Proceedings of the Geologists' Association xxx (2019) xxx–xxx

Contents lists available at ScienceDirect

Proceedings of the Geologists' Association

journal homepage: www.elsevier.com/locate/pgeola

Revision of the Early Cretaceous genus *Paraspiticeras* Kilian, 1910 (Ancyloceratoidea, Ammonoidea)

Evgeny Yu. Baraboshkin*, Irina A. Mikhailova

M.V. Lomonosov Moscow State University, Vorobjovy Gory, Moscow 119234, Russian Federation

ARTICLE INFO

Article history:
Received 10 January 2019
Received in revised form 8 May 2019
Accepted 13 June 2019
Available online xxx

Keywords:
Heteromorph ammonoid
Paraspiticeras
Early Cretaceous
Biostratigraphy
Crimea
Phylogeny

ABSTRACT

A study of heteromorph ammonoids from the Hauterivian – Barremian succession of the south-western Crimea, has prompted revision the genus *Paraspiticeras* Kilian. The results suggest that *Paraspiticeras* was probably descended from the early Hauterivian heteromorph *Crioceratites* by recoiling of the spiral. Its taxonomic position as representative of Subfamily Paraspiticeratinae Vermeulen, 2009 of Family Emericiceratidae Vermeulen, 2004 of Superfamily Ancyloceratoidea Gill, 1871 seems to be reasonable. The genus can be split into 3 subgenera: *P.* (*Paraspiticeras*) s.s., *P.* (*Blascoceras*) and *Paraspiticeras* (*Lepinayceras*). The absence of the descendants of *Paraspiticeras* in the late Barremian makes impossible to consider it as the direct ancestor of the Aptian Douvilleiceratoidea.

1. Introduction

Representatives of the heteromorph genus *Paraspiticeras* Kilian attract the interest of ammonoid specialists, since they are considered as a possible ancestor of the Douvilleiceratoidea, one of the important Aptian-Albian ammonoid Superfamilies (Mikhailova and Baraboshkin, 2009). In most of the known localities *Paraspiticeras* are rare, and the genus itself is traditionally considered as Barremian (Wright et al., 1996). *Paraspiticeras* were collected from the condensed section of "cephalopod limestones" in South-Western Crimea (Fig. 1). Most of these ammonoids come from the Hauterivian part of the section (Baraboshkin, 1997). This pushed us to revise *Paraspiticeras*, the preliminary data of which were published in Baraboshkin and Mikhailova (2009).

2. Material and methods

There are 23 specimens of *Paraspiticeras* in the collection, now housed in Earth Science Museum of the Moscow State University, which were studied by standard methods. The suture line was drawn with the binocular microscope MBS-1 with a drawing adaptor.

3. Geological setting

Paraspiticeras were collected in two localities in the watershed of the Kacha and Bodrak rivers in the South-Western Crimea: on the southern slope of the Belaya Mountain, near Verkhorechie Village and in the valley in the base of the southern slope of the Selbukhra Mountain, near Nauchnyi Village (Fig. 1). The locality of Belaya Mountain (Fig. 2) is better exposed and was described by Baraboshkin (1997). The "cephalopod limestone" represents the following succession (after Baraboshkin, 1997, with changes) (Fig. 1).

Member VI has a thickness of 1.7 m and represents rhythmically-bedded, bioturbated grey-green muddy sandstone-siltstone to silty mudstones (0.05-0.23 m thick) with carbonaceous debris, limonite gravel and small phosphatic pebbles, in alternation with brownish Fe-oolitic sandy wackestones to carbonate sandstones (0.05-0.25 m). Remains of *Hibolites* sp., *Crioceratites duvali* Lev., *C.* aff. *duvali*,*Crioceratites* cf. *tenuicostatus* Thom. and *C.* sp. were reported from this interval by (Baraboshkin, 1997). This member was referred to the Crioceratites duvali Zone of basal upper Hauterivian.

Member VII has a total thickness of 1.8–2 m. It comprises 3 parts. The lower part of brownish Fe-oolitic sandy bioclastic wackestones (0.4 m) contains glauconite, small phosphorite- and limonite-replaced fossil remains, carbonaceous debris and large number of ammonoids, nautiloids, bivalves, forams, brachiopods, echinoids, crinoids, etc. A number of highly-condensed ammonoid zones were recognised in this limestone (Baraboshkin, 1997). The

* Corresponding author.
E-mail address: EJBaraboshkin@mail.ru (E. Yu. Baraboshkin).

https://doi.org/10.1016/j.pgeola.2019.06.006
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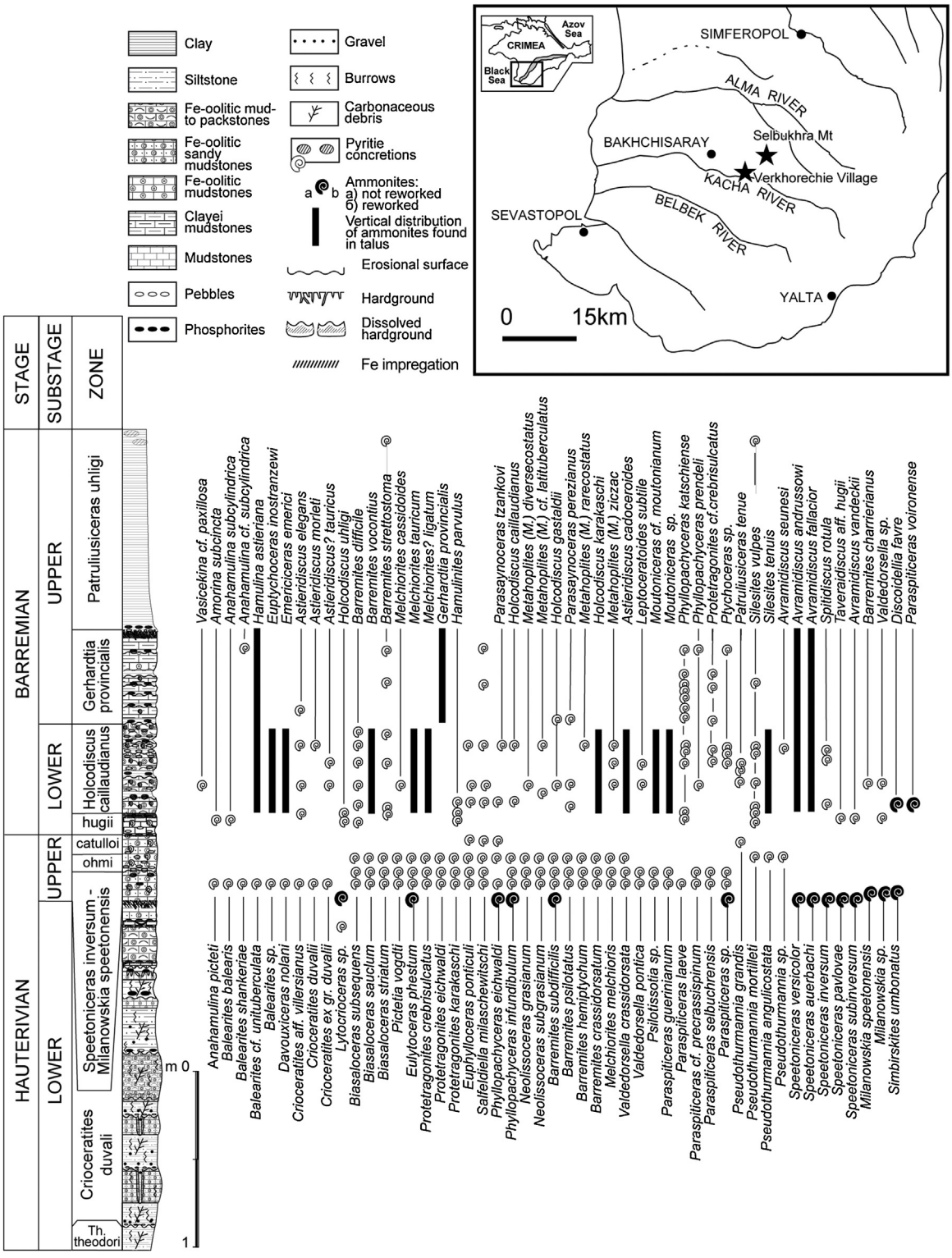

Fig. 1. Locality map, lithology, stratigraphy and ammonoid distribution (after Baraboshkin, 1997 with changes) in Verkhorechie Village section, south slope of Belaya Mt.

presence of *Speetoniceras inversum, Milanowskia speetonensis,* and *Craspedodiscus discofalcatus* Boreal Zones was distinguished by the finds of reworked index species and other ammonoids in the lower 0.2 m of the limestone. The limestone above that level (0.2 m) contains *Pseudothurmannia picteti* Sark., *"P." ohmi* (Winkler), *P. mortilleti* (Pict.), *P. angulicostata* (dOrb.), *"P." catulloi* (Parona), and others of "Pseudothurmannia ohmi" Zone. The zone could be subdivided into ohmi and catulloi Subzones. A pink-brownish wackestone (0.05-0.1 m) of lower Barremian Taveraidiscus hugii Zone is in the top of the lower part.

The middle part of reddish sandy bioclastic nodular wackestones (0.5-0.55 m) contains rare quartz, glauconite and limonite grains and again a large number of ammonoids, nautiloids, brachiopods, forams and other fossils. The interval is characterised by the presence of zonal index *Holcodiscus caillaudianus* (D'Orb.). Rare reworked *Nicklesia pulchella* (D'Orb.) were found at the base.

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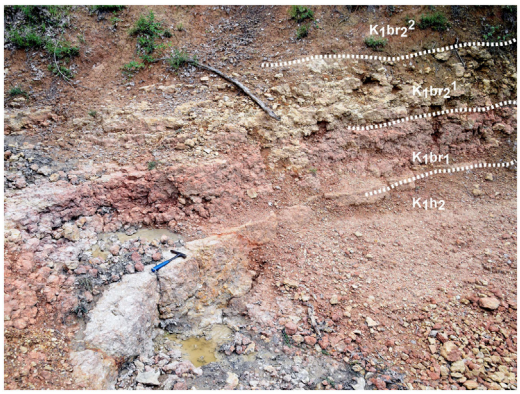

Fig. 2. Verkhorechie Village section, south slope of Belaya Mt., Mountain Crimea.

The upper part of grey to pale bioclastic wackestones (0.5-0.55 m) contains rare silt-size quartz grains and numerous fossils, mainly forams, ammonoids, brachiopods and crinoids. Rare *Gerhardtia provincialis* (D'Orb.), the upper Barremian Zonal index ammonoids, were found in this interval.

Most of *Paraspiticeras* were collected in the upper Hauterivian brownish limestones of member VII and the only sample of *Paraspiticeras* (*B.*) *voironense* (Pictet et De Loriol) comes from the lower Barremian reddish limestones.

4. Systematic palaeontology

Ammonoids examined in this study are stored at the Earth Science Museum of the Moscow State University (ESM MSU), Moscow, Russian Federation, collection No.101.

For the size parameters of ammonite shells, the following abbreviations are used: D – shell diameter, H – whorl height, U – umbilicus diameter and W – whorl width. Ratio of the whorl height to whorl width (H/W) is indicated.

Class Cephalopoda Zittel, 1884
Order Ammonoidea Zittel, 1884
Suborder Ancyloceratina Wiedmann, 1966
Superfamily Ancyloceratoidea Gill, 1871
Family Emericiceratidae Vermeulen, 2004
Subfamily Paraspiticeratinae Vermeulen, 2009
Genus *Paraspiticeras* Kilian, 1910

Aspidoceras: Uhlig, 1883, p. 237; Haug, 1889, p. 205; Sarasin and Schöndelmayer, 1901, p. 62.

Paraspiticeras: Kilian, 1910, p. 7; Spath, 1921, p. 316; Roman, 1938, p. 397; Wright, 1957, p. 383; Wiedmann, 1966, S. 26; Dimitrova, 1967, p. 168; Wright et al., 1996, p. 266; Aguirre-Urreta and Rawson, 1993, p. 56; Vermeulen, 2004, p. 79, Vermeulen, 2006, p. 149; Baraboshkin and Mikhailova, 2009, p. 38.

Type species: *Aspidoceras percevali* Uhlig (1883, p. 238, pl. XXVI, Fig. 2a, 2b), by subsequent designation of Spath (1921, p. 316).

Diagnosis: Initial whorl open, then evolute, with round or depressed rapidly enlarging whorls; ribs strong, rounded, simple or bifurcated, sometimes looped, crossing venter with slight forward bend; one to two more or less prominent lateral tubercles and (in some forms) umbilical tubercles on inner whorls; ribs and tubercles tending to weaken or disappear on outer whorls. Suture quadrilobate throughout (changed after Wright et al., 1996, p. 267).

Discussion: Kilian (1910, p. 7) originally included 3 Barremian species in *Paraspiticeras*: *P. percevali* (Uhlig), *P. pachycyclum* (Uhlig) and *P. guerinianum* (D'Orbigny). Later, Kilian (1913, p. 255) added *P. voironense* (Pictet et De Lorlol) from the Hauterivian, *P. nieri* (Pictet) from the Berriasian and *P. nodulosum* (Catullo) from Biancone (probably from Berriasian according to Aguirre-Urreta and Rawson (1993)). Wright (1957, p. L383) gave a diagnosis of the genus, which was described by Wiedmann (1966, p. 55) as "Cheloniceratid with open early spire". He also described the new species *P. schindewolfi* Wiedmann. Dimitrova (1967) added to this list *P. beneckei*, which Haug (1889, p. 206) previously related to *P. pachycyclum*. Later, two new Barremian species were described: *P. caucasicum* form the Caucasus (Egoyan, 1989, p. 138) and *Paraspiticeras groeberi* from Argentina (Aguirre-Urreta and Rawson, 1993, p. 58). These new data were considered in the new volume of the Treatise on Ammonoidea (Wright et al., 1996), where they placed

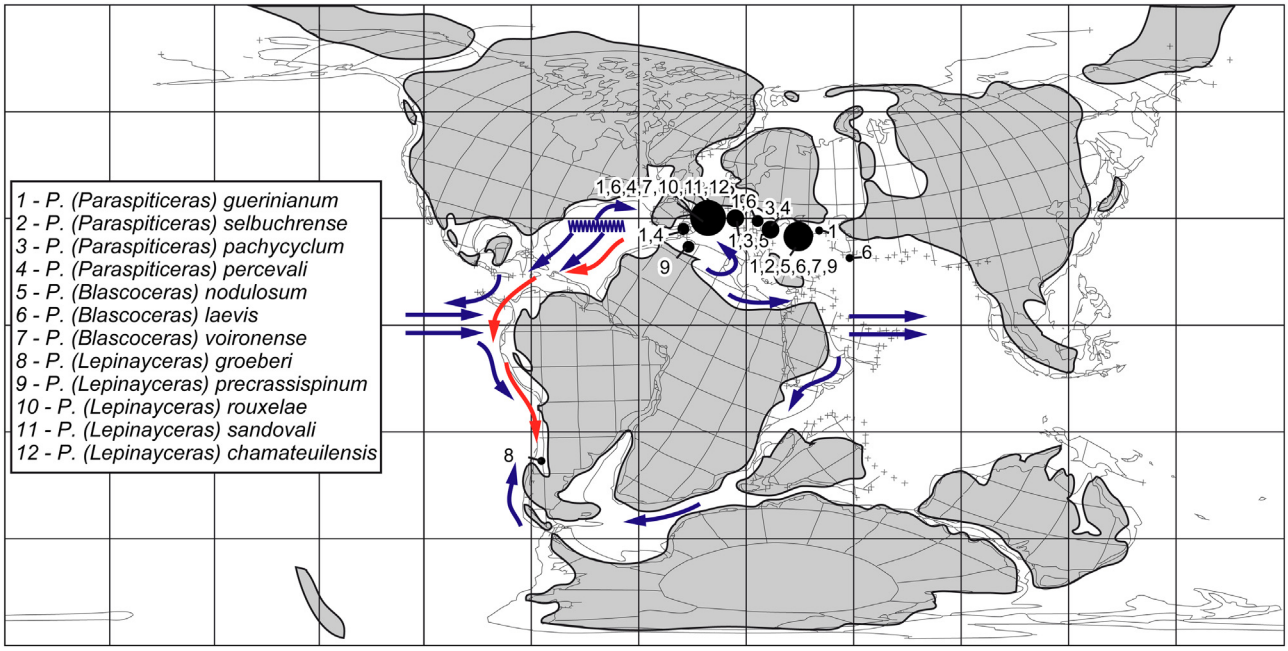

Fig. 3. Geographic distribution of *Paraspiticeras*. Continental outlines for the early Cretaceous (Smith and Briden, 1977), late Hauterivian shorelines – author's data based on numerous sources. Arrows indicate surface current reconstruction, zigzag line – position of the high-pressure zone in the atmosphere, size ot the circule reflects number of species of *Paraspiticeras* (Baraboshkin et al., 2007).

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Paraspiticeras into Subfamily Rolobоceratinae Casey of Family Douvilleiceratidae Parona & Bonarelli.

Vermeulen (2004) referred *Crioceratites tuberosus* of Busnardo et al. (2003) to *Paraspiticeras* and revised the taxonomic position of the genus replacing it into Emericiceratidae Vermeulen. The state of knowledge on *Paraspiticeras* was summarised in the "Fossilium Catalogus" of Klein et al. (2007).

In 2009 Vermeulen recognised *Paraspiticeras dollai* and proposed the new Subfamily Paraspiticeratinae Vermeulen. Finally, he revised *Paraspiticeras* and split it into genera *Paraspiticeras* s.s., *Blascoceras* Vermeulen, Lazarin, Leroy et Mascarelli (with *B. laevis* (Fallot et Termier), *B. nodulosum* (Catullo), *B. voironensis* (Pictet et De Loriol)) and *Lepinayceras* Vermeulen, Lazarin, Leroy et Mascarelli, with *L. chamateuilensis* sp. nov., *L. groeberi* (Aguirre-Urreta), *L. precrassispinum* (Roch), *L. rouxelae* sp. nov., *L. sandovali* sp. nov. (Vermeulen et al., 2012).

Summarizing the above, one can note that there are highly debatable questions in the taxonomy of *Paraspiticeras* both in specific and generic level as well as in the higher taxonomic level.

In our opinion, three groups of species could be distinguished in the *Paraspiticeras*. They differ in the style of ornamentation having similar features at the same time.

1. The *Paraspiticeras percevali* group includes the type species *P. percevali* (Uhlig, 1883), *P. guerinianum* (D'Orbigny, 1850), *P. pachycyclum* (Uhlig, 1883), *P. selbuchrense* Baraboshkin et Mikhailova, sp. nov. The group has diagnostic features of the genus. Species differ mainly by the presence of single or bifurcating ribs and the smoothness of the large whorls. We regard this group as *Paraspiticeras* (*Paraspiticeras*) s.s.

2. The *Paraspiticeras leave-voironense* group includes *P. laeve* (Fallot et Termier, 1923) and *P. voironense* (Pictet et De Loriol, 1858). This group is characterised by the smooth strongly depressed whorls with strong lateral tubercles through all stages. The group was recognised as genus *Blascoceras* Vermeulen, Lazarin, Leroy et Mascarelli (Vermeulen et al., 2012) with the *Blascoceras nodulosum* (Catullo) as a type of the genus. Unfortunately, the holotype of *B. nodulosum* was not preserved.

According to Vermeulen et al. (2012), *Blascoceras* differs from *Paraspiticeras* by less rounded cross-section, constant presence of the lateral tubercles, early smoothing of the ribs and by the stratigraphic distribution limited to the uppermost Hauterivian. Our collection demonstrates that lateral tubercles could exist in all stages in *Paraspiticeras* s.s. (the holotype of *P. selbuchrense*); *B. nodulosum* from Angles section (Vermeulen et al., 2012, fig.7) has well-developed ribs in the adult whorls, similar to *P. pachycyclum*. The holotype of *Paraspiticeras laeve* itself represents medium size whorls of *Paraspiticeras*. It has the same features as the inner whorls of the specimen of *P. guerinianum* (pl. 1, Fig. 3a-b) with simple monotuberculated ribs smoothed at the venter. Therefore, we cannot exclude that *P. laeve* is, in fact, is a synonym of *P. guerinianum*.

Vermeulen et al. (2012) supposed that the range of *Blascoceras* is restricted to the uppermost Hauterivian, but *P. (B.) voironense* (pl. 2, Fig. 6) characterises Nicklesia pulchella - Holcodiscus caillaudianus Zones of the lower Barremian. The loss of the holotype of *P. nodulosum* questions its age. Catullo (1848, p. 143) indicated co-occurrence of this ammonoid with Valanginian – Hauterivian belemnite *Duvalia dilatata* (Blainv.), Aguirre-Urreta and Rawson

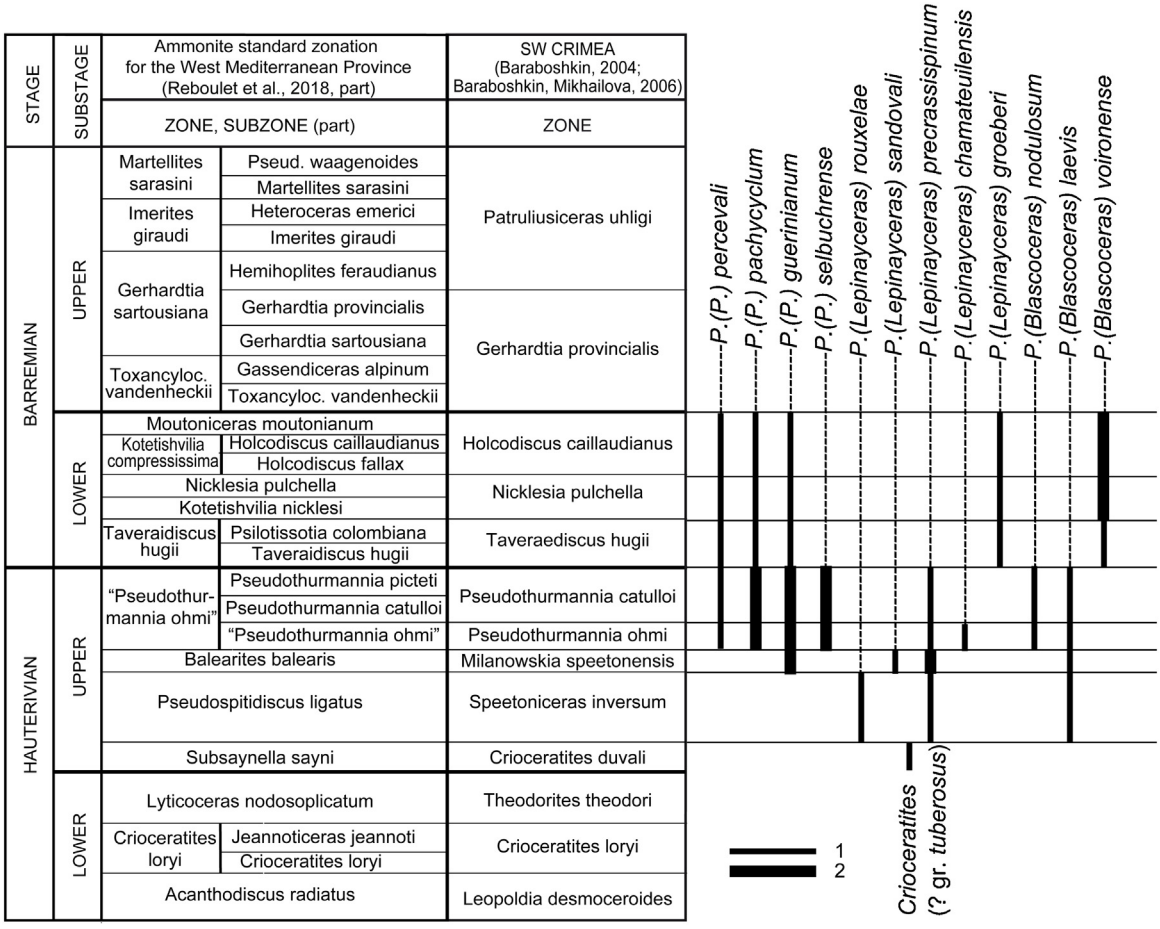

Fig. 4. Stratigraphic ranges of *Paraspiticeras*: 1 - total, 2 - in the south-western Crimea.

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(1993, p. 56) supposed its Berriasian age, while Vermeulen et al. (2012) attributed it to upper Hauterivian.

3. The *Paraspiticeras precrassispinum* group was described as the genus *Lepinayceras* Vermeulen, Lazarin, Leroy et Mascarelli (Vermeulen et al., 2012) with the new species *L. sandovali* as a type of that genus. *L. chamateuilensis* sp. nov., *L. groeberi* (Aguirre-Urreta and Rawson, 1993), *L. precrassispinum* (Roch, 1930), *L. rouxelae* sp. nov. were included in *Lepinayceras*. These ammonoids have two rows of tubercles (lateral and umbolateral) at the adult stage.

Lepinayceras differs from *Paraspiticeras* s.s. it by less regular ribbing, the presence of two lateral tubercles at the adult stage and by higher cross-section (Vermeulen et al., 2012); it ranges from the Plesiospitidiscus ligatus Zone to the Pseudothurmannia mortilleti Zone. Vermeulen et al. (2012), however, figured a rather different ammonoid with the name *Lepinayceras*. *Lepinayceras sandovali* is bituberculated species with rather coarse branched main and intercalated ribs and relatively narrow cross-section. *Lepinayceras rouxelae* is bituberculated ammonoid with very smooth ribs. *Lepinayceras precrassispinum* and very similar *L. chamateuilensis* in having inner whorls close to *Paraspiticeras guerinianum* with well-developed lateral tubercles, branched main and intercalated secondary ribs. The adult stage of *L. precrassispinum* demonstrates main ribs with two tubercles smoothing with an age. Highly variable early Barremian (? to late Hauterivian: Mourgues (2007)) *Lepinayceras groeberi* (Aguirre-Urreta and Rawson, 1993) was also included in this new genus.

It seems that *Lepinayceras* artificially combines very different ammonoids and needs a serious revision based on representative material.

Therefore, representatives of *Blascoceras* and *Lepinayceras* have a number of transitions to *Paraspiticeras s.s.* in terms of the shell morphology and stratigraphic range. Because of that we regard them as subgenera of *Paraspiticeras*.

There are several other ammonoids referred by different authors to *Paraspiticeras.*

Kilian (1913, p. 255) placed *Ammonites Nieri* Pict. into *Paraspiticeras.* Now it is referred to *Pseudohimalayites* (Klein and Hoedemaeker, 1999).

Paraspiticeras beneckei(Haug) is based on *Aspidoceras Beneckei* (Haug, 1889, p. 206, pl. VIII, Fig. 3). We already doubt on the independence of this species (Baraboshkin and Mikhailova, 2009), and now we are prone to think that "*P. beneckei*" is a synonym of *P. pachycyclum* (Uhlig). *Paraspiticeras beneckei*, figured by Dimitrova (1967, p. 169, pl.83, Fig. 4, pl.84, Fig. 3) is very close to the outer whorl of the lectotype of *P. guerinianum* (Cottreau, 1937, pl. 77, fig. 15).

Barremian *Paraspiticeras schindewolfi* described by Wiedmann (1966, p. 55) in very small specimens, whose specific features have not yet been formed. Identification of this species is problematic.

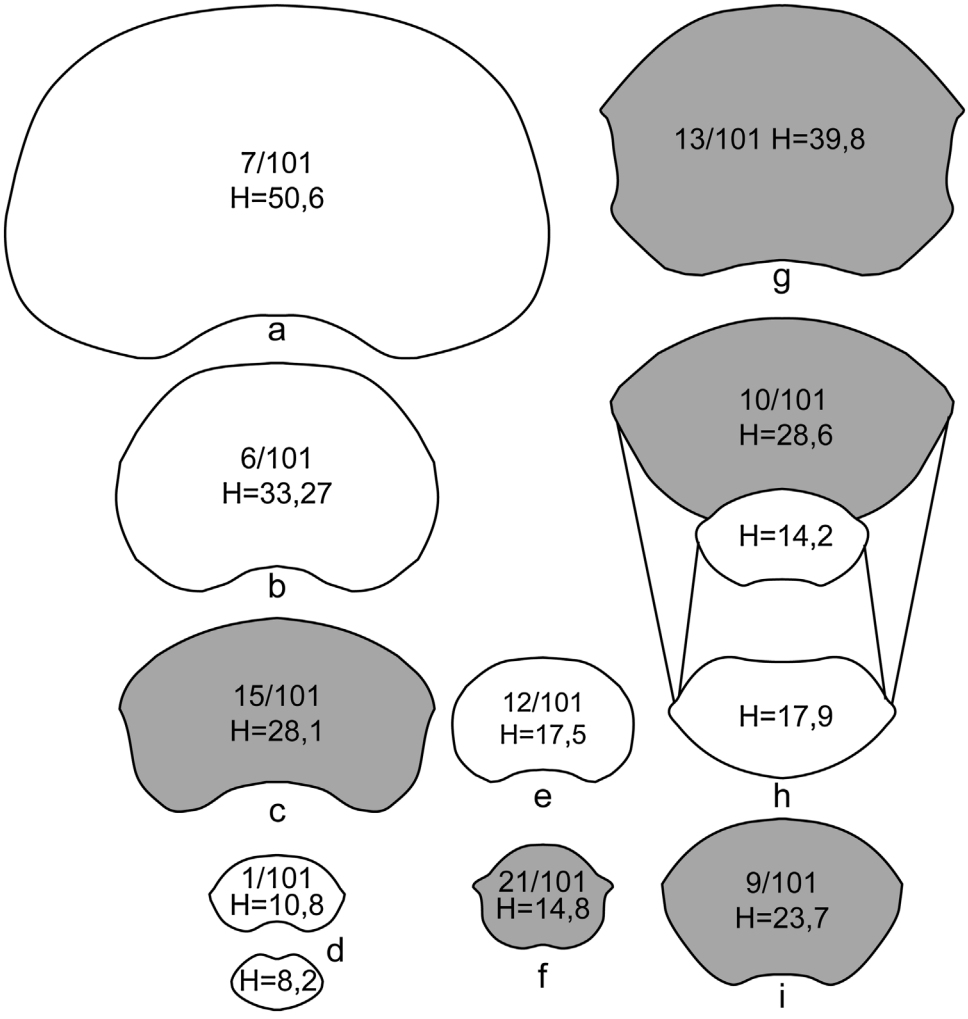

Fig. 5. Whorl sections through phragmocone and body chamber (in grey) of *Paraspiticeras*. Number of samples and whorl height (H, in mm) indicated directly at the sections: a, *P. (P.) guerinianum*, ESM MSU 7/101; b, *P. (P.) guerinianum*, ESM MSU 6/101; c, *P. (P.) selbuchrense*, ESM MSU 15/101; d, *P. (P.)* cf. *guerinianum*, ESM MSU 1/101; e, *P. (P.)* cf. *pachycyclum*, ESM MSU 12/101; f, *P. (Blascoceras) voironense*, ESM MSU 21/101; g, *P. (Lepinayceras)* cf. *precrassispinum*, ESM MSU 13/101; h, *P. (P.) selbuchrense*, ESM MSU 10/101; i, *P. (P.) selbuchrense*, ESM MSU 9/101.

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"*Paraspiticeras depressum*" was mentioned in a few papers from Venezuelan Andes with a reference on the determinations of J.-P. Thieuloy in the PhD Thesis of Stephan (1982). To our knowledge such ammonoid was not published by J.-P. Thieuloy.

Paraspiticeras caucasicum (Egoyan, 1989, p. 138) is a junior synonym of *Paraspiticeras guerinianum* (D'Orbigny), see below.

"Paraspiticeras jourdani" (Delanoy, 1995, p. 45) is a misspelling of *Paraspinoceras jourdani*.

Crioceratites tuberosum Busnardo, 2003, referred to *Paraspiticeras* (Vermeulen, 2004, p. 80; Vermeulen in Klein et al., 2007), has evolute uncoiled shell with three-tuberculated ribs, which is not typical for that genus. Therefore, we do not see any ground to attribute this ammonoid to *Paraspiticeras*.

Paraspiticeras (*P.*) *dollai* described by Vermeulen (2009) is based on a single poorly preserved quarter-whorl sample, which we cannot accept as a well justified species.

To summarise above, we regard *Paraspiticeras* as three subgenera:

Paraspiticeras (*Paraspiticeras*): *P. (P.) percevali* (Uhlig, 1883), *P. (P.) pachycyclum* (Uhlig, 1883), *P. (P.) guerinianum* (D'Orbigny, 1850),?*P. (P.) schindewolfi* Wiedmann, 1966, *P. (P.) selbuchrense* Baraboshkin et Mikhailova sp. nov.

Paraspiticeras (*Blascoceras*): *P. (B.) nodulosum* (Catullo, 1848),?*P. (B.) laevis* (Fallot et Termier, 1923), *P. (B). voironensis* (Pictet et De Loriol, 1858).

Paraspiticeras (*Lepinayceras*): *P. (L.) sandovali* Vermeulen et al., 2012,?*P. (L.) precrassispinum* (Roch, 1930),?*P. (L.) chamateuilensis* Vermeulen et al., 2012 (=? a synonym of *P. (L.) precrassispinum*),?P. *(L.) rouxelae* Vermeulen et al., 2012,? *P. (L.) groeberi* (Aguirre-Urreta and Rawson, 1993).

Distribution: The most of *Paraspiticeras* are distributed in southern Europe and northern Africa except of *P. groeberi* from Argentina and Chile (Fig. 3), but their stratigraphic ranges are different (Fig. 4). Previously *Paraspiticeras* was regarded as Barremian (Wright, 1957), but after appearance of numerous papers with the detailed stratigraphy, it ranges from upper Hauterivian to Barremian (see references in the text below).

Subgenus *Paraspiticeras* (*Paraspiticeras*) Kilian, 1910

Paraspiticeras (Paraspiticeras) guerinianum (D'Orbigny, 1850)

Pl. 1, fig. 1-4, 6; Pl. 2, Fig. 5; text-Fig. 5a, b, d; 6b

Ammonites Guerinianus: D'Orbigny, 1850, p. 99, n° 596;

Ammonites Guerinianus: Pictet and Campiche, 1860, p. 355.

Aspidoceras Guerinianum: Uhlig, 1883, p. 238, pl. XXVI, Fig. 1a, 1b.

? *Aspidoceras Guerini*: Haug, 1889, S.205(13).

? *Aspidoceras* cf. *Guerini*: Haug, 1889, S.205(13).

? *Aspidoceras Guerinianum*: Sarasin and Schöndelmayer, 1901, p. 63, pl. VIII, fig. 1, 2, 3.

Paraspiticeras guerinianum: Kilian, 1910, p. 255.

Ammonites Guerinianus: Cottreau, 1937, p. 54, pl. LXXVII, fig. 11, 12, 15, text-fig. on page 55 (only).

Paraspiticeras guerinianum: Fulop, 1958, pl. VIII, fig. 7.

Paraspiticeras cf. *guerinianum:* Wiedmann, 1966, text-fig. 27b.

Paraspiticeras beneckei: Dimitrova, 1967, p. 169, pl.83, Fig. 4, pl.84, Fig. 3

Paraspiticeras guerinianus: Thomel, 1980, p. 130, fig. 258.

Paraspiticeras ex gr. *percevali*: Mikhailova and Doguzhaeva, 1985, pl. IV, Fig. 1.

Paraspiticeras guerinianum: Avram et al., 1995, p. 119, pl. 9, fig. 8.

Paraspiticeras caucasicum: Egoyan, 1989, p. 138, pl. XI, Fig. 1а, 1б, 1в, 2а, 2б, 2в, 2г, 3.

? *Paraspiticeras* sp.: Hoedemaeker et al., 1995, pl.9, fig.11.

Paraspiticeras cf. *guerini:* Arnaud et al., 1998, p. 18, pl. 2, Fig. 4.

Paraspiticeras guerinianum: Busnardo et al., 2003, p. 54, pl. XXVII, fig.1, pl. XXVII, Fig. 3 (only);

Paraspiticeras guerinianum: Vermeulen, 2004, p. 80.

non Paraspiticeras guerinianum: Company et al., 2005, fig.5A

Paraspiticeras percevali: Vašiček, 2006, p. 435, pl. 4, fig. 3, 4.

Paraspiticeras guerinianum: (D'Orbigny, 1850) Főzy, 2015, tab. LIX, 6a, 6b.

Paraspiticeras guerinianum: Baraboshkin and Mikhailova, 2009, tab.1, fig.1, 3.

Paraspiticeras cf. *guerini*: Lukeneder, 2012, Fig. 4L, P1/66.

Paraspiticeras guerinianum: Lukeneder, 2018, fig.7D.

Lectotype. Specimen 596 (Cottreau, 1937, pl. LXXVII, Fig.15) from the D'Orbigny collection. Chosen by Klein et al. (2007). Hauterivian of Cheiron, Basses-Alpes, France.

Material. 9 specimens (ESM MSU 1/101, 3-7/101, 18-20/101, 23/101) from the upper Hauterivian of the southern slope of the Selbukhra Mountain.

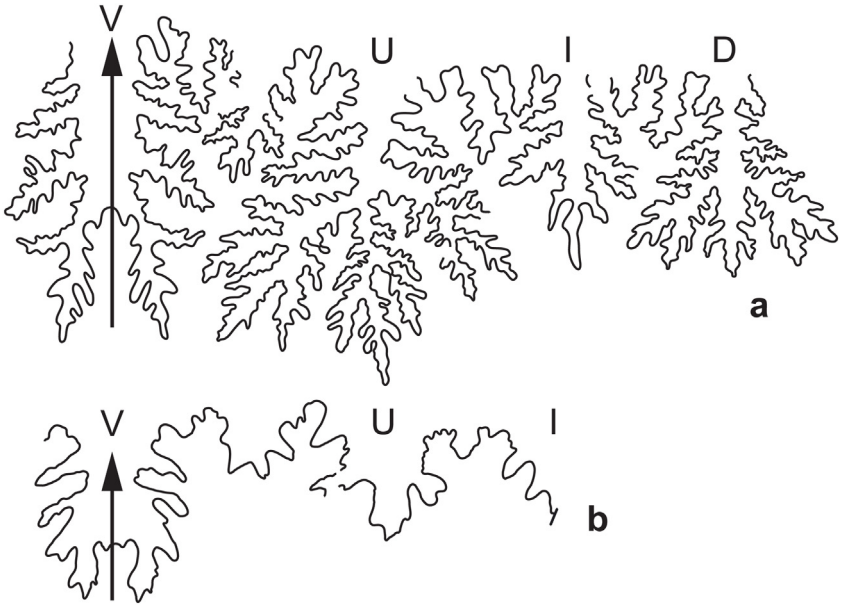

Fig. 6. Suture lines: a - *Emericiceras* cf. *emerici* (Lev.), ESM MSU 7/5, Karagach Village at H = 17.6 mm (from Mikhailova and Doguzhaeva (1985, Fig. 1); b - *Paraspiticeras (P.) guerinianum*, ESM MSU 23/101, at H =9.1 mm; south slope of Selbukhra Mt.

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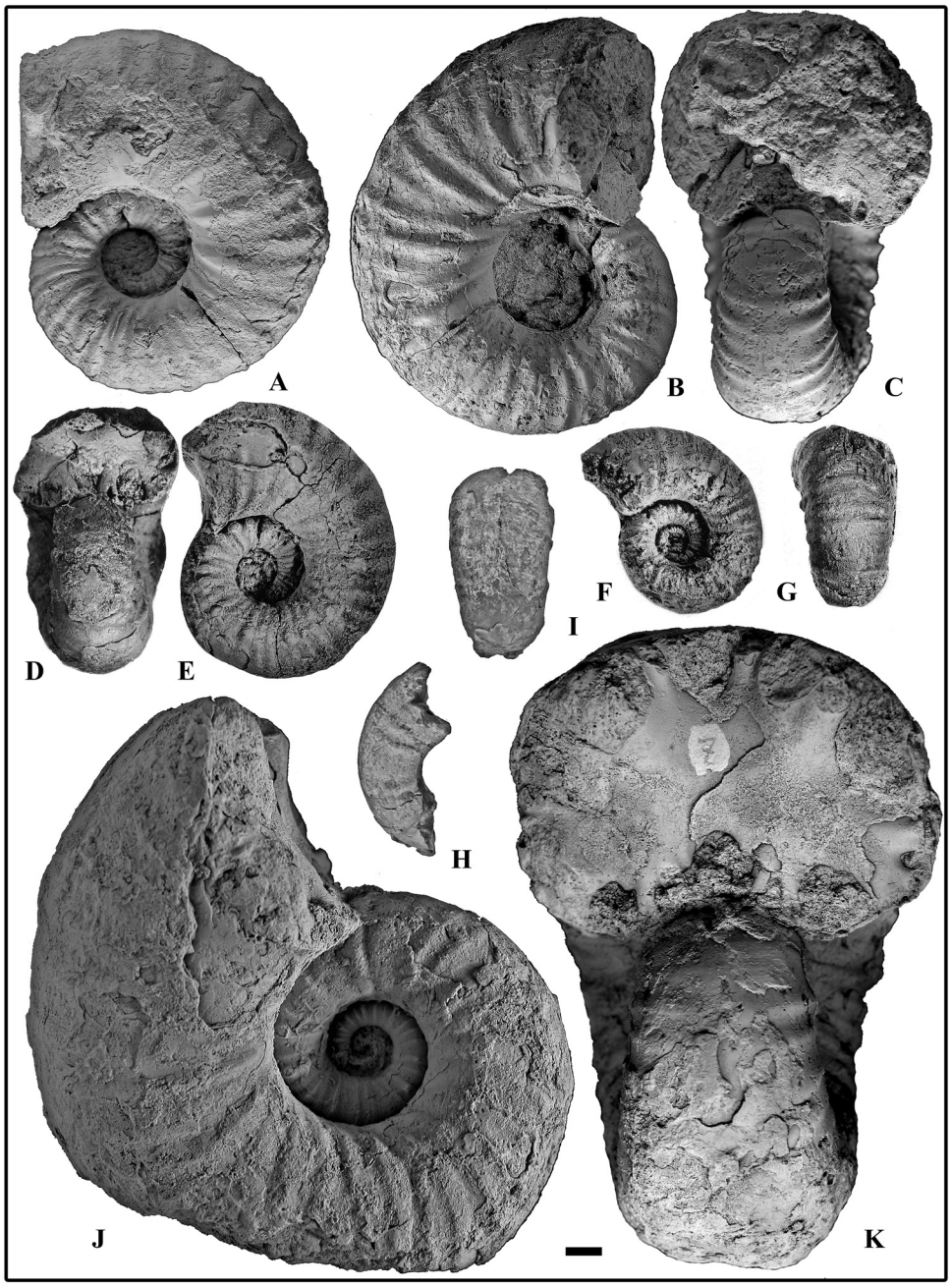

Plate 1. *Paraspiticeras* from the upper Hauterivian of southern slope of Selbukhra Mt., Mountain Crimea. 1–4. *Paraspiticeras (P.) guerinianum*; 1, ESM MSU 17/101; 2, ESM MSU 6/101, 2a - lateral view, 2b - ventral view; 3, ESM MSU 5/101, 3a - ventral view, 3b - lateral view; 4, ESM MSU 14/101, 4a - lateral view, 4b - ventral view; 5. *Paraspiticeras (P.)* cf. *pachycyclum*, ESM MSU 12/101, 5a - lateral view, 5b - ventral view; 6. *Paraspiticeras (P.) guerinianum,* ESM MSU 7/101, 4a - lateral view, 4b - ventral view. All specimens x 1, except of Fig. 5, coated with ammonium chloride. Scale bar is 1 cm.

Shape. Evolute inflated shell, with depressed rounded subrectangular whorl section, widest in the mid-side to lower 1/3 side in the largest whorls. Umbilicus is wide, umbilical wall is subvertical, vertical with age, umbilical bend is gradual.

Lectotype is a large form with ribbing, smoothed at the last whorl with the prevailing single ribs. However, there are 2-3 bifurcated or intercalating ribs (or both) per whorl with a branch point located just below the mid-side. The branch point is marked with a small thickening. Tubercles of different size are developed on the internal whorls, their number varies.

Dimensions (in mm) of measured specimens.

Specimen	D	U	H	W	H/W
1/101			10.6	16.5	0.64
4/101	35.8	12.8	15	19.8	0.76
5/101	52.6	16.1	21.4	38.6	0.55
6/101	72.7	21.4	34.3	40.2	0.85
7/101	110	32	51.2	73.3	0.70
18/101	102.3	29.5	46.8	66.2	0.71
19/101	52.9	13.2	25.8	30.5	0.85
20/101	67.3	19.2	30.5	40.6	0.75
23/101	23	8.5	9.1	12.7	0.72

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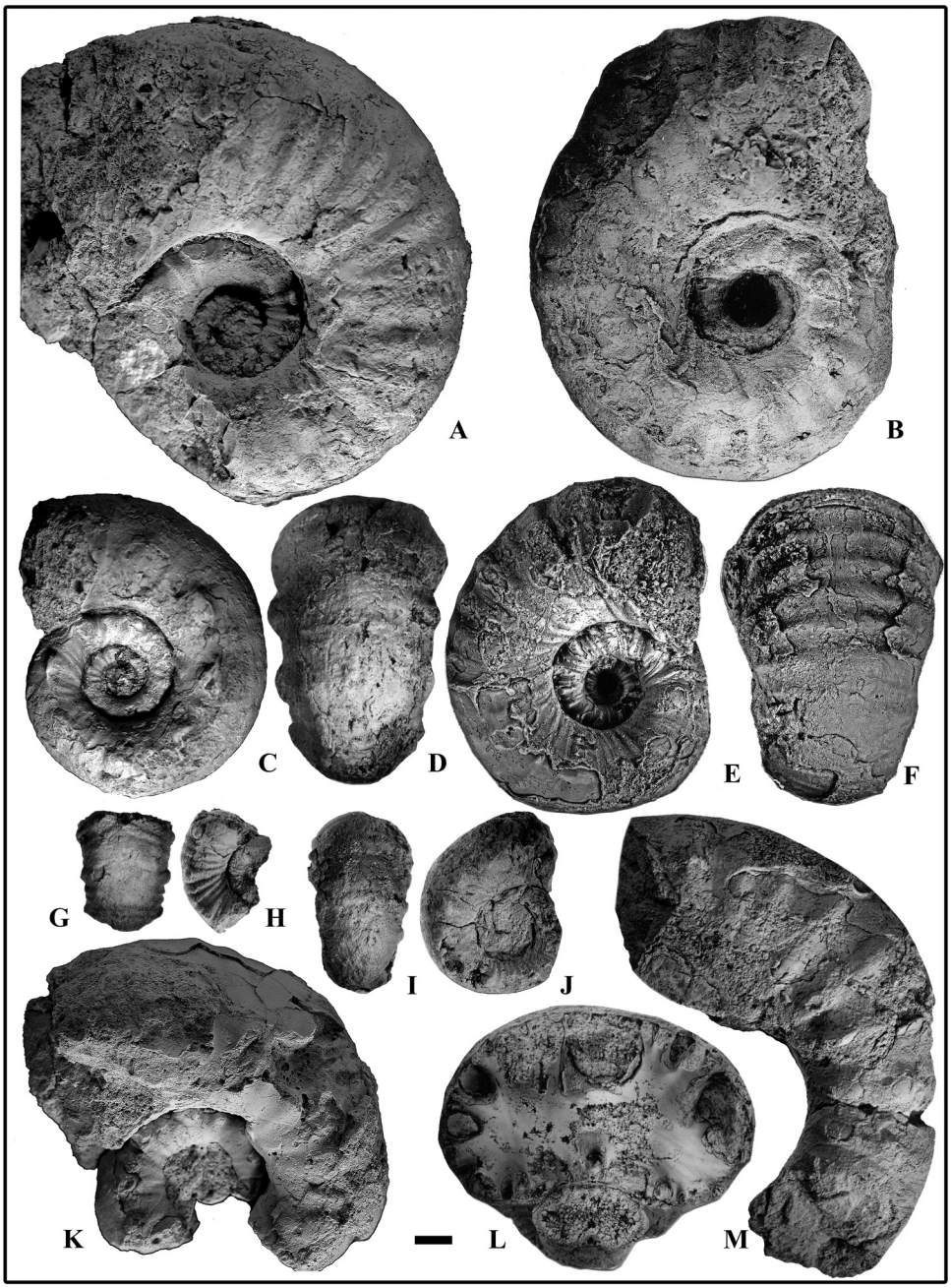

Plate 2. *Paraspiticeras* from the upper Hauterivian -Barremian of Mountain Crimea. 1–4, 7–8. *Paraspiticeras* (*P.*) *selbuchrense* Baraboshkin et I. Mikhailova, sp. nov.; 1 - ESM MSU 17/101; 2, ESM MSU 16/101; 3, ESM MSU 9/101, 3a - ventral view, 3b - lateral view; 4, holotype ESM MSU 15/101, 4a - lateral view, 4b - ventral view; 7, ESM MSU 10/1017. a - ventral view, 7b - lateral view; 8, ESM MSU 1/101; 5. *Paraspiticeras* (*P.*) cf. *guerinianum*, ESM MSU 1/101, 5a - ventral view, 5b - lateral view; 6. *Paraspiticeras* (*P.*) *voironense*, ESM MSU 21/101, K1br1, 6a - ventral view, 6b - lateral view; 9. *Paraspiticeras (Lepinayceras)* cf. *precrassispinum* (Roch, 1930), ESM MSU 13/101. All specimens x 1, coated with ammonium chloride. Scale bar is 1 cm. Specimens on figs. 1–4, 7–8 are from the upper Hauterivian of southern slope of Selbukhra Mt. Specimens on figs. 5, 9 are from the upper Hauterivian and specimen on fig. 6 is from the lower Barremian of southern slope of Belaya Mt. near Verkhorechie Village.

The sculpture is represented by simple and bifurcated ribs of similar thickness. Branching ribs (8–10 per whorl) form a thickening or a small elongated tubercle at the branching point, the most prominent and well-marked in the early whorls. 1–3 simple ribs are located between the branching ribs. The number of ribs at the ventral side is 36 (at D =70 mm); they are smoothed in the middle of the venter. 1–2 umbilical ribs join on the lateral tubercle forming a loop. At the adult whorls (D > 110 mm), branching ribs become intercalating.

Comparison and comments: The specimen of Cottreau (1937, fig. 13–14) is a small involute ammonoid with numerous ribs and does not belong to *Paraspiticeras*. Perhaps the same applies to the juvenile specimen in fig. 12. Other specimens of D'Orbigny (1850) vary significantly.

The ornamentation of *Paraspiticeras laeve* (Fallot and Termier, 1923) is represented by simple fine ribs with side tubercles. Inner whorls of our specimen (pl.1, fig.3) at the D = 35–40 mm are almost identical to the *Paraspiticeras leave*, but outer whorl (D > 40 mm) is much closer to *P. guerinianum*. *Aspidoceras Guerinianum* (Sarasin and Schöndelmayer, 1901, p. 63, pl. VIII, Figs. 1–3) also has well-developed lateral tubercles on each rib, which is similar to *P. (L.) leave*, and to our sample of *Paraspiticeras guerinianum* (pl.1, fig.3).

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Therefore, they could represent inner whorls of one of the variations of *P. guerinianum*.

Paraspiticeras ex gr. *percevali* figured in longitudinal section by Mikhailova and Doguzhaeva (1985, pl. IV, Fig. 1) from the Crimea demonstrates the same sculpture as in our samples. The age and the locality of that sample (ESM MSU 3201) were mistaken: it was found in the upper Hauterivian of Verkhorechie Village.

Paraspiticeras beneckei of Dimitrova (1967, p. 169, pl.83, Fig. 4, pl.84, Fig. 3) is close to the outer whorl of the lectotype of *P. guerinianum* with bifurcated and simple ribs.

Paraspiticeras caucasicum of Egoyan (1989, p. 138, pl. XI, Fig. 1–3) is based on a single specimen. It demonstrates depressed rounded subrectangular whorl section and costulation similar to early whorls of *P. guerinianum* with main monotuberculated bi-trifurcated ribs and 2–3 intercalated ribs. Outer whorl is poorly preserved, so it is difficult to judge on its features.

Paraspiticeras guerinianum of Company et al. (2005, Fig. 5A) is a large specimen with predominantly simple ribs smoothed with age, which is much close to *Paraspiticeras percevali.*

Paraspiticeras percevali of Vašiček (2006, p. 435, pl. 4, Figs. 3,4) represents two specimens of different size with similar inner whorls and very close to our samples. Outer whorl of the largest sample (Fig. 3) has smooth simple and bifurcated ribs, so it is much closer to *P. (P.) guerinianum* rather than to *P. (P.) percevali.*

Paraspiticeras guerinianum of Lukeneder (2018, fig.7D) is a fragment of small bituberculated whorl, so it should be referred to *Paraspiticeras (Lepinayceras).*

Distribution: The upper part of the Pseudothurmannia picteti (= angulicostata) Zone of the upper Hauterivian of Romania (Patrulius and Avram, 2004) and Switzerland (Busnardo et al., 2003); upper Hauterivian of Italy (Lukeneder and Lukeneder, 2014); the Barremian of Hungary (Fülop, 1958); lower Barremian of France (D'Orbigny, 1850, Cottreau, 1937), Spain (Wiedmann, 1966); lower Barremian of the North-Western Caucasus (Egoyan, 1989); lower Barremian Kotetishvilia compressissima Zone of Slovakia (Vašiček, 2006).

Paraspiticeras (Paraspiticeras) cf. *pachycyclum* (Uhlig, 1883)

Pl. 1, Fig. 5a, b; text-fig. 5e

Holotype: Specimen of *Aspidoceras pachycyclus*, figured by Uhlig (1883, p. 239, pl. XXVII, Fig. 1) from Barremian of Skalitz, Silesia.

Material. One specimen (ESM MSU 12/101), representing fragment of the phragmocone from the upper Hauterivian of the southern slope of the Selbukhra Mt.

Shape. Evolute, depressed, with a low oval cross-section, the widest in the middle part. Umbilicus is wide, with steep umbilical wall and gradual umbilical bend.

The sculpture is represented by irregular ribs, thickened on varying degrees on the lateral sides, but not forming tubercles. Ribs are smoothed in the direction of the umbilical suture and ventral bends.

Dimensions (in mm) of measured specimens.

Specimen	H	W	H/W
9/101	19.4	25.4	0.676

Comparison. *Paraspiticeras pachycyclum* (Uhlig) seems to be the closest to our sample because of rare costulation, absence of tubercles and smoothing of the sculpture.

Distribution. *Paraspiticeras pachycyclum* was reported from the Barremian of Silesia (Uhlig, 1883), upper Hauterivian of France (Kilian, 1910); lower Barremian Holcodiscus perezianum and Barremites cassidoides Zones (Breskovski, 1975), Pseudothurmannia ohmi Zone of Morocco (Ettachfini, 2004). Our sample was found lost in the upper Hauterivian part of the section.

Paraspiticeras (Paraspiticeras) selbuchrense Baraboshkin et I. Mikhailova, sp. nov.

Pl. 2, fig. 1–4, 7–8; text-fig. 5c, h, I

Paraspiticeras laeve: Baraboshkin and Mikhailova, 2009, tab.1, Fig. 2.

Derivation of the name: from Selbukhra Mountain, near Nauchnyi Town.

Holotype. Specimen ESM MSU No.15/101, representing large phragmocone and the very beginning of the living chamber; upper Hauterivian of Selbukhra Mountain.

Material. 7 specimens from the upper Hauterivian of Selbukhra Mountain (ESM MSU 8–10/101, 14–17/101).

Shape. Evolute, strongly inflated, with a low elliptical whorl section, the widest in the mid-side, in the strong tubercles. Umbilicus is wide, umbilical wall is subvertical, vertical with age, umbilical bend.

Dimensions (in mm) of measured specimens.

Specimen	D	U	H	W	H/W
9/101	54.9	20.3	20.5	34	0.60
10/101	70.6	22	28.2	44.8	0.63
13/101			38.5	42.4	0.91
14/101	39.7	14	16.8	23.3	0.72
15/101 holotype	61.8	20.3	27	40	0.68
16/101	90	25.2	40	61.2	0.65
17/101	94	25.7	42.6	55	0.77

Three stages are recognisable in the development of the *P. (P.) selbuchrense*: early ribbed (D<40-50 mm), medium smooth, with strong tubercles (D = 40–60) and coarse-ribbed with bifurcated ribs and large tubercles (D > 50–60). The sculpture of the larger whorls is represented by coarse ribs (9–10 per whorl) branching into 2 or 3 secondary ribs with appearance of a large lateral tubercle in the branching point. One of the branches is thicker than the other; they cross the ventral side with a noticeable flattening. Secondary ribs become more prominent with age. Rarely (1–2 times per whorl) two umbilical ribs are connected on the lateral tubercle, forming a loop. There are simple thinner ribs present between the branched ribs. They get thicker or form a small tubercle in the mid-side. The number of ribs on the ventral side reaches 26 (D =65 mm). Simple ribs disappear when D > 50 mm, and when D > 70 mm they could appear again. The middle whorls are almost smooth, with wary rare ribs, but with strong tubercles, which strongly resembles *P. (P.) leave*. Inner whorls have 2–5 simple ribs between the thicker tuberculated ribs.

Comparison. The new species is close to *P. guerinianum*, and differs by very inflated whorls and coarse branched ribs with large lateral tubercles on the outer whorls. The medium whorls are similar to *P. leave* but can be distinguished by larger sparked tubercles and presence of ribs at the outer whorls.

Distribution. Upper Hauterivian of the Crimea.

Subgenus *Paraspiticeras (Lepinayceras)* (Vermeulen, Lazarin, Leroy et Mascarelli, 2012)

Paraspiticeras (*Lepinayceras*) cf. *precrassispinum* (Roch, 1930)

Pl. 2, fig. 9; text-fig. 5g

Lectotype. Sample No. ID163, Institute Dolomieu, Université de Grenoble France (Roch, 1930, p. 317, Pl. XIV, Fig. 2a, b), upper Hauterivian, Igueni Ouram, Maroc; refigured by Vermeulen et al. (2012, p. 329, Fig. 4).

Material.Sample ESM MSU 13/101, representing a fragment of the terminal part of the phragmocone and the beginning of the body chamber from the upper Hauterivian of the Verkhorechie Village.

Description. The shell is evolute, moderately inflated, with an oval cross-section, the widest in the middle of the sides. Umbilicus is wide, umbilical wall subvertical, umbilical bend gradual with gentle transition to the sides.

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The sculpture is represented by simple radial ribs (9 on a quarter of the whorl) with two rows of small tubercles at the umbilical and ventral bends. The ribs quickly smoothed in the umbilicus and the venter direction. The ventral side is completely smooth.

Internal whorls of the holotype represent main bifurcated and finer intercalated ribs. A large tubercle appears at the bifurcation point.

Dimensions (in mm) of measured specimens.

Specimen	H	W	H/W
13/101	38.5	42.4	0.91

Comparison. *P. (L.) precrassispinum* differs from other *Paraspiticeras* in having bituberculated ribs at the adult stage, while in the younger whorls they are monotuberculated.

Lepinayceras chamateuilensis Vermeulen et al., 2012 is probably a synonym of *P. (L.) precrassispinum*, which differs by more involute whorls and slightly curved ribs.

Distribution. *P. (L.) precrassispinum* was reported from the upper Hauterivian *Balearites balearis* Zone (Autran, 1989, pl. 12, Fig. 3) and Plesiospitidiscus ligatus Zone (Bulot et al., 1992, p. 50) from SE France; upper Hauterivian of the Morocco and the Crimea.

Subgenus *Paraspiticeras (Blascoceras)* (Vermeulen, Lazarin, Leroy et Mascarelli, 2012)

Paraspiticeras (Blascoceras) voironense (Pictet et De Loriol, 1858)

Pl. 2, Fig. 6a, b; text-fig. 5f.

Ammonites Voironensis: Pictet and De Loriol, 1858, p. 19, pl. II, Fig. 5.

Ammonites Voironensis: Pictet and Campiche, 1860, p. 355.

Paraspiticeras Voironense: Kilian, 1910, p. 255.

Paraspiticeras voironense: Baraboshkin and Mikhailova, 2009, tab.1, fig.4.

Blascoceras voironensis: Vermeulen et al., 2012, p. 338.

Holotype: *Ammonites Voironensis:* Pictet and De Loriol, 1858, p. 19, pl. II, Fig. 5a, b, Hivernages, Voirons Mountain, region of Genève, Switzerland.

Material. One specimen ESM MSU 21/101 from the lower Barremian of south slope of Belaya Mt. section, Verkhorechie Village.

Shape. Evolute, moderately inflated, with an oval relatively high whorl section, the widest in the mid-side. Venter is smooth and rounded. Umbilicus is wide, umbilical wall is steep, but not vertical, umbilical bend is gradual.

Dimensions (in mm) of measured specimens.

Specimen	D	U	H	W	H/W
21/101	34.7	12.4	14.4	17.6	0.82

The sculpture is represented by frequent thin ribs on the umbilical wall, looped by two or three in a sharp lateral tubercle. Short simple ribs occur between tubercles. They reach the ventral bend and then disappear. The outer whorls have smoothed secondary ribs poorly recognisable at the venter.

Comparison. *Paraspiticeras voironense* differs from *P. laeve* by higher narrow whorl section, by the presence of thin umbilical ribs and rare intercalated ribs.

Distribution. Hauterivian – Barremian of Switzerland, lower Barremian of the Crimea.

5. Position of *Paraspiticeras* in the ammonoid system

The genus *Paraspiticeras*, defined by Kilian (1910) more than 100 years ago, attracted the attention of palaeontologists as a possible ancestor of the Superfamily Douvilleiceratoidea. Based on the similarity in shape and sculpture of these ammonoids he considered *Douvilleiceras* as a possible descendant of *Paraspiticeras*. However, the attempt to bring together the Tithonian - Berriasian fine-ribbed *Spiticeras* of the Superfamily Perisphinctaceae, and *Paraspiticeras* seems rather strange. Djanelidze (1922) completely refuted this point of view.

The papers of Wiedmann and Schindewolf discussing *Paraspiticeras* appeared almost simultaneously in 1966. The material of excellent preservation from the Barremian of Alicante province (Southern Spain), available from Wiedmann and partially transferred to Schindewolf, was studied thoroughly by them.

In the holotype of juvenile *P. schindewolfi* (Wiedmann, 1966, tab. 4, Fig. 2) the protoconch, the first and second whorls are uncoiled. A similar umbilical hole was later found in two specimens of *"P. ex gr. percevali"* (= *P. guerinianum* in this paper) from the south-western Crimea. The septal tubes are partially preserved, and the siphon is located in a distance from the ventral side at the beginning of the third whorl (Mikhailova and Doguzhaeva, 1985, fig.).

The presence of the umbilical hole was also observed in other Early Cretaceous ammonoids: *Caspianites* Casey (Bogdanova and Mikhailova, 1975), *Luppovia* Bogd., Kakab. et I.Mich. (Kakabadze et al., 1978), *Matheronites* Renngarten (Bogdanova, 1971), *Audouliceras* Thomel (Mikhailova and Baraboshkin, 2007), *Turkmeniceras* Tovbina (Bogdanova, 1971), *Theodorites* (Baraboshkin and Mihailova, 2006), etc.

These genera belong to the Suborder Ancyloceratina and are included either in the Superfamily Ancyloceratoidea, which has a heteromorph shell, or in the Superfamily Deshayesitaceae (*Turkmeniceras*) and the Superfamily Douvilleiceratoidea (*Paraspiticeras*), with planispiral shell. The umbilical hole in *Paraspiticeras* is rounded, but slice-like in *Turkmeniceras*, probably due to it genetic relation with the genus *Deshayesites*. Therefore, its inclusion in the Superfamily Deshayesitaceae does not cause objections. Wiedmann (1966) noted that the shape of the umbilical hole in *Paraspiticeras* is not properly rounded. This is correct: a gap begins with a straight shaft replaced by gentle arc and then by a spiral.

Wiedmann (1966) established the Suborder Ancyloceratina with heteromorph ancestors (Superfamily Ancyloceratoidea), heteromorph (Superfamily Scaphitaceae) and monomorph (Superfamily Deshayesitaceae and Douvilleiceratoidea) descendants. The phylogenetic scheme of Schindewolf (1966, Fig. 430) differs by the separation of Superfamilies Douvilleiceratoidea and Parahoplitaceae.

We cannot agree with the proximity of *Paraspiticeras* and *Scaphites*. First representatives of Scaphitaceae appear in the late Albian. Their shape and the suture line are fundamentally different from what is typical for the Douvilleiceratoidea (Michailova, 1983, p. 179). In *Paraspiticeras* (Fig. 6b) one can see a clear excess of the V/U saddle over the adjacent saddle, like in *Cheloniceras cornuelianum* D'Orb. (Michailova, 1983, p. 108). Comparison of the morphogenesis of *Cheloniceras cornuelianum* and *Scaphites teshioensis* reflects the fundamentally different ways of generation of the new elements of the suture line (Michailova, 1983, p. 91). Gildner (2003), however, showed on the base of a mathematical analysis that the suture lines of *Paraspiticeras* stands apart from *Douvilleiceras* and *Cheloniceras*, but has more similarities with *Scaphites*.

At the same time, there is an obvious similarity between the unique feature of the bifurcation of the umbilical lobe in *Paraspiticeras* and cheloniceratids, noted by Wiedmann (1966). That was the main argument of Wiedmann (1966) and Schindewolf (1966) on the proximity of *Paraspiticeras* and the early Douvilleiceratoidea. Schindewolf (1966) figured the early stages of *Paraspiticeras* morphogenesis, which did not allow to hit the features of Douvilleiceratoidea: the separation of umbilical and innerlateral lobes, and Wiedmann (1966, fig. 38) demonstrated the beginning of this process with the division of the umbilical lobe into a larger U_1 and a smaller U_2 and a noticeable increase in the outer saddle V/U.

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Wiedmann (1966; Wiedmann in Kullmann and Wiedmann, 1970) suggested phylogenetic relations in Douvilleiceratoidea, indicating Hauterivian *Leptoceras* as the ancestor of *Paraspiticeras*, which has a tendency of re-coiling of the shell. It is now known that *Leptoceras* s. s. is Berriasian – Valanginian genus, and morphologically similar *Leptoceratoides* Thieuloy is Barremian in age. Since the first *Paraspiticeras* appear in the late Hauterivian, there is a rather large time gap (~4 Ma) with *Leptoceras* and the transitional forms are not yet found.

Unfortunately, our samples are not sufficiently well preserved in order to describe the morphogenesis of the suture line, but we thought that the dichotomy of the umbilical lobe did not yet appear in *Paraspiticeras* (Fig. 6b), it is trifurcate, similar to *Emericiceras* (Fig. 6a). Therefore, it is possible that *Paraspiticeras* derives from larger late Hauterivian heteromorphs, like *Crioceratites* (Baraboshkin and Mikhailova, 2009). One of the probable ancestors of *Paraspiticeras* is *Crioceratites tuberosum* Busnardo, which Vermeulen (2004, p. 80; Vermeulen in Klein et al., 2007) regarded as *Paraspiticeras*. Vermeulen (2004, 2006) was the first who referred *Paraspiticeras* to the Family Emericiceratidae Vermeulen of the Suborder Ancyloceratina Wiedmann. Vašíček (2009) supported Vermeulen's proposal.

Busnardo et al. (2003) regarded *Paraspiticeras* as a descendant of simbirskitids and referred it to ?Polyptychitidae. They argued that *Paraspiticeras* has similarities with *Simbirskites* and that they appear in Tethys during Boreal invasion.

Wright (1957, p. L383) derived Cheloniceratinae Spath, 1923, from late Hauterivian *Raspailiceras* (= *Plesiospitidiscus* Breistroffer now, Family Desmoceratidae), which was questioned by Casey (1961, p. 176), who aligned it with Roloboceras. In 1996 Wright (p. 266) placed *Paraspiticeras* in the Subfamily Roloboceratinae after Casey (1961). Sharikadze (2015) agreed that this genus is "not true representative of Douvilleiceratoidea" and it is better to include it into Ancyloceratidae (p. 190), but in the phylogenetic scheme (Fig. 124) he began Douvilleiceratoidea with *Paraspiticeras*.

Vermeulen (2004) regarded the Moroccan species *P. precrassisipinum* (Roch) as a descendant *Paraspiticeras*. Later he thought that *Paraspiticeras* (*Blascoceras*) was older than *Paraspiticeras* s.s. (Vermeulen et al., 2012). Our data do not confirm the ideas of Vermeulen et al. (2012) on the subgeneric and species relations of *Paraspiticeras*. It seems that *P. (Lepinayceras) rouxelae, P. (Blascoceras) nodulosum* and *P. (Blascoceras) laevis* are the oldest representatives of *Paraspiticeras* (Fig. 4). Who was the direct ancestor of *Paraspiticeras* is still a question.

Even more difficult is the problem with the descendants of *Paraspiticeras*. Traditionally, it is related to the early Aptian *Prochelonicera*s Spath, *Cheloniceras* Hyatt or *Roloboceras* Casey (Wiedmann, 1966; Wright et al., 1996). Vermeulen et al. (2012) and our data demonstrated the absence of *Paraspiticeras* in the upper Barremian, so the 3 million years gap between its disappearance and the appearance of the first Douvilleiceratoidea does not allow us to consider this genus as their direct ancestor.

6. Conclusions

There are a number of conclusions coming from the present study.

1 *Paraspiticeras* is rather variable ammonoid, which could be split into 3 subgenera. *P. (Paraspiticeras) s.s.* includes *P. (P.) percevali* (Uhlig, 1883), *P. (P.) pachycyclum* (Uhlig, 1883), *P. (P.) guerinianum* (D'Orbigny, 1850),? *P. (P.) schindewolfi* Wiedmann, 1966, *P. (P.) selbuchrense* Baraboshkin et Mikhailova sp. nov. *P. (Blascoceras)* includes *P. (B). nodulosum* (Catullo, 1848),? *P. (B). laeve* (Fallot et Termier, 1923), *P. (B). voironense* (Pictet et De Loriol, 1858). *P. (Lepinayceras)* includes *P. (L.) sandovali* Vermeulen et al., 2012,? *P. (L.) precrassispinum* (Roch, 1930), ? *P. (L.) chamateuilensis* Vermeulen et al., 2012,? *P. (L.) rouxelae* Vermeulen et al., 2012,? *P. (L.) groeberi* (Aguirre-Urreta and Rawson, 1993). *P. (Lepinayceras)* is heterogeneous subgenus and should be revised in the future.

2 Stratigraphic range of *Paraspiticeras* is not simply Barremian, as it was thought before. It is late Hauterivian to early Barremian. There is ~3 Ma gap between disappearance of *Paraspiticeras* in the early Barremian and the appearance of the first representatives of Douvilleiceratoidea.

3 Presence of the umbilical hole, style of the suture line development and absence of direct descendants of *Paraspiticeras* in the late Barremian demonstrate more evidences to include it into Ancyloceratoidea Gill, 1871 rather than into Douvilleiceratoidea Parona et Bonarelli, 1897. It is reasonable, therefore, to attribute them to the Subfamily Paraspiticeratinae Vermeulen, 2009 of the Family Emericiceratidae Vermeulen, 2004.

4 The direct ancestor of *Paraspiticeras* is not known. There is possibility that it was derived from an uncoiled crioceratid like *Crioceratites tuberosum*, but farther investigations are required.

Acknowledgements

This work was supported by the Russian Foundation of Basic Research (grant 06-05-64167), FTP "Scientific Schools" (grant НШ-841.2008.5) and Scientific Program "Trans-Realm correlation of the Phanerozoic biostratigraphic units". We thank J. Klein (Amsterdam) for the help with the literature, V. Arkadiev (Sankt-Petersburg University) and anonymous reviewer for improving the manuscript. We also thank Alastair Ruffel (Queen's University Belfast) for the correction of the English spelling.

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Please cite this article in press as: E.Yu. Baraboshkin, I.A. Mikhailova, Revision of the Early Cretaceous genus *Paraspiticeras* Kilian, 1910 (Ancyloceratoidea, Ammonoidea), Proc. Geol. Assoc. (2020), https://doi.org/10.1016/j.pgeola.2019.06.006

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