1971: pl. VIII figs 2a–e, 3a–e) compares to with *Hypacanthoplites subangulata* while that of Khalilov (1988: pl. XI fig. 4) is of doubtful identification.

## Discussion

### Affinities between *Protacanthoplites* and *Acanthohoplites*

*Protacanthoplites abichi* and *Acanthohoplites aschiltaensis* share the same suture line, and same juvenile (Royerianum stage) as well as subadult ontogeny (Abichi and Crassicostatum-like stages). The lectotype of *Protacanthoplites abichi*, however, lacks the later growth stages of *Acanthohoplites aschiltaensis* (Tobleri and Aschiltaensis stages), but this could reflect its immaturity evidenced by the non-approximated suture lines, and incomplete body chamber.

Comparison with material from Akusha, i.e., the type locality of *Protacanthoplites abichi*, supports this view. Indeed, some individuals of *Acanthohoplites aschiltaensis* from that locality have a long and robust Abichi stage, but shorter later growth stages compared to the other ones matching the lectotype PMU.24105 (compare with Bogdanova & Mikhailova 2016: pls 14–15 for example). Since both species co-occur here, and more generally in the '*Acanthohoplites aschiltaensis*–*Acanthohoplites uhligi*

Zone' of Dagestan, a synonymy between *Protacanthoplites abichi* and *Acanthohoplites aschiltaensis* is likely. In the lack of date priority between the two taxa, the species *Acanthohoplites aschiltaensis* is here retained as the senior valid name by its long quoting history and its historical use as a zonal index of the upper Aptian. This meets former agreements of Wright *et al.* (1996), Szives (2008), and Bogdanova & Mikhailova (2016: 802) who previously acknowledged the synonymy of *Acanthohoplites* over *Protacanthoplites*.

#### Variability in *Acanthohoplites aschiltaensis*

Based on the type material and figured specimens from Dagestan (Bogdanova & Mikhailova 2016), *Acanthohoplites aschiltaensis* is represented by two distinct morphotypes, consisting in (i) small- to moderate-sized individuals, having a subophiocone to subvirgacone coiling, and generally the four main ontogenetic stages of the lectotype PMU.24105, viz. Royerianum, Abichi, Crassicostatum-like and Tobleri stages; and (ii) large-sized virgacone individuals further developing a long Aschiltaensis stage in the adult as in the paralectotype PMU.24107. These variabilities thus concern the adult size, general coiling, and change in adult ornamentation. This may conform to the expression of a classical (i.e., morpho-dimensional) dimorphism of sexual nature. Revision on an in situ palaeopopulation from Dagestan is, therefore, needed to confirm this hypothesis.

A revised synonymy list of *Acanthohoplites aschiltaensis*, taking account the putative dimorphism, is given in the Appendix. It can be seen that *Acanthohoplites aschiltaensis* has mostly been misidentified in the literature. Reliable occurrences are reported from Dagestan (Anthula 1900; Kazansky 1914; Bogdanova & Mikhailova 2016), Mangyshlak (Sinzow 1908), SE France (Thomel 2015), probably from northern Spain (Frau 2020a, 2020b) and Morocco (Luber *et al.* 2017).

#### Conclusions

Based on the revision of the type material of *Parahoplites abichi* and *Parahoplites aschiltaensis*, we confirm that these species are synonyms, and may illustrate a dimorphic pair. The species *Parahoplites aschiltaensis* is retained as the senior name. As a consequence, the genus *Protacanthoplites* should be synonymised with *Acanthohoplites* by priority in the date of publication. In their *Fossilium Catalogus*, Klein & Bogdanova (2013) listed ninety species and subspecies (including nomina nuda) for both *Acanthohoplites* and *Protacanthoplites*. A revision is far beyond the scope of this work, but it shows the extent of the challenge we were facing before a full understanding of the Aptian Acanthohoplitidae.

#### Acknowledgements

This work is dedicated to the late Luc G. Bulot (1963–2022) who had introduced me to the taxonomy of the Aptian Acanthohoplitidae. This work benefited from the (extensive) loan of Uppsala specimens thanks to Jan Ove R. Ebbestad (Palaeontological Museum of Uppsala). Warm thanks are also due to Alexander Lukeneder and Ivo Gallmetzer (Naturhistorisches Museum Wien) for their help with literature, photographs, and casts of Vienna specimens. Valuable inputs were provided by the reviewers Ottilia Szives (Hungarian Natural History Museum) and Christian Klug (Universität Zürich), as well as the topical editor Marie-Béatrice Forel (National Museum of Natural History).

#### References

- Anthula D.J. 1900. Über die Kreidefossilien des Kaukasus mit einem allgemeinen Überblick über die Entwicklung der Sedimentärbildungen des Kaukasus. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients* 12 (for 1899): 55–160 (1–106).
- Avram E. 1974. *Egoianiceras* nouveau sous-genre du genre *Colombiceras* Spath, 1923 (Ammonitina). *Dări de Seamă ale Ședințelor* 3. *Paleontologie* 60 (for 1972–1973): 3–10.

- Bather F.A. 1888. Shell-growth in Cephalopoda (Siphonopoda). *Journal of Natural History* 1: 298–309. <https://doi.org/10.1080/00222938809460727>
- Bogdanova T.N. & Mikhailova I.A. 2016. Middle Aptian biostratigraphy and ammonoids of the Northern Caucasus and Transcaspia. *Paleontological Journal* 50 (8): 725–933. <https://doi.org/10.1134/S0031030115100019>
- Bulot L.G., Latil J.-L., Hairabian A. & Fournillon A. 2014. New insight on the genus *Nolaniceras* Casey, 1961 (Ammonoidea, Cretaceous) and its consequences on the biostratigraphy of the Aptian Stage. *Proceedings of the Geologists' Association* 125: 227–232. <https://doi.org/10.1016/j.pgeola.2013.12.006>
- Cuvier G. 1797. *Tableau élémentaire de l'histoire naturelle des Animaux*. Baudouin, Paris. <https://doi.org/10.5962/bhl.title.11203>
- Dimitrova N. 1967. *Fossils of Bulgaria. IV. Lower Cretaceous-Cephalopoda (Nautiloidea & Ammonoidea)*. Bulgarian Academy of Sciences, Sofia.
- Drushchits V.V. 1956. On systematics of the family Parahoplitidae. *Scientific Reports of the Moscow State University. Geology* 176: 105–113.
- Eristavi M.C. 1961. Aptian and Albian ammonites of the north Caucasus. *Trudy Geologicheskogo Instituta Akademia Nauk Gruzinskoi SSR* 12 (17): 41–77.
- Frau C. 2020a. New insight on the age and significance of the Aparein black shales in the Basque-Cantabrian Basin, northern Spain. *Newsletters on Stratigraphy* 54 (1): 1–16. <https://doi.org/10.1127/nos/2020/0583>
- Frau C. 2020b. New insight on the age and significance of the Aparein black shales in the Basque-Cantabrian Basin, northern Spain – Reply to comments made by Fernández-Mendiola *et al.* (2021). *Newsletters on Stratigraphy* 54 (4): 501–505. <https://doi.org/10.1127/nos/2021/0675>
- Frau C., Pictet A. & Caïssa M. 2020. The affinities between the Lower Cretaceous Ammonoidea *Ammonites crassicostatus* d'Orbigny, 1841 and *Ammonites gargasensis* d'Orbigny, 1841. *Paleontología Mexicana* 9 (1): 53–72.
- Fritel P.H. 1906. Sur les variations morphologiques d'*Acanthoceras Milletianum*, d'Orb; sp. *Le Naturaliste*, 28<sup>e</sup> Année, Série 2 472: 245–247.
- Glazunova A.E. 1953. *Ammonites of the Aptian and Albian of Kopet-Dagh, Lesser and Great Balkan and Mangyshlak*. Gosgeolizdat, Moscow.
- Haeckel E. 1866. Allgemeine Entwicklungsgeschichte der Decabrachia (Cephalopoda, Coleoidea). *Palaeontographica, Abteilung A* 245: 63–81. <https://doi.org/10.1127/pala/245/1997/63>
- Hoffmann R., Howarth M.K., Fuchs D., Klug C. & Korn D. 2022. The higher taxonomic nomenclature of Devonian to Cretaceous ammonoids and Jurassic to Cretaceous ammonites including their authorship and publication. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 305 (2): 187–197. <https://doi.org/10.1127/njgpa/2022/1085>
- Kazansky P. 1914. *Description d'une Collection des Céphalopodes des Terrains Crétacés du Daghestan*. Tomsk.
- Kennedy W.J., Gale A., Bown P.R., Caron M., Davey R.J., Grocke D. & Wray D.S. 2000. Integrated stratigraphy across the Aptian-Albian boundary in the Marnes Bleues, at the Col de Pré-Guittard, Arnayon (Drôme), and at Tartonne (Alpes-de-Haute-Provence), France: a candidate Global Boundary Stratotype Section and Boundary Point for the base of the Albian Stage. *Cretaceous Research* 21: 591–720. <https://doi.org/10.1006/cres.2000.0223>

- Khalilov A.G. 1988. Nautiloids and ammonites. *In: Alizade A.A. (ed.) Cretaceous Fauna of Azerbaydzhan: 330–389.*
- Klein J. & Bogdanova T. 2013. Lower Cretaceous Ammonites VI. Douvilleiceratoidea & Deshayesitoidea. *Fossilium Catalogus I: Animalia - Pars 151.* Backhuys Publishers, Leiden.
- Klug C., Korn D., Landman N.H., Tanabe K., De Baets K. & Naglik C. 2015. Chapter 1 – Describing ammonoid conchs. *In: Klug C., Korn D., De Baets K., Kruta I. & Mapes R.H. (eds) Ammonoid Paleobiology: from Anatomy to Ecology. Topics in Geobiology 43: 3–24.*  
[https://doi.org/10.1007/978-94-017-9630-9\\_1](https://doi.org/10.1007/978-94-017-9630-9_1)
- Kvantaliani I.V. 1971. *The Aptian Ammonites of Abkhazia.* Georgian Polytechnical Institute, Tbilisi.
- Luber T.L., Bulot L.G., Redfern J., Frau C., Arantegui A. & Masrour M. 2017. A revised ammonoid biostratigraphy for the Aptian of NW Africa: Essaouira-Agadir Basin, Morocco. *Cretaceous Research 79: 12–34.* <https://doi.org/10.1016/j.cretres.2017.06.020>
- Luppov N.P. 1961. Ammonites from the Lower Cretaceous deposits of the southwest spurs of the Hissar range. *Trudy VNIGI, new series 46 (2): 175–218.*
- Luppov N.P. & Drushchits V.V. 1958. Mollusca-Cephalopoda 11. Ammonoidea (ceratites and ammonites) and Endocochlia. *In: Orlov Y.A. (ed.) Fundamentals of Paleontology, Vol. 6.* Gosudarstvennoe Nauchno-tekhnicheskoe Izdatel'stvo Literatury po Geologii i Okhrane Nedr, Moskva.
- Michelin H. 1834. Coquilles fossiles de Gérodot (Aube). *Magazine de Zoologie, Paris, n° 3, Classe V: pl. 35.* Available from <https://www.biodiversitylibrary.org/page/50547302> [accessed 28 Jul. 2023].
- Mikhailova I.A. 1957. On the systematic position of the families Parahoplitidae Spath and Deshayesitidae Stoyanow. *Vestnik Moskovskogo Universiteta, Biologiya 3: 173–182.*
- Mordvilko T.A. 1962. *Lower Cretaceous Deposits of the Southeast Northern Caucasus and Ciscaucasia), part 2.* Akademii Nauk SSSR, Moscow–Leningrad.
- Orbigny A.d'. 1841. *Paléontologie française. Tome premier. Terrains crétacés. Céphalopodes.* Librairie Victor Masson, Paris. <https://doi.org/10.5962/bhl.title.50510>
- Reboulet S., Ottilia S., Aguirre-Urreta B., Barragán R., Company M., Frau C., Kakabadze M.V., Klein J., Moreno-Bedmar J.A., Lukeneder A., Pictet A., Ploch I., Raisossadat S.N., Vašíček Z., Baraboshkin E.J. & Mitta, V. 2018. Report on the 6<sup>th</sup> International Meeting of the IUGS Lower Cretaceous Ammonite Working Group, the Kilian Group (Vienna, Austria, 20<sup>th</sup> August 2017). *Cretaceous Research 91: 100–110.* <https://doi.org/10.1016/j.cretres.2018.05.008>
- Roman F. 1938. *Les Ammonites jurassiques et crétacées. Essai de Genera.* Masson, Paris.
- Seunes J. 1887. Note sur quelques ammonites du Gault. *Bulletin de la Société géologique de France, troisième série 15 (7): 557–571.*
- Sharikadze M.Z. 2015. *Aptian Ammonites of the Caucasus.* Publishing house Universal, Tbilisi.
- Sharikadze M.Z., Kakabadze M.V. & Hoedemaeker P.J. 2004. Early Albian Douvilleiceratidae, Acanthohoplitidae and Parahoplitidae of Colombia. *Scripta Geologica 128: 313–514.*
- Sinzow I.T. 1908. Untersuchung einiger Ammonitiden aus dem Unteren Gault Mangyschlaks und des Kaukasus. *Zapiski Imperatorskogo S.-Peterburgskogo Mineralogicheskogo Obshchestva, series 2 45 (for 1907): 455–519.*
- Sinzow I.T. 1913. Beiträge zur Kenntnis der unteren Kreideablagerungen des Nord Kaukasus. *Travaux du Musée géologique Pierre le Grand près l'Académie Impériale des Sciences de St. Pétersbourg 7: 93–117.*

Stoyanow A. 1949. Lower Cretaceous stratigraphy in southeastern Arizona. *Memoir Geological Society of America* 38: 1–169. <https://doi.org/10.1130/MEM38-p1>

Stoyanow A. 1958. Suture of *Acanthohoplites aschiltaensis* (Anthula). *Geological Society of America Bulletin* 69 (5): 607–610. [https://doi.org/10.1130/0016-7606\(1958\)69\[607:SOAAA\]2.0.CO;2](https://doi.org/10.1130/0016-7606(1958)69[607:SOAAA]2.0.CO;2)

Szives O. 2008. Two new species of *Constrictoceras* nov. gen. (Ammonoidea) from the Early Cretaceous (Aptian) of Hungary. *Geobios* 41: 297–305. <https://doi.org/10.1016/j.geobios.2006.12.005>

Thomel G. 2015. *Atlas des Faunes d'Ammonites Pyriteuses de l'Étage Aptien des Alpes de Provence*. Unpublished online work. Available from <http://www.cephalopodes-cretaces.com/pages/ammonites/atlas-des-ammonites-de-l-aptien/> [accessed 26 Jul. 2023].

Tovbina S.Z. 1970. A new genus of the family Parahoplitidae. *Paleontological Journal* 3: 56–65.

Wright C.W., Callomon J.J. & Howarth M.K. 1996. *Cretaceous Ammonoidea. Treatise on Invertebrate Paleontology. Part L, Mollusca 4 Revised*. The Geological Society of America & The University of Kansas Boulder, Colorado & Lawrence.

*Manuscript received: 29 January 2023*

*Manuscript accepted: 15 March 2023*

*Published on: 16 August 2023*

*Topic editor: Marie-Béatrice Forel*

*Desk editor: Pepe Fernández*

Printed versions of all papers are also deposited in the libraries of the institutes that are members of the *EJT* consortium: Muséum national d'histoire naturelle, Paris, France; Meise Botanic Garden, Belgium; Royal Museum for Central Africa, Tervuren, Belgium; Royal Belgian Institute of Natural Sciences, Brussels, Belgium; Natural History Museum of Denmark, Copenhagen, Denmark; Naturalis Biodiversity Center, Leiden, the Netherlands; Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; Leibniz Institute for the Analysis of Biodiversity Change, Bonn – Hamburg, Germany; National Museum of the Czech Republic, Prague, Czech Republic.



## Appendix

Synonymy list of *Acanthohoplites aschiltaensis* (Anthula, 1900), including hypothesis on its morpho-dimensional dimorphism.

[?m]

- 1900 *Parahoplites aschiltaensis* Anthula, p. 117(63), pl. X(IX) figs 2a–b, (?) 3a–b.  
 1900 *Parahoplites abichi* Anthula, p. 118(64), pl. IX(VIII) fig. 2a–c.  
 non 1907 *Parahoplites* cfr. *aschiltaensis* Anthula – Burckhardt, p. 192, pl. XLII fig. 8 (= ?*Colombiceras* sp. indet.).  
 non 1907 *Parahoplites* sp. gr. *aschiltaensis* Anthula – Burckhardt, p. 192, pl. XLII figs 9–10, pl. XLIII figs 1, 3, 7 (= ?*Colombiceras* sp. indet.).  
 non 1908 *Acanthohoplites abichi* (Anthula) – Sinzow, p. 490, pl. VI figs 1–1a, 2–3 (= *Acanthohoplitidae* spp. indet.).  
 non 1908 *Acanthohoplites aschiltaensis* v. *aplanata* Sinzow, p. 481, pl. V figs 4–7 (= “*Hypacanthoplites*” *aplanatus*).  
 non 1913 *Acanthohoplites aschiltaensis* var. *aplanata* Sinzow – Sinzow, p. 111, pl. 6 fig. 4 (= *Egoianiceras* gr. *lautum laxa*).  
 1914 *Acanthohoplites aschiltaensis* (Anthula) – Kazansky, p. 67, pl. III fig. 47a–c.  
 1938 *Acanthohoplites aschiltaensis* (Anthula) – Rouchadze, p. 197, text-fig. 13a–b (= ?Anthula, 1900, pl. X(IX) fig. 3b).  
 1938 *Acanthohoplites aschiltaensis* (Anthula) – Roman, p. 348, pl. XXXIV figs 330–331 (= Anthula, 1900, pl. X(IX) figs 2a, 3a), text-figs 330–331 legend pl. XXXIV (= Anthula, 1900, pl. X(IX) fig. 3b).  
 1949 *Acanthohoplites aschiltaensis* (Anthula) – Luppov *et al.* in Luppov, p. 231, pl. LXVIII figs 3, 4a–b (= Anthula, 1900, pl. X(XI) figs 2a–b, 3a), text-fig. 59 (= Anthula, 1900, pl. X(IX) fig. 3b).  
 1952 *Acanthohoplites aschiltaensis* (Anthula) – Basse, p. 655, pl. XX fig. 2, 2a (= Anthula, 1900, pl. X(IX) fig. 2a–b).  
 non 1953 *Acanthohoplites aschiltaensis* (Anthula) – Glazunova, p. 42, pl. VIII figs 1a–b, 2, 3a–b, text-fig. 17 (= *Egoianiceras* ex. gr. *angulatum*).  
 non 1955 *Acanthohoplites abichi* (Anthula) – Eristavi, p. 100, pl. IV fig. 5 (= *Acanthohoplitidae* sp. indet.).  
 ? 1956 *Acanthohoplites aschiltaensis* (Anthula) – Drushchits, p. 108, text-figs 5a–r, 6, 7a–e.  
 ? 1957 *Acanthohoplites abichi* (Anthula) – Mikhailova, text-fig. 5a–r.  
 1957 *Acanthohoplites aschiltaensis* (Anthula) – Arkell *et al.*, p. L387, fig. 504: 4a–c (= Anthula, 1900, pl. X(IX) figs 3a–b, 4).  
 ? 1958 *Acanthohoplites abichi* (Anthula) – Mikhailova, p. 101, text-fig. 1a–3 (= specimen Mikhailova, 1957, text-fig. 5a–r).  
 non 1960 *Acanthohoplites aschiltaensis* (Anthula) – Kudryavtsev, p. 319, pl. VII figs 2a–b, 3a–b, text-fig. 108 (= *Acanthohoplites* ex gr. *bigoureti*).  
 non 1960 *Acanthohoplites abichi* (Anthula) – Kudryavtsev, p. 321, pl. VIII fig. 3a–b, text-fig. 110 (= ?*Acanthohoplites* sp. indet.).  
 non 1961 *Acanthohoplites abichi* (Anthula) – Eristavi, p. 58, pl. IV fig. 2 (= *Acanthohoplitidae* indet. juv.).  
 non 1963 *Acanthohoplites* aff. *aschiltaensis* (Anthula) – Cantú-Chapa, p. 46, pl. XVI(V) fig. 2d (= *Riedelites* ex gr. *alexandrinus*).  
 non 1963 *Acanthohoplites* aff. *abichi* (Anthula) – Cantú-Chapa, p. 47, pl. XVII(VII) fig. 4 (= ?*Constrictoceras* sp. indet.).  
 1965 *Acanthohoplites aschiltaensis* (Anthula) – Casey, text-fig. 151a–e (= Anthula, 1900, pl. XI(X) figs 2a–b, 3a–b, 4).  
 non 1965 *Acanthohoplites abichi* (Anthula) – Egoian, p. 130, pl. V fig. 4a–b (= “*Hypacanthoplites*” ex gr. *multispinatus*).

- non 1966 *Acanthopliotes aschiltaensis* (Anthula) – Filipescu & Grigorescu, p. 424(8), pl. II fig. 15 (= *Acanthohoplitidae* sp. indet.).
- non 1967 *Acanthohoplites abichi* (Anthula) – Dimitrova, p. 187, pl. LXXXIX fig. 6–6a (= *Egoianiceras* ex gr. *angulatum*).
- pars 1967 *Acanthohoplites aschiltaensis* (Anthula) – Dimitrova, p. 185, text-fig. 84 (= Anthula, 1900, pl. X(XI) fig. 3b), non pl. LXXXIX fig. 4 (= *Acanthohoplitidae* sp. indet.).
- non 1967 *Parahoplites melchioris* Anthula – Wachendorf *et al.*, p. 289, pl. 36 fig. 5 (= *Acanthohoplitidae* sp. indet.).
- non 1969 *Acanthohoplites abichi* (Anthula) – Egoian, p. 162, pl. XXIII fig. 31 (= Egoian, 1965, pl. V fig. 4a–b).
- ? 1970 *Protacanthopliotes abichi* (Anthula) – Tovbina, p. 59, text-figs 3a–д, 4a–3.
- ? 1970 *Acanthohoplites aschiltaensis* (Anthula) – Tovbina, text-figs 5a–3, 6a–л.
- non 1971 *Acanthohoplites aschiltaensis* (Anthula) – Kemper, pl. 25 fig. 4a–c (= *Acanthohoplites* sp. juv. indet.).
- non 1971 *Acanthohoplites abichi* (Anthula) – Kvantaliani, p. 47, pl. V fig. 2a–b, text-fig. 25a–д (= ?*Colombiceras bogdonovae*).
- pars 1971 *Acanthohoplites aschiltaensis* (Anthula) – Kvantaliani, p. 54, text-fig. 14 (= Anthula, 1900, pl. X(IX) fig. 2a–b), non pl. VII fig. 3a–b and pl. VIII fig. 1a–b, text-figs 29a–3, 30, 70 top (= “*Hypacanthopliotes*” *subangulatus*).
- non 1975 *Acanthohoplites aschiltaensis* (Anthula) – Förster, p. 203, pl. 9 fig. 3a–b, text-fig. 59 (= “*Hypacanthopliotes*” *malgachensis*).
- non 1977 *Acanthohoplites aschiltaensis* (Anthula) – Contreras y Montero, p. 15, pl. V figs 1–3, pl. VI fig. 4 (= *Riedelites* ex gr. *estersernae*).
- non 1981 *Acanthohoplites* ex gr. *aschiltaensis* (Anthula) – Drushchits *et al.*, p. 102, pl. 1 fig. 3 (= *Acanthohoplitidae* indet.).
- non 1982 *Acanthohoplites aschiltaensis* (Anthula) – Kemper, pl. 8.4-2 fig. 3a–c (= Kemper, 1971, pl. 25 fig. 4a–c).
- non 1982 *Acanthohoplites aschiltaensis* (Anthula) – Leshchukh, p. 127, pl. X figs 6–7 (= *Acanthohoplitidae* indet.).
- non 1982 *Protacanthopliotes abichi* (Anthula) – Tovbina, p. 64, pl. I fig. 3a–б, text-fig. 2 (= *Egoianiceras* ex gr. *angulatum*).
- non 1987 *Acanthohoplites* cf. *aschiltaensis* (Anthula) – Autran & Delanoy, p. 418, pl. I fig. 4 (= ?*Hypacanthopliotes* sp. indet.).
- non 1988 *Acanthohoplites abichi* (Anthula) – Khalilov, p. 352, pl. X fig. 4a–б (= *Chaschupseceras* ex gr. *causicum*).
- non 1990 *Acanthohoplites* cf. *aschiltaensis* (Anthula) – Ivanov & Stoykova, pl. I fig. 8 (= ?*Colombiceras* ex gr. *tobleri*).
- 1996 *Acanthohoplites aschiltaensis* (Anthula) – Wright *et al.*, p. 275 fig. 215: 2a–c (= Anthula, 1900, pl. X(IX) figs 3a–b, 4).
- non 1999 *Acanthohoplites aschiltaensis* (Anthula) – Szives, p. 405, pl. I fig. 6 (= *Nodosohoplites* ex gr. *subplanatus*).
- non 2001 *Acanthohoplites* cf. *aschiltaensis* (Anthula) – Avram *et al.*, pl. III fig. 16 (= *Acanthohoplitidae* spp.).
- non 2003 *Acanthohoplites aschiltaensis* (Anthula) – Méndez Franco, pl. 7 figs 7–10, 1111 (= ?*Penaceras* sp. indet.).
- non 2004 *Protacanthopliotes abichi* (Anthula) – Sharikadze *et al.*, p. 392, pl. 81 figs 1a–c, 2a–c (= ?*Constrictoceras* ex gr. *originalis*).
- non 2004 *Acanthohoplites* ex gr. *aschiltaensis* (Anthula) – Sharikadze *et al.*, p. 403, pl. 84 fig. 2a–c (= ?*Colombiceras* sp. indet.).

- non 2005 *Protacanthoplites abichi* (Anthula) – Sharikadze in Kotetishvili *et al.*, p. 395, pl. 102 fig. 4a–b (= ? *Acanthohoplites* ex gr. *bigoureti* juv.).
- non 2005 *Acanthohoplites aschiltaensis aschiltaensis* (Anthula) – Kvantaliani in Kotetishvili *et al.*, p. 399, pl. 103 fig. 4a–b (= *Acanthohoplitidae* sp. indet. close to “*Acanthohoplites*” *tsagarelii*).
- non 2005 *Acanthohoplites aschiltaensis* (Anthula) – Avila Licona, p. 38, pl. 2 fig. 5a–b (= ? *Penaceras* sp. indet.).
- non 2006 *Acanthohoplites aschiltaensis* (Anthula) – Raisossadat, p. 916 fig. 5d (= “*Hypacanthoplites*” *uhligi*).
- non 2007 *Acanthohoplites abichi* (Anthula) – Szives *et al.*, p. 69, pl. IX figs 2a–b, 3a–b, 6a–b, 8a–b, 15a–b, pl. X fig. 5a–b (= *Acanthohoplitidae* spp. indet.).
- non 2007 *Acanthohoplites aschiltaensis* (Anthula) – Szives *et al.*, p. 68, pl. IX figs 12a–b, 13a–b, 14a–b, (= Szives, 1999, pl. I fig. 6), 16a–b, 17a–b, 18a–b, 20a–b (= *Acanthohoplitidae* spp. indet.).
- 2012 *Acanthohoplites aschiltaensis* (Anthula) – Mikhailova & Bogdanova, text-fig. 1b–г (= Anthula, 1900, pl. X(IX) fig. 2a–b).
- 2015 *Acanthohoplites aschiltaensis* (Anthula) – Thomel, pl. 62 figs 8–10/37–39, 13–14, 15–18, 19–20/32–33, 21–24, 25–28, 29–31/34–36; pl. 64 figs 17–20, 25–28.
- 2015 *Hypacanthoplites malgachensis* (Breistroffer) – Thomel, pl. 64 figs 1–2/29–30.
- 2016 *Acanthohoplites aschiltaensis* (Anthula) – Bogdanova & Mikhailova, p. 855, pl. 14 figs 1a–c, 2a–c, 3a–b, pl. 15 figs 1a–b, 2a–b.
- ? 2017 *Protacanthoplites abichi* (Anthula) – Luber *et al.* fig. 9.17–20.
- non 2019 *Protacanthoplites abichi* (Anthula) – Lehmann *et al.*, p. 220 fig. 4e (= *Acanthohoplites* ex gr. *bigoureti*).
- 2020a *Acanthohoplites* cf. *aschiltaensis* (Anthula) – Frau fig. 4d–e; supplementary material, p. 3, fig. 1d–e [cum. syn.].

[?M]

- 1900 *Parahoplites aschiltaensis* Anthula, p. 117(63), pl. X(IX) fig. 4, pl. XI(X) fig. 1.
- pars 1908 *Acanthohoplites aschiltaensis* (Anthula) – Sinzow, p. 478, pl. V fig. 1, non pl. VI figs 19–21 (= *Hypacanthoplites propinquus*).
- 1908 *Acanthohoplites aschiltaensis* var. *rotundata* (Anthula) – Sinzow, p. 479, pl. V figs 2–3.
- non 1960 *Acanthohoplites aschiltaensis rotundata* (Anthula) – Kudryavtsev, p. 320, pl. IX fig. 1a–b (= *Acanthohoplites stephanoides*).
- non 1961 *Acanthoplites aschiltaensis* v. *rotunda* (Anthula) – Eristavi, p. 55, pl. II fig. 9 (= *Acanthohoplitidae* sp. indet.).
- non 1981 *Acanthohoplites aschiltaensis rotundatus* (Anthula) – Chiriac, p. 81, pl. 13 fig. 1a–b (= Ammonoidea indet.).
- non 1961 *Acanthoplites aschiltaensis* var. *subangulata* (Anthula) – Luppov, p. 280, pl. I fig. 2a–b, 3a–b (= *Acanthohoplites stephanoides*).
- non 1971 *Acanthohoplites aschiltaensis subangulata* (Anthula) – Kvantaliani, p. 54, pl. VIII fig. 2a–e, 3a–e (= *Acanthohoplites stephanoides*).
- non 1988 *Acanthohoplites aschiltaensis subangulata* (Anthula) – Khalilov, p. 353, pl. XI fig. 4 (= *Acanthohoplitidae* sp. indet.).
- ? 2017 *Acanthohoplites aschiltaensis* (Anthula) – Luber *et al.*, fig. 11.1–2.

### Supporting references

- Anthula D.J. 1900. Über die Kreidefossilien des Kaukasus mit einem allgemeinen Überblick über die Entwicklung der Sedimentärbildungen des Kaukasus. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients* 12 (for 1899): 55–160 (1–106).
- Arkell W.J. with contributions by Wright C.W. & Osborne White H.J. 1947. *The Geology of the Country around Weymouth, Swanage, Corfe & Lulworth*. Memoirs of the Geological Survey of Great Britain, England and Wales.
- Autran G. & Delanoy G. 1987. Mise en évidence d'un niveau à ammonites aptiennes dans la Basse Vallée du Var (Alpes-Maritimes, France) conséquences paléogéographiques. *Géobios* 20 (3): 415–422. [https://doi.org/10.1016/S0016-6995\(87\)80051-7](https://doi.org/10.1016/S0016-6995(87)80051-7)
- Avila Licona J.A. 2005. *Análisis bioestratigráfico basado en fauna de ammonites del Aptiano (Cretácico Inferior) del área del Cañón de la Boca, Nuevo León*. Bachelor Thesis, Universidad Nacional Autónoma de México, Facultad de Ciencias, México D.F.
- Avram E., Bordea S., Cociuba I., Huza R. & Preda I. 2001. Ammonite assemblages of the Ecleja Formation (Northern Apuseni Mts., Romania). *Romanian Journal of Stratigraphy* 79: 13–20.
- Basse E. 1952. Ammonoidea. In: Piveteau J. (ed.) *Traité de Paléontologie vol. 2*. Masson, Paris.
- Bogdanova T.N. & Mikhailova I.A. 2016. Middle Aptian biostratigraphy and ammonoids of the Northern Caucasus and Transcaspi. *Paleontological Journal* 50 (8): 725–933. <https://doi.org/10.1134/S0031030115100019>
- Burckhardt C. 1907. La faune jurassique de Mazapil avec un appendice sur les fossiles du crétacique inférieur. *Instituto Geológico de México Boletín* 23 (for 1906): 1–216. <https://doi.org/10.5962/bhl.title.40977>
- Cantú-Chapa A. 1963. Étude biostratigraphique des ammonites du centre et de l'est du Mexique (Jurassique supérieur et Crétacé). *Mémoires de la Société géologique de France, série 5* 99: 1–103.
- Casey R. 1965. A monograph of the Ammonoidea of the Lower Greensand 6. *Palaeontographical Society* 118 (for 1964): 399–546. <https://doi.org/10.1080/25761900.2022.12131694>
- Chiriac M. 1981. *Amoniti Cretacici din Dobrogea de Sud, Studiu biostratigrafic*. Editura Academiei Republicii Socialiste Romania, Bucuresti.
- Contreras y Montero B. 1977. Bioestratigrafía de las formaciones Taraises y la Peña (Cretácico inferior), de la Goleta, Coahuila y Minillas, Nuevo León. *Revista del Instituto Mexicano del petróleo* 9 (1): 8–29.
- Dimitrova N. 1967. *Fossils of Bulgaria. IV. Lower Cretaceous-Cephalopoda (Nautiloidea & Ammonoidea)*. Bulgarian Academy of Sciences, Sofia.
- Drushchits V.V. 1956. On systematics of the family Parahoplitidae. *Scientific reports of the Moscow State University, Geology* 176: 105–113.
- Drushchits V.V., Mikhailova I.A. & Nerodenko V.M. 1981. Zonal division of the Apt sediments of southwest Crimea. *Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody Otdel Biologicheskii* 56 (1): 95–103.
- Egoian V.L. 1965. Some ammonites from the Clansayan of the Western Caucasus. *Trudy Krasnodarskogo Filiala Vsesojuznogo Neftegazovogo. NauchnoIssledovatel'skogo Instituta* 16: 112–160.
- Egoian V.L. 1969. Ammonites from the Clansayan of the Western Caucasus. *Trudy Krasnodarskogo Filiala Vsesojuznogo Neftegazovogo. NauchnoIssledovatel'skogo Instituta* 19: 126–317.

- Eristavi M.C. 1955. *Lower Cretaceous Fauna of Georgia*. Akademiia nauk Gruzinskoi SSR, Monograph 6, Gruzinskoi.
- Eristavi M.C. 1961. Aptian and Albian ammonites of the north Caucasus. *Trudy Geologicheskogo Instituta Akademia Nauk Gruzinskoi SSR* 12 (17): 41–77.
- Filipescu M. & Grigorescu D. 1966. Contribuții la Cunoașterea faunei cretacice din flisul carpaților orientali. *Studii și cercetări de geologie, geofizică, geografie. Seria Geologie* 11 (2): 417–432.
- Förster R. 1975. Die geologische Entwicklung von Sud-Mozambique seit der Unterkreide und die Ammoniten-Fauna von Unterkreide und Cenoman. *Geologisches Jahrbuch B* 12: 1–324.
- Frau C. 2020a. New insight on the age and significance of the Aparein black shales in the Basque-Cantabrian Basin, northern Spain. *Newsletters on Stratigraphy* 54 (1): 1–16.  
<https://doi.org/10.1127/nos/2020/0583>
- Glazunova A.E. 1953. *Ammonites of the Aptian and Albian of Kopet-Dagh, Lesser and Great Balkan and Mangyshlak*. Gosgeolizdat, Moscow.
- Ivanov M. & Stoykova K. 1990. Aptian and Albian stratigraphy of the Ruse in the central part of the Moessian Platform. *Geologica Balcanica* 20 (5): 45–71.
- Kazansky P. 1914. *Description d'une collection des Céphalopodes des Terrains Crétacés du Daghestan*. Tomsk.
- Kemper E. 1971. Zur Gliederung und Abgrenzung des norddeutschen Aptium mit Ammoniten. *Geologisches Jahrbuch* 89: 359–390.
- Kemper E. 1982. Die Ammoniten des späten Apt und frühen Alb Nordwestdeutschlands. *Geologisches Jahrbuch* 65: 553–577.
- Khalilov A.G. 1988. Nautiloids and ammonites. In: Alizade A.A. (ed.) *Cretaceous fFauna of Azerbaydzhan*: 330–389.
- Kotetishvili E.V., Kvantaliani I.V., Kakabadze M.V. & Tsirekidze L.R. 2005. *Atlas of Early Cretaceous Fauna of Georgia*.
- Kudriavtsev M.P. 1960. Ammonites. In: Drushchits V.V. & Kudriavtsev M.P. (eds) *Atlas of the Lower Cretaceous Faunas of the Northern Caucasus and the Crimea*. Vsesoyuznyi Nauchno-Issiedovatel'skii Institut Prirodnykh Gazov, Moskva.
- Kvantaliani I.V. 1971. *The Aptian Ammonites of Abkhazia*. Georgian Polytechnical Institute, Tbilisi.
- Lehmann J., Mosavinia A. & Wilmsen M. 2019. Parahopliteid ammonites and narrowing down the Aptian/Albian boundary interval in northern Iran. *Cretaceous Research* 94: 207–228.  
<https://doi.org/10.1016/j.cretres.2018.10.004>
- Leshchukh R.J. 1982. *Lower Cretaceous Ammonites of the Ukrainian Carpathians*. Naukova Dumka, Kiev.
- Luber T.L., Bulot L.G., Redfern J., Frau C., Arantegui A. & Masrour M. 2017. A revised ammonoid biostratigraphy for the Aptian of NW Africa: Essaouira-Agadir Basin, Morocco. *Cretaceous Research* 79: 12–34. <https://doi.org/10.1016/j.cretres.2017.06.020>.
- Luppov N.P. 1961. Ammonites from the Lower Cretaceous deposits of the southwest spurs of the Hissar range. *Trudy VNIGI, new series* 46 (2): 175–218.
- Luppov N.P., Bodylevsky V.I. & Glazunova A.E. 1949. Class Cephalopoda. In: Luppov N.P. (ed.) *Atlas of Index Forms of the Fossil Faunas of the USSR vol. 10*. Gostgeolizdat, Moskva & Leningrad.

- Méndez Franco A.L. 2003. *Bioestratigrafía de Ammonites y Variaciones de Litofacias en una Secuencia estratigráfica del Barremiano-Aptiano (Cretácico Inferior) del Área del Cañón de La Huasteca, Estado de Nuevo León*. Bachelor Thesis, Universidad Nacional Autónoma de México, Facultad de Ciencias, México D.F.
- Mikhailova I.A. 1957. On the systematic position of the families Parahoplitidae Spath and Deshayesitidae Stoyanow. *Vestnik Moskovskogo Universiteta, Biologiya* 3: 173–182.
- Mikhailova I.A. 1958. Some data on the genus *Acanthohoplites* Sinzow and *Hypacanthoplites* Spath. *Vestnik Moskovskogo Universiteta, Biologiya* 1: 101–108.
- Mikhailova I.A. & Bogdanova T.N. 2012. Genus *Parahoplites* Anthula, 1899: composition, evolution, and distribution. In: Leonova T.B., Barskov, I.S. & Mitta V.V. (eds) *Contributions to Current Cephalopod Research: Morphology, Systematics, Evolution, Ecology and Biostratigraphy*. Proceedings of Conference (Moscow, 9–11 April, 2012). Russian Academy of Sciences, Borissiak Paleontological Institute, Moscow.
- Raisossadat S.N. 2006. The ammonite family Parahoplitidae in the Sanganeh Formation of the Kopet Dag Basin, north-eastern Iran. *Cretaceous Research* 27 : 907–922.  
<https://doi.org/10.1016/j.cretres.2006.04.003>
- Roman F. 1938. *Les Ammonites jurassiques et crétacées. Essai de genera*. Masson, Paris.
- Rouchadze I. 1938. Les ammonites Aptiennes du Caucase du Nord. *Bulletin de l'Institut géologique de Géorgie* 4 (2): 115–174 (191–209).
- Sharikadze M.Z., Kakabadze M.V. & Hoedemaeker P.J. 2004. Early Albian Douvilleiceratidae, Acanthohoplitidae and Parahoplitidae of Colombia. *Scripta Geologica* 128: 313–514.
- Sinzow I.T. 1908. Untersuchung einiger Ammonitiden aus dem Unteren Gault Mangyschlaks und des Kaukasus. *Zapiski Imperatorskogo St.-Peterburgskogo Mineralogicheskogo Obshchestva, series 2* 45 (for 1907): 455–519.
- Sinzow I.T. 1913. Beiträge zur Kenntnis der unteren Kreideablagerungen des Nord Kaukasus. *Travaux du Musée géologique Pierre le Grand près l'Académie Impériale des Sciences de St. Pétersbourg* 7: 93–117.
- Szives O. 1999. Ammonite biostratigraphy of the Tata Limestone Formation (Aptian–Lower Albian), Hungary. *Acta Geologica Hungarica* 42 (4): 401–411.
- Szives O., Csontos L., Bujtor L. & Fözy I. 2007. Aptian-Campanian ammonites of Hungary. *Geologica Hungarica, Series Palaeontologica* 57: 1–187.
- Thomel G. 2015. *Atlas des Faunes d'Ammonites pyriteuses de l'Étage Aptien des Alpes de Provence*. Unpublished online work. Available from <http://www.cephalopodes-cretaces.com/pages/ammonites/atlas-des-ammonites-de-l-aptien/> [accessed 25 Jul. 2023].
- Tovbina S.Z. 1970. A new genus of the family Parahoplitidae. *Paleontological Journal* 3: 56–65.
- Tovbina S.Z. 1982. New representatives of the family Parahoplitidae of the Turkmenia. *Annual of the All-Union Paleontological Society* 25: 60–79.
- Wachendorf H., Bettenstaedt F. & Ernst G. 1967. Zur Unterkreide Stratigraphie von Süd-Mozambique. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 129 (3): 272–303.
- Wright C.W., Callomon J.J. & Howarth M.K. 1996. *Cretaceous Ammonoidea. Treatise on Invertebrate Paleontology. Part L, Mollusca 4 Revised*. The Geological Society of America & The University of Kansas Boulder, Colorado & Lawrence, Kansas.