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

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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, Ammonoida, Aptian, Dagestan, taxonomy.

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Introduction

This paper continues the taxonomic revision of the most iconic taxa of the family Acanthohoplitidae Stoyanow, 1949 (Cephalopoda, Ammonoida) 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 *Gargasiceras 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).

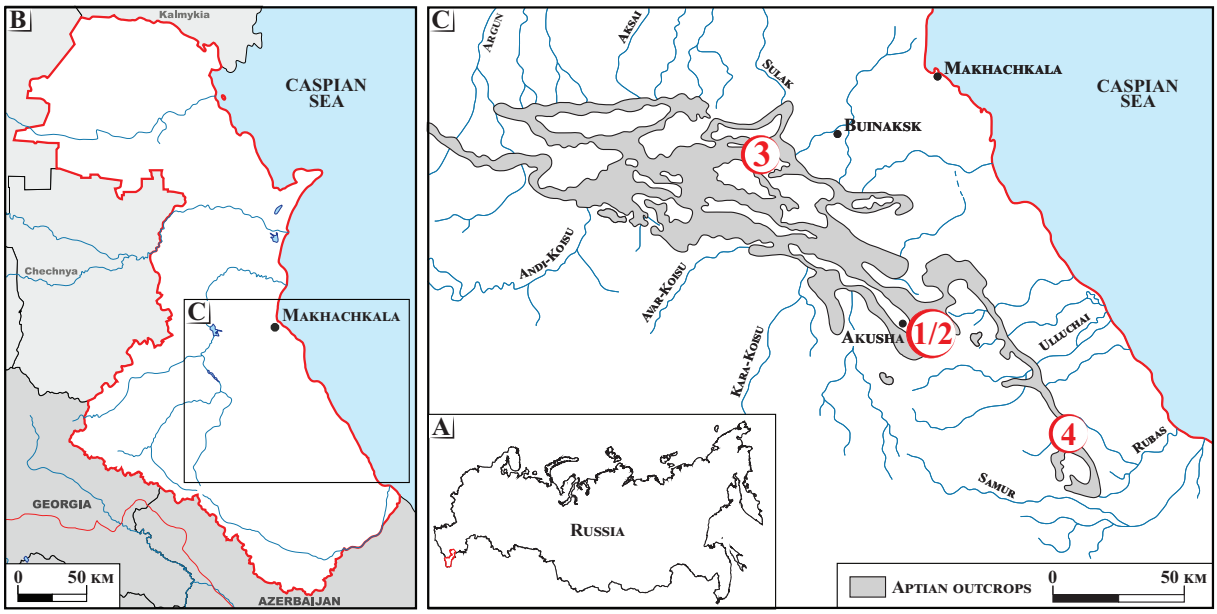

Fig. 1. A–B. Locality map of Dagestan, Russia. **C**. The main localities cited in the text located southwest of the Makhachkala town (after Bogdanova & Mikhailova 2016).

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 ~ 0.41), weakly depressed (Ww/Wh ~ 1.08), very evolute (U/Wh ~ 1.18) subophiocone coiling (U/D ~ 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 crassicostatum* 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.

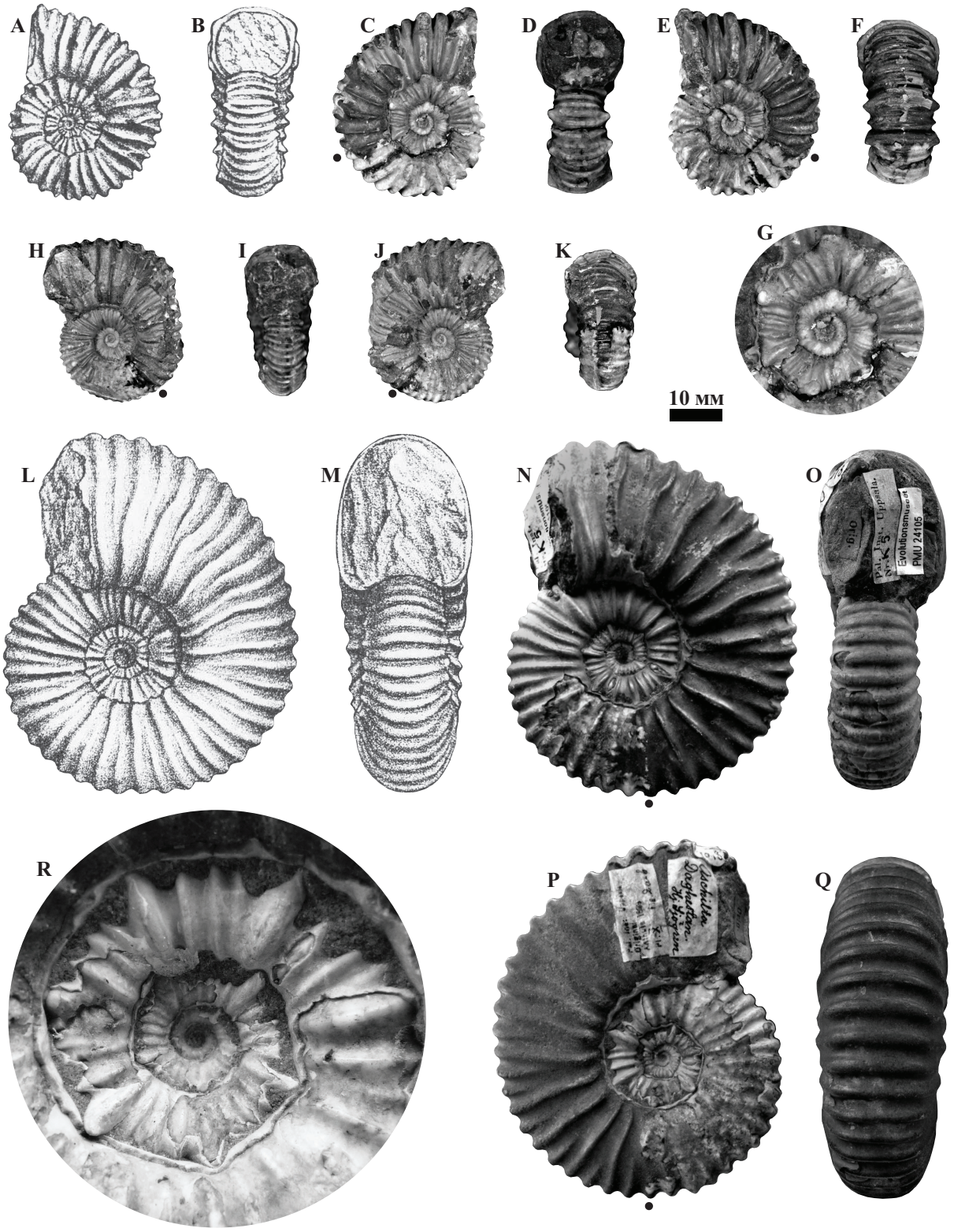

Fig. 2. A–K. *Parahoplites abichi* Anthula, 1900. **A**–**B**. Reproduction of the original hand-drawing. **C**–**G**. Lectotype (IPUW 1900-3a). **G**. Focus on its inner whorls. **H**–**K**. Syntype (IPUW 1900-3b), which is here excluded from the species. – **L–R**. *Parahoplites aschiltaensis* Anthula, 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 ~ 0.39), weakly depressed (Ww/Wh ~ 1.02), very evolute (U/Wh ~ 0,91) subvirgacone coiling (U/D ~ 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 ~ 0.35), weakly compressed (Ww/Wh ~ 0.82), subevolute (U/Wh ~ 0.76) and subvirgacone coiling (U/D ~ 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 ~ 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).

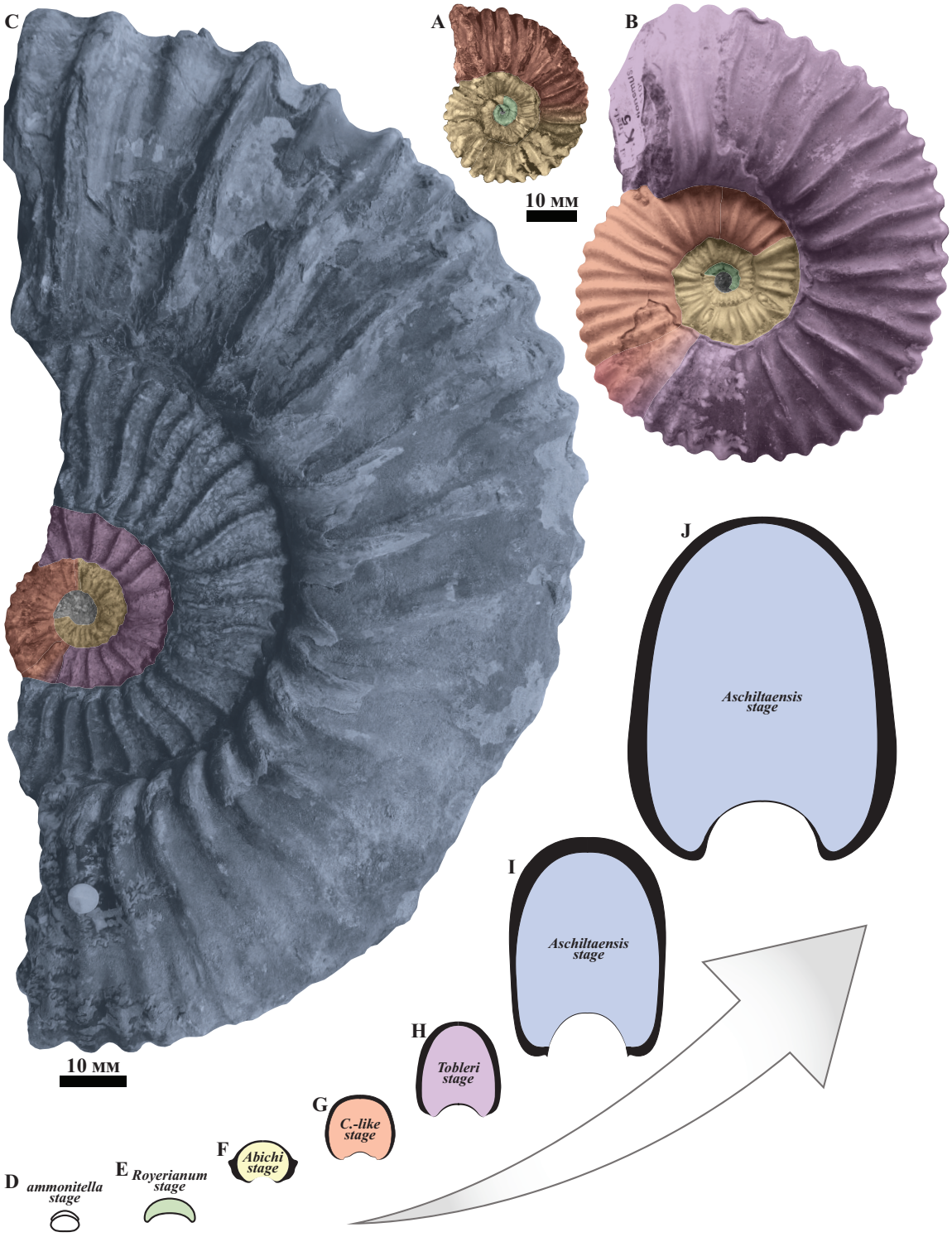

Fig. 3. Illustration of the ontogenetic stages observed after the ammonitella (not seen), including Royerianum (green), Abichi (yellow), Crassicostatum-like (orange), Tobleri (violet), and Aschiltaensis (blue). **A**. *Protacanthoplites abichi* (Anthula, 1900), lectotype (IPUW 1900-3a). **B**. *Acanthohoplites 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 ~ 0.39) with extremely discoidal (Ww/D ~ 0.25), very evolute (U/Wh ~ 1.19) and weakly compressed coiling (Ww/Wh ~ 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 ~ 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 ~ 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.

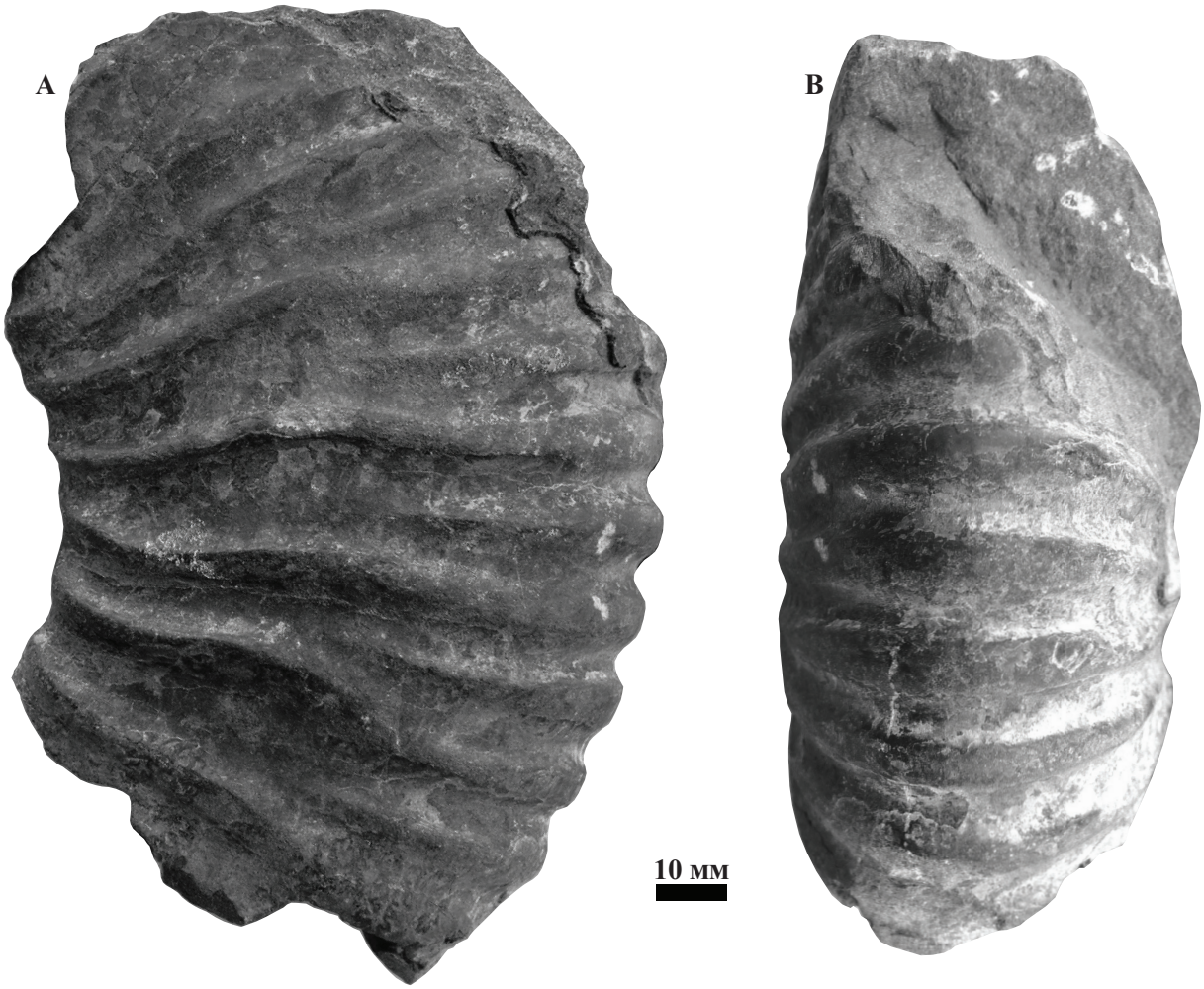

Fig. 4. *Acanthohoplites aschiltaensis* (Anthula, 1900), paralectotype (PMU.24106). Scale bar = 10 mm.

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 ~ 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 ~ 0.33) and weakly compressed (Ww/Wh ~ 0.94) coiling, while the umbilicus is more open (U/Wh ~ 1.19). Specimen PMU.24108 further displays a lower number of ventral ribs (estimated at ~ 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 ~ 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 *Cheloniceras* 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 '*Acanthoplites aschiltaensis*–*Acanthoplites 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.

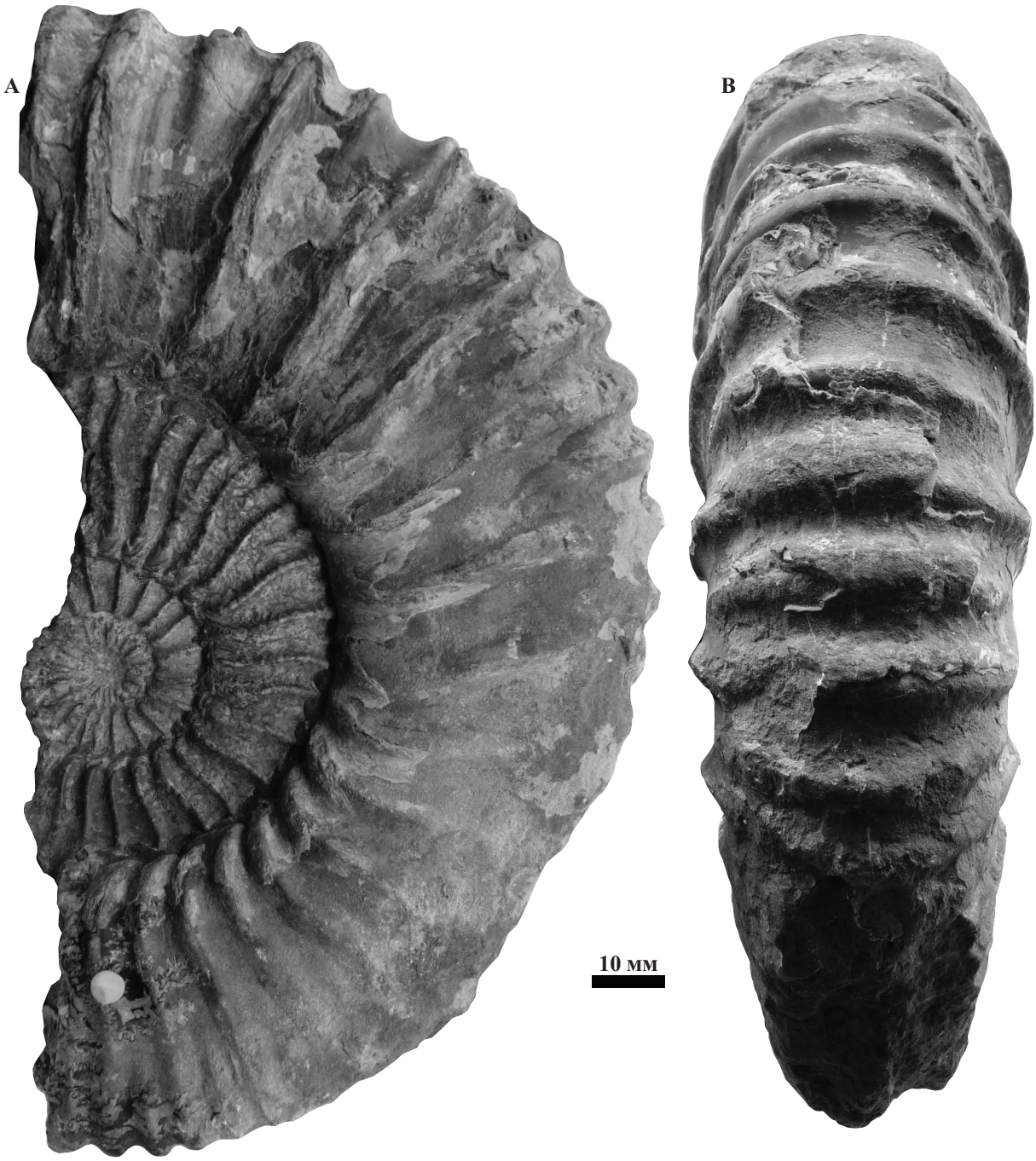

Fig. 5. *Acanthohoplites aschiltaensis* (Anthula, 1900), paralectotype (PMU.24107). Scale bar = 10 mm.

Subspecies of *Acanthohoplites aschiltaensis*

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

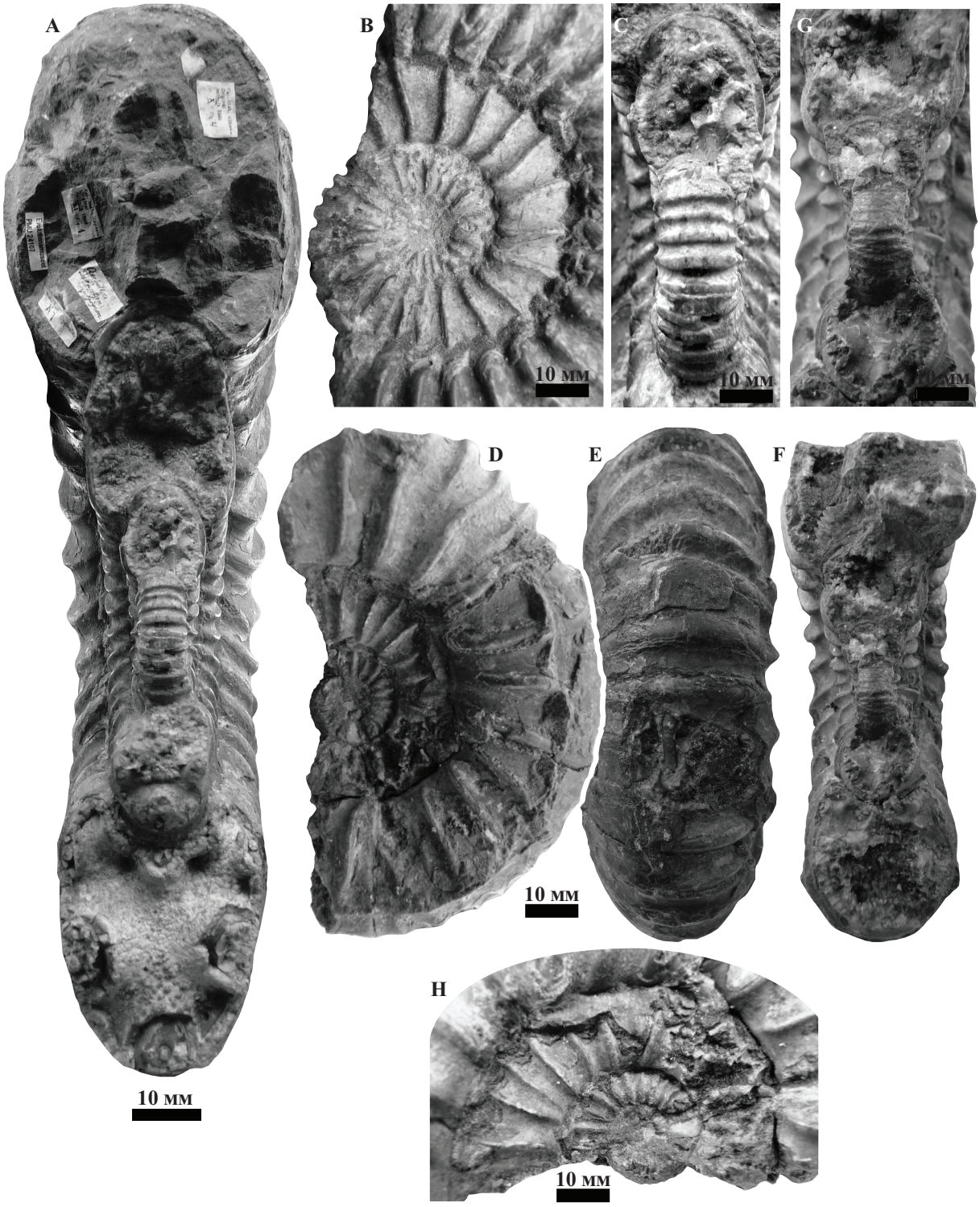

Fig. 6. *Acanthohoplites aschiltaensis* (Anthula, 1900). **A–C**. Paralectotype (PMU.24107). **D–H**. Paralectotype (PMU.24108). Scale bars = 10 mm.

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

The subspecies is based on a single, incomplete, moderate-sized phragmocone of an acanthohoplitid 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 ~ 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 acanthohoplitids 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–в), 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, acanthohoplitids from the southwest termination of the Gissar Range, Uzbekistan (Luppov 1961: pl. I figs 2a–в, 3a–в). 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 '*Acanthoplites aschiltaensis–Acanthoplites 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.

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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 *Acanthoplites aschiltaensis* v. *aplanata* Sinzow, p. 481, pl. V figs 4–7 (= "*Hypacanthoplites*" *aplanatus*).
non 1913 *Acanthoplites 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 *Acanthoplites 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 *Acanthoplites abichi* (Anthula) – Eristavi, p. 100, pl. IV fig. 5 (= Acanthohoplitidae sp. indet.).
? 1956 *Acanthoplites aschiltaensis* (Anthula) – Drushchits, p. 108, text-figs 5а–г, 6, 7а–е.
? 1957 *Acanthoplites abichi* (Anthula) – Mikhailova, text-fig. 5а–г.
1957 *Acanthoplites 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. 1а–з (= specimen Mikhailova, 1957, text-fig. 5а–г).
non 1960 *Acanthohoplites aschiltaensis* (Anthula) – Kudryavtsev, p. 319, pl. VII figs 2а–в, 3а–в, text-fig. 108 (= *Acanthohoplites* ex gr. *bigoureti*).
non 1960 *Acanthohoplites abichi* (Anthula) – Kudryavtsev, p. 321, pl. VIII fig. 3а–б, text-fig. 110 (= ?*Acanthohoplites* sp. indet.).
non 1961 *Acanthoplites 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. 4а–в (= *"Hypacanthoplites*" ex gr. *multispinatus*).

non 1966 *Acanthoplites 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. 4а–в).
? 1970 *Protacanthoplites abichi* (Anthula) – Tovbina, p. 59, text-figs 3а–д, 4а–з.
? 1970 *Acanthohoplites aschiltaensis* (Anthula) – Tovbina, text-figs 5а–з, 6а–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. 2а–в, text-fig. 25а–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. 3а–в and pl. VIII fig. la–в, text-figs 29а–з, 30, 70 top (= "*Hypacanthoplites*" *subangulatus*).
non 1975 *Acanthohoplites aschiltaensis* (Anthula) – Förster, p. 203, pl. 9 fig. 3a–b, text-fig. 59 (= ''*Hypacanthoplites*'' *malgachensis*).
non 1977 *Acanthohoplites aschiltaensis* (Anthula) – Contreras y Montero, p. 15, pl. V figs 1–3, pl. VI fig. 4 (= *Riedelites* ex gr. *esthersernae*).
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, 197l, pl. 25 fig. 4a–c).
non 1982 *Acanthohoplites aschiltaensis* (Anthula) – Leshchukh, p. 127, pl. X figs 6–7 (= Acanthohoplitidae indet.).
non 1982 *Protacanthoplites abichi* (Anthula) – Tovbina, p. 64, pl. I fig. 3а–б, text-fig. 2 (= *Egoianiceras* ex gr. *angulatum*).
non 1987 *Acanthohoplites* cf. *aschiltaensis* (Anthula) – Autran & Delanoy, p. 418, pl. I fig. 4 (=?*Hypacanthoplites* sp. indet.).
non 1988 *Acanthohoplites abichi* (Anthula) – Khalilov, p. 352, pl. X fig. 4а–б (= *Chaschupseceras* ex gr. *caucasicum*).
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 *Protacanthoplites 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–в (= ? *Acanthohoplites* ex gr. *bigoureti* juv.).
non 2005 *Acanthohoplites aschiltaensis aschiltaensis* (Anthula) – Kvantaliani *in* Kotetishvili *et al*., p. 399, pl. 103 fig. 4a–в (= 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. 1в–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 figs1a–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. la–в (= *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-в, 3a-в (= *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.).
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