



UPPER APTIAN AMMONITES FROM ROUSSILLON, SOUTHERN FRANCE

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Frau, C. (2023): Upper Aptian ammonites from Roussillon, southern France. – Fossil Imprint, 79(1): 89–101, Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (on-line).

Abstract: The present contribution describes a new rich ammonite material from the Aptian-type area, Vaucluse, France, made accessible by the expansion of the wine cellar of Domaine de Château-Blanc at Roussillon, located at ca. 8 km northwest of Apt. This temporary outcrop exposed a few meters of sandstones and sandy, glauconitic marls, characterising the fifth unit of the Aptian-type series. The ammonite specimens are preserved as crushed, internal moulds with phosphatised shells, and are assigned to the Acanthohoplitidae *Egoianiceras angulatum*, *Egoianiceras lautum*, ?*Egoianiceras exiquecostatum*, and *Acanthohoplites* sp., together with poorly-preserved Parahoplitidae (*Parahoplites* sp.). This assemblage is coeval to the Falot black shale episodes occurring in the nearby Vocontian Basin, and correlates to the uppermost *Epicheloniceras martini* Zone of Dutour (2005), or the lower *Colombiceras tobleri* Zone of Dauphin (2002), an age which challenges the younger ammonite-age calibration previously established for the fifth unit.

Key words: Acanthohoplitidae, Ammonites, Aptian, Apt, Roussillon, Vaucluse, France.

Received: April 29, 2023 | Accepted: July 12, 2023 | Issued: November 7, 2023

Zoobank: <http://zoobank.org/urn:lsid:zoobank.org:pub:6EC605A3-DFA8-4861-A257-1BFC13768E87>

Introduction

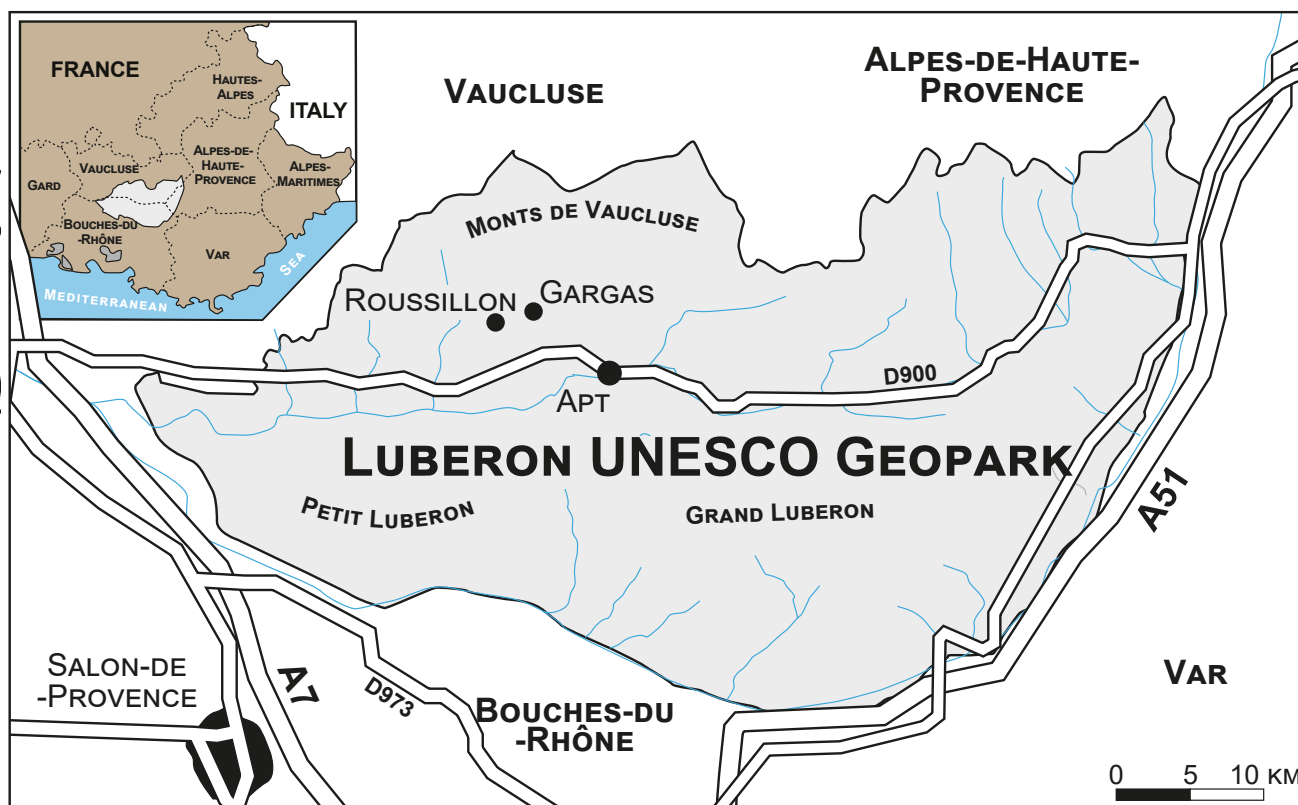
The historical outcrops of the Aptian unit-stratotype located in the Luberon UNESCO Geopark (Vaucluse, southern France) are no longer accessible in the vicinity of the Apt town, due to extensive urbanization launched in the early 1960s (Moullade 1965, Dutour 2005, Moullade et al. 2017, Frau et al. 2017, 2018, 2020). Our understanding of the sedimentary succession is based on a composite litho-log reconstructed at the nearby locality of Gargas (Text-fig. 1). Here, Moullade (1965) defined eight successive lithological units (Text-fig. 2a). The first four units span the upper lower and lower upper Aptian, according to Dutour (2005), and Frau et al. (2017, 2018, 2020), with ammonite evidence of the upper *Deshayesites forbesi* Zone to the *Epicheloniceras martini* Zone of the Standard Mediterranean Ammonite Zonation (SMAZ of Reboulet et al. 2018). Macrofossils are rare in the three overlying formations, and the age of these units remains unclear, as they yield mostly non-diagnostic belemnites (Moullade 1965). A single horizon with ammonites has been reported in the fifth unit by Kilian and Leenhardt (1890), and Moullade (1965), including mention of the Acanthohoplitidae *Diadochoceras nodosocostatum* (D'ORBIGNY, 1841) and *Protacanthoplites bigoureti* (SEUNES, 1887). This fauna would be diagnostic of a latest Aptian age (i.e., “Clansayésien” of Moullade 1965), but the corresponding fauna lacks illustration.

New ammonite discoveries from the fifth unit have been made by Dutour (2005) at Roussillon, ca. 8 km northwest of Apt (Text-fig. 1). The author reported the species *Eogaudryceras (Eotetragonites) duvali* (D'ORBIGNY, 1841), *Melchiorites alpina* (KILIAN, 1913), *Valdedorsella akuschaense* (ANTHULA, 1900), *Pseudohaploceras falcistriatum* (ANTHULA, 1900), *Diadochoceras nodosocostatum* (D'ORBIGNY, 1841) and *Sinzowia* sp. This association would be indicative of the upper Aptian *Nolaniceras nolani* Zone of the SMAZ. Unfortunately, the nominative index species is lacking in the corresponding fauna, and the age-diagnostic species *Diadochoceras nodosocostatum* (D'ORBIGNY, 1841) was not illustrated for further confirmation.

The study of new ammonite discoveries from Roussillon sheds new light on dating of the fifth unit of the Aptian-type series.

Geological context

The Luberon UNESCO Geopark mostly occupies the eye-shaped Apt plain bordered by the Luberon Massif to the south and by the mountains of the Monts de Vaucluse to the North. The rock basement of the Apt plain consists of shallow-marine biocalcarene-dominated platform carbonates dipping to the south (= Unit 1 of Moullade 1965). This is overlain by a ca. 80 m thick Aptian to lower Cenomanian



Text-fig. 1. Luberon UNESCO Geopark (Vaucluse, southern France), including localities cited in text (modified from Frau et al. 2017).

marine succession, starting with marly limestones and marls (Units 2 to 4 of Moullade 1965), transitioning upwards into sandy marls and variegated sandstones (Units 5 to 8 of Moullade 1965). This succession was deposited in the distal part of the Provence platform, opening northward to the Vocontian basinal settings (Tendil et al. 2018).

The yellowish marls of Unit 2 mark the final drowning of the Urganian series, dated by ammonites to the upper *Deshayesites forbesi* Zone *auctorum* (Frau et al. 2017, 2018). It has been shown that these yellowish marls are locally capped by a glauconitic discontinuity, including a short hiatus at the climax of Oceanic Anoxic Event 1a (Frau et al. 2017). This discontinuity is not reported by Moullade (1965), likely due to poor outcropping conditions at the time of logging. Above, Unit 3 consists of blueish marly limestones yielding large *Procheloniceras* SPATH 1923 ammonites, for which a description is pending. The age of Unit 3 thereby remains largely unclear, as none of the subsequent authors have yet found a new *in situ* record of this fauna. The following Unit 4 is the thickest one, consisting of ~ 57 m thick, dark grey-blue coloured marls, with dispersed pyritic nodules. It includes as its base a blueish marly interval yielding a rich pyritic ammonite fauna from the lower/upper Aptian boundary interval, which is the upper *Deshayesites deshayesi* Zone, *Dufrenoyia furcata* Zone and lower *Epicheloniceras martini* Zone (Dutour 2005, Frau et al. 2017, 2020). Only the lower part of the *Epicheloniceras martini* Zone is identified by ammonites, as they become rarer in the top of Unit 4.

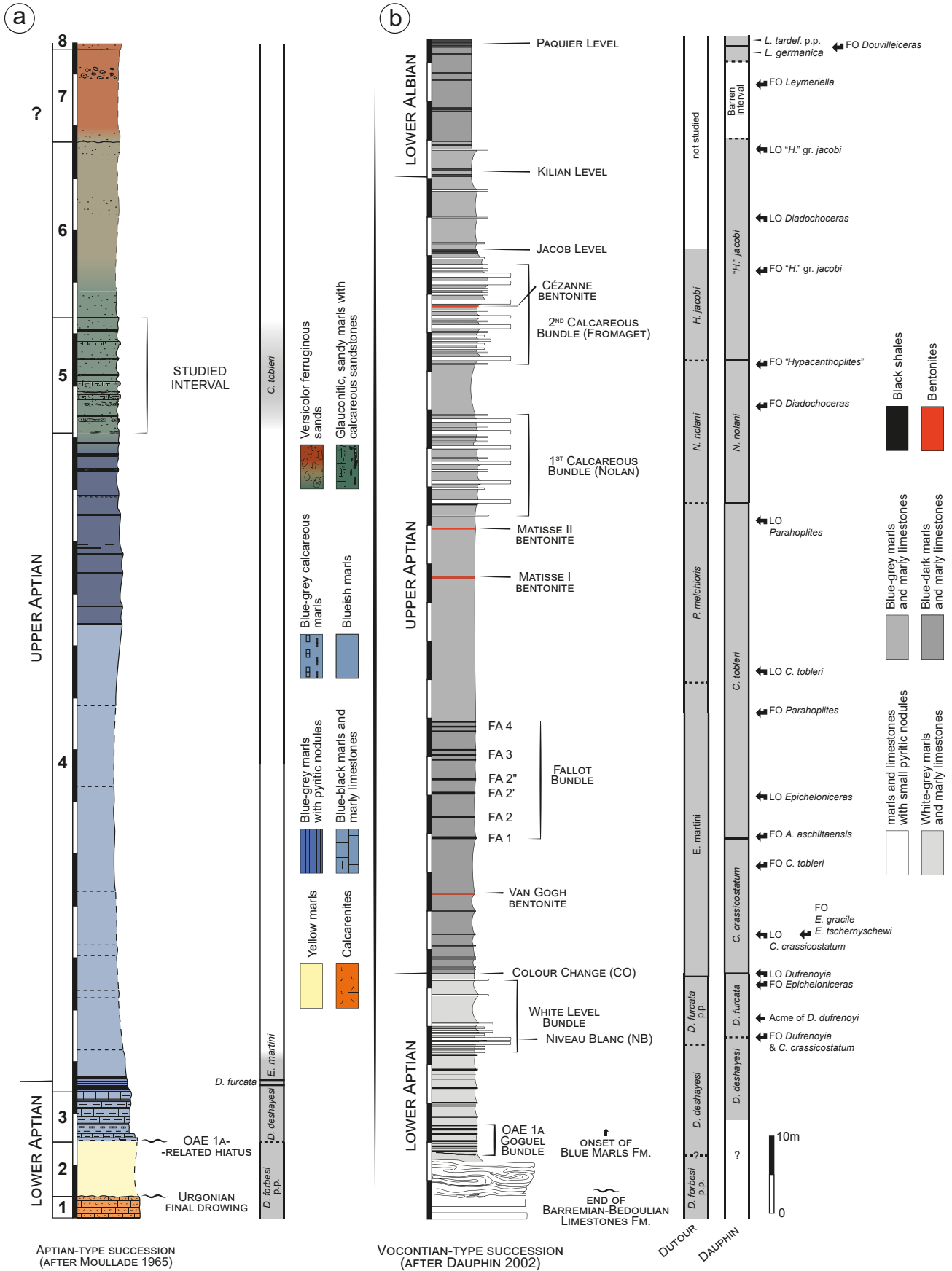
A rich ammonite fauna was collected in the overlying Unit 5 by Dutour (2005), taking advantage of an opportunity

made by the expansion of the wine cellar of Domaine de Château-Blanc at Roussillon. These works temporarily exposed a few meters of sandstones and sandy, glauconitic marls of the fifth unit. The ammonite specimens are preserved as crushed, internal moulds with phosphatised shells (Text-fig. 3a). Some of them are possibly mature individuals, as they have nearly complete body chambers with preserved peristomes. They occur with common bivalves *Plicatula* sp., *Panopea* sp. (Text-fig. 3b), rare belemnites *Hibolithes* sp. and nautiloids *Cymatoceras neckerianus* (Pictet, 1847) (Text-fig. 3c). The late palaeontologist Luc Georges Bulot had the opportunity to collect fossils from this temporary outcrop. This paper provides the first description of his material left to the present author before his recent passing (July 2022). The material will be housed at the Maison du Parc Naturel Régional du Lubéron after completion of its study.

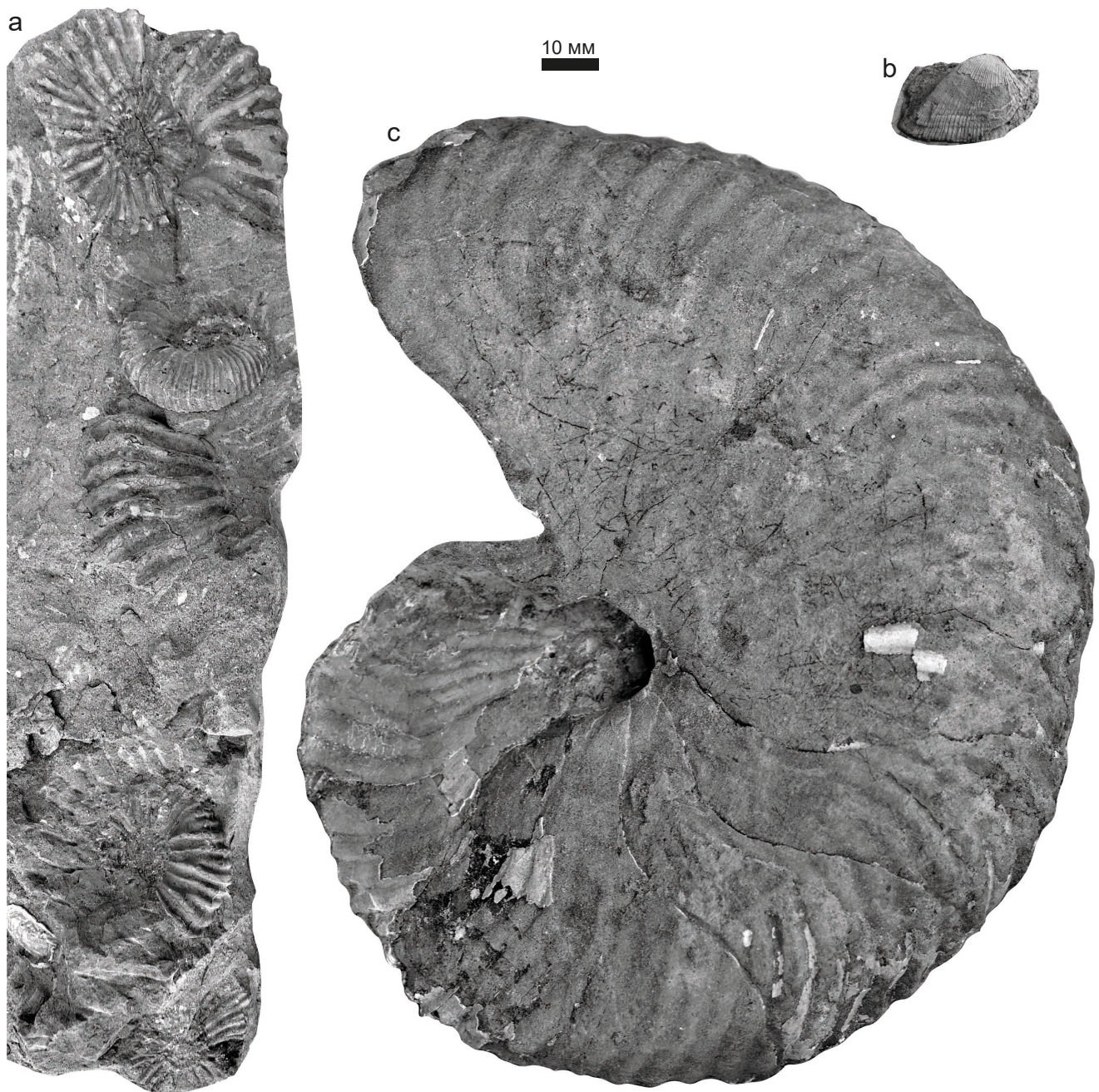
Palaeontological study

The suprageneric classification follows Hoffmann et al. (2022) and Frau et al. (2020).

In the paleontological description, mentions are made of the ornamental stages of basal Acanthohoplitidae: Ammonitella, Royerianum, Gargasense, Crassicostatum, and Tobleri – all defined by Frau et al. (2020). The reader is referred to this paper for the definitions of those ornamental stages. The following abbreviations indicate: D: total diameter; U: umbilical width; Wh: whorl height; Ww: whorl width. All dimensions are given in millimetres in Table 1. The suture terminology is that of Korn et al. (2003).



Text-fig. 2. a: Composite sedimentary column of Aptian-type area, reconstructed by Moullade (1965), including eight successive lithological units. **b:** Composite sedimentary column of Vocontian-type area reconstructed by Dauphin (2002), with main marker beds (Bréhéret 1997, Dauphin 2002, Dutour 2005). This is compared to Dauphin's and Dutour's ammonite zonation for Aptian Stage, with main ammonite bioevents.



Text-fig. 3. a: Rock sample showing various crushed, internal molds of ammonites with phosphatized shells. b: Bivalve *Panopea* sp. c: Nautiloid *Cymatoceras neckerianus* (Pictet, 1847). Scale bar 10 mm.

Superorder Ammonoida HAECKEL, 1866

Order Ammonitida HAECKEL, 1866

Superfamily Acanthohoplitoidea STOYANOW, 1949

Family Acanthohoplitidae STOYANOW, 1949

Genus *Egoianiceras* AVRAM, 1974

Type species. *Colombiceras angulatum* EGOIAN, 1969, by original designation.

Emended diagnosis. Diminutive acanthohoplitids, very small to moderate size, up to $D \sim 45$ mm: *E. angulatum* (EGOIAN, 1969), or possibly 60 mm: *E. multicostatum* (AVRAM, 1974)]. Shell shape discoidal ($Ww/D \sim 0,36-0,37$), strongly compressed ($Ww/Wh \sim 0,36-0,37$), very evolute ($U/Wh \sim 0,75-1$), subvirgacone coiling ($U/D \sim 0,33-0,37$). Whorl section compressed, subquadrate, sometimes with

flattened venter in juvenile, generally becoming suboval with rounded venter in adult. No evidence of ventral furrow at any growth stage. Four ornamental stages resembling those of *Colombiceras crassicostratum* (D'ORBIGNY, 1841). Embryonic (Ammonitella) stage poorly characterised, followed by short Royerianum stage, with reniform whorl section, crateriform umbilicus, spaced and flat-topped ribs angulate at shoulders or bearing small tubercles, smooth interspaces. Gargasense juvenile stage variable; sometimes long and gracile, made of dense, sharp, rather uniform, simple, bifurcate and intercalate ribs lacking tubercles, otherwise short and robust, made of irregular alternation of primary and secondary ribs. In that case, primary ribs are simple, bifurcate, rarely trifurcate, sometimes inflated, with or without tubercle-like thickenings at point of

Table 1. Measurements of Roussillon's specimens and selected types of species *Egoianiceras angulatum* (EGOIAN, 1969), *Egoianiceras lautum* (GLAZUNOVA, 1953), and *Egoianiceras exiquestata* (EGOIAN, 1969).

Species	Collection number	D	U	Wh	Ww	U/D	Wh/D	Ww/D	Ww/Wh	U/Wh
<i>Egoianiceras angulatum</i>	MEA-310	45	15.2	16.3	16	0.338	0.362	0.356	0.356	0.933
<i>Egoianiceras angulatum</i>	MEA-310	35	11.6	13.2	13	0.331	0.377	0.371	0.371	0.879
<i>Egoianiceras angulatum</i>	MEA-157 (= holotype)	29.5	10.3	11.5	11	0.349	0.390	0.373	0.373	0.896
<i>Egoianiceras angulatum</i>	MEA-311	25	8.6	9.5	9.3	0.344	0.38	0.372	0.372	0.905
<i>Egoianiceras angulatum</i>	MEA-312	23.5	7.7	8.8	8.9	0.328	0.374	0.379	0.379	0.875
<i>Egoianiceras angulatum</i>	LGB-ROU.2	-	-	15.3	-	-	-	-	-	-
<i>Egoianiceras angulatum</i>	LGB-ROU.4	-	9.7	14.5	-	-	-	-	-	0.669
<i>Egoianiceras angulatum</i>	LGB-ROU.5a	46	15	17.4	-	0.326	0.378	-	-	0.862
<i>Egoianiceras angulatum</i>	LGB-ROU.5b	36.35	12.96	14.1	-	0.357	0.388	-	-	0.919
<i>Egoianiceras angulatum</i>	LGB-ROU.6	-	-	24.78	15.5	-	-	-	-	-
<i>Egoianiceras angulatum</i>	LGB-ROU.13a	32.13	10.17	11.9	-	0.317	0.370	-	-	0.855
<i>Egoianiceras angulatum</i>	LGB-ROU.14	26.6	10.5	9.2	-	0.395	0.346	-	-	1.141
<i>Egoianiceras angulatum</i>	LGB-ROU.11a	59.4	21.5	20.4	10.3	0.362	0.343	0.173	0.173	1.054
<i>Egoianiceras angulatum</i>	LGB-ROU.12b	-	15.6	-	-	-	-	-	-	-
<i>Egoianiceras lautum lautum</i>	RAS-I	14	5	5.2	6	0.357	0.371	0.429	0.429	0.962
<i>Egoianiceras lautum lautum</i>	RAS-II	17.5	6	7	7	0.343	0.4	0.4	0.4	0.857
<i>Egoianiceras lautum lautum</i>	RAS-III	24	9	9	9.2	0.375	0.375	0.383	0.383	1
<i>Egoianiceras lautum laxa</i>	I	21.2	7.8	8	7	0.368	0.377	0.330	0.330	0.975
<i>Egoianiceras lautum laxa</i>	II	26.8	10	9.8	8	0.373	0.366	0.299	0.299	1.020
<i>Egoianiceras lautum laxa</i>	III	30	12.2	10.2	10	0.407	0.34	0.333	0.333	1.196
<i>Egoianiceras lautum laxa</i>	IV	30.5	11	12	11.4	0.361	0.393	0.374	0.374	0.917
<i>Egoianiceras lautum</i>	LGB-ROU.3	40.2	16.3	12.2	6	0.303	0.303	0.149	0.149	1.336
<i>Egoianiceras lautum</i>	LGB-ROU.10b	25.2	8.87	11.1	-	0.352	0.440	-	-	0.799
<i>Egoianiceras lautum</i>	LGB-ROU.11b	-	-	-	-	-	-	-	-	-
<i>Egoianiceras lautum</i>	LGB-ROU.11e	-	10.9	-	-	-	-	-	-	-
<i>Egoianiceras lautum</i>	LGB-ROU.12a	28	8.8	12.7	-	0.314	0.454	-	-	0.693
<i>Egoianiceras nolani exiquestata</i>	MEA-243	39	12	15.5	12.5	0.308	0.397	0.321	0.321	0.774
<i>Egoianiceras nolani exiquestata</i>	LGB-ROU.1	45	15.7	17	-	0.349	0.378	-	-	0.924
<i>Acanthohoplites</i> sp.	LGB-ROU.11d	34.3	10.5	12.8	-	0.306	0.373	-	-	0.820
<i>Parahoplites</i> sp	LGB-ROU.7	-	-	61.45	23.5	-	-	-	-	-
<i>Parahoplites</i> sp	LGB-ROU.8	125	24	58	-	0.192	0.464	-	-	0.414

furcation. Secondaries variable in number, generally one to four, atuberculate, sometimes bifurcate or coalescent on primaries. All ribs and branches tend to be flat-topped over venter. Progressive change toward short *Crassicostatum* sub-adult stage made of enlarged simple and bifurcate, rarely trifurcate primary ribs, separated by one or two, rarely three secondaries. No elongated tubercles at point of furcation of primaries. Ribbing changes into Tobleri adult stage, sometimes irregularly disposed but generally alternation of spaced, slightly flexuous, primary rib, with or without slight retrocurvature at umbilical margin, generally one secondary rib starting at variable height on flank. Ribs become sharper, but often cuneiform and flat-topped over venter. Peristome marked by smooth interspace, followed by discrete simple rib. Suture line quinquelobate. Ventral lobe has bifid median saddle. Umbilical lobe deeper than ventral lobe, rather symmetrical outlines with long central branch. First umbilical, inner, and dorsal lobes remain poorly characterised.

Remarks. With the introduction of the subgenus *Egoianiceras*, AVRAM (1974) separated the group of *Colombiceras crassicostatum angulata* EGOIAN, 1969 supposedly lacking lateral tubercles on the primary ribs of the early whorls. This species comes from mid-late Aptian aged outcrops of the Khokodz River Basin in southwestern Russia (Egoian 1969), but occurrences of the species were later reported from Romania (Avram 1974), Colombia (Sharikadze et al. 2004), SE France (Dauphin 2002), and northern Spain (Frau 2021a, b). Avram (1974) also erected the species *Colombiceras (Egoianiceras) multicostatum* AVRAM, 1974, based on Romanian *Colombiceras*, but the author failed to give a clear diagnosis for separating his taxon from *Colombiceras (Egoianiceras) angulatum* EGOIAN, 1969. Regarding this, Sharikadze et al. (2004) identified the lack of tubercles as a non-reliable diagnostic feature, because some of the type specimens of *Colombiceras (Egoianiceras) angulatum* EGOIAN, 1969 bear sort of tubercle-like thickenings on the early whorls, a detail previously noted by Egoian (1969: 163). On that basis, *Egoianiceras* has been discarded, or considered doubtfully necessary by subsequent authors (Sharikadze et al. 2004, Wright et al. 1996, Bogdanova and Mikhailova 2016).

The fact is that a distinction can be made between *Egoianiceras* and *Colombiceras*, thanks to the recent account of Frau et al. (2020) revising the type species *Colombiceras crassicostatum* (D'ORBIGNY, 1841). *Egoianiceras* is of smaller adult size, and possesses a more compressed subquadrate whorl section, with indistinct flattened venter in the early whorls. There is never a ventral furrow as in the juveniles of *Colombiceras crassicostatum* (D'ORBIGNY, 1841). Moreover, *Egoianiceras* more quickly reaches its adult shell morphology made of a suboval whorl section with a rounded venter. Regarding its ontogeny, *Egoianiceras* shares the post-embryonic Royerianum stage of *Colombiceras crassicostatum* (D'ORBIGNY, 1841), but the following Gargasense and *Crassicostatum* stages are reduced, attenuated or substantially modified, and never develop strong lateral tubercles on the primary ribs. However, some sort of thickenings can occur. Ribbing changes in the adult whorl into the Tobleri adult stage of *Colombiceras*

crassicostatum (D'ORBIGNY, 1841), but the ribbing is rather irregular, due to more common simple ribs, variable lengths of secondaries, the presence of additional primaries, and sharper ventral ribs over the venter. On the whole, we suggest keeping *Colombiceras* and *Egoianiceras* separate, pending a better understanding of their representatives and clarification of their phyletic relationships. This agrees with the earlier suggestions of Dauphin (2002), and Frau et al. (2020).

Specific content. Here we group into *Egoianiceras* the species *Egoianiceras angulatum* (EGOIAN, 1969), *Egoianiceras lautum* (GLAZUNOVA, 1953), and doubtfully, *Egoianiceras multicostatum* (AVRAM, 1974), pending revision. We provisionally refer to '*Egoianiceras*' the three subspecies *Acanthohoplites nolani exiquecostatus* EGOIAN, 1969, *Acanthohoplites nolani nolani* EGOIAN, 1969, and *Acanthohoplites nolani nodosus* EGOIAN, 1969, pending more material to be studied.

Through most of their distribution area, *E. angulatum* (EGOIAN, 1969), and *E. lautum* (GLAZUNOVA, 1953) co-occur, and seem to be linked by specimens intermediate in ribbing (see discussion below). Such specimens call for attention, as it has been proven that brady-*versus* tachymorphic ontogenetic development is the dominant controlling factor in the variability of basal acanthohoplites (Frau et al. 2020). Re-examination of *in situ* Trans-Caspian material is needed to solve the taxonomy of *Egoianiceras*.

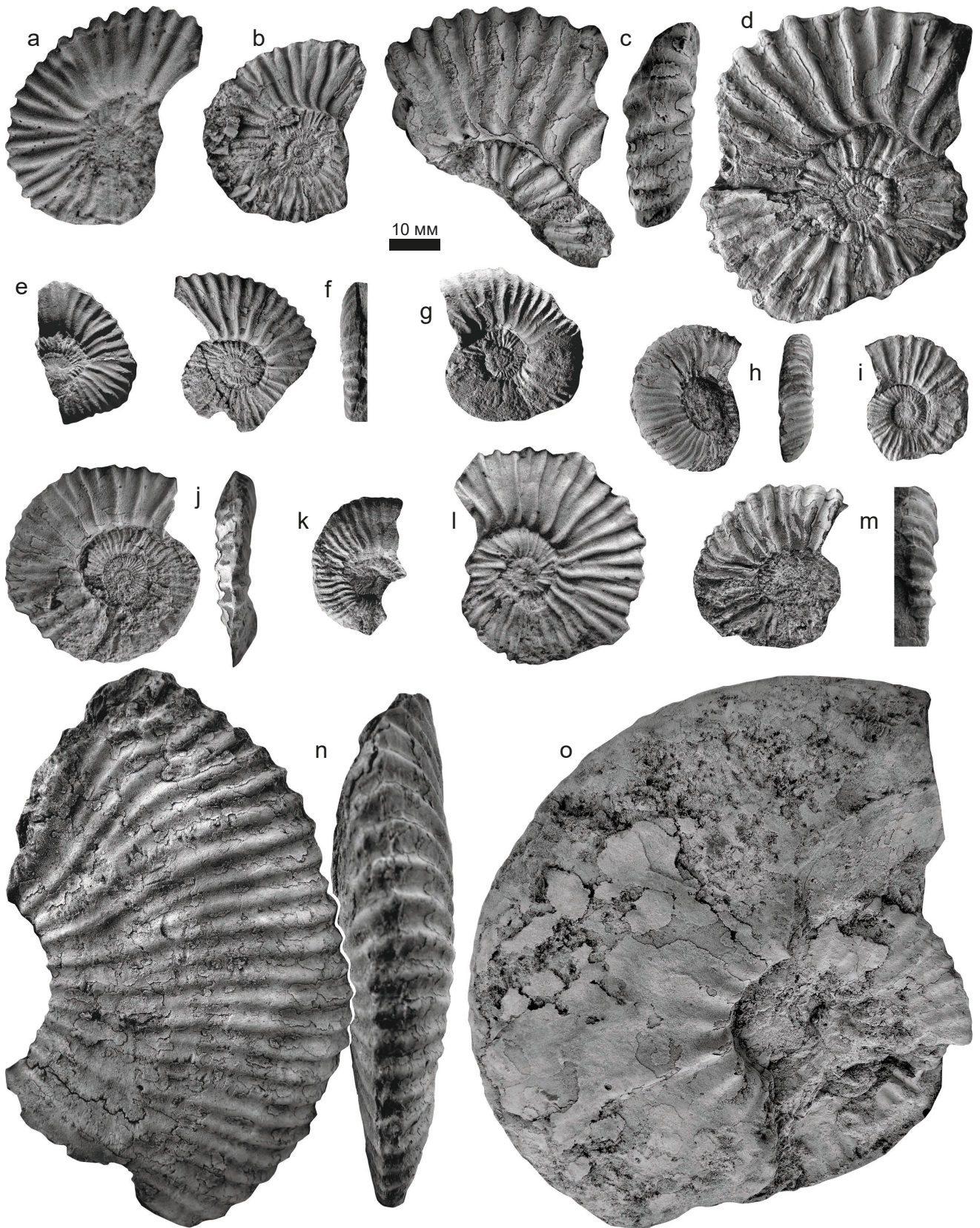
By comparison with the type species, *Egoianiceras multicostatum* (AVRAM, 1974) reaches a greater adult size (D = 60 mm), has almost twice as many ribs on the last whorl, and all of them are distinctly flexuous on the flank, becoming flat-topped and cuneiform over the venter. Bifurcate primaries are frequent through most of the ontogeny. These features bring it closer to the group of *Colombiceras caucasicum* (LUPPOV, 1949) according to Frau et al. (2020). Pending revision, the affinities between *Egoianiceras multicostatum* and *Colombiceras caucasicum* remains in doubt, particularly as Luppov (1949: 230) mentioned a short stage with distinct tubercles in the early whorls of the latter taxon.

***Egoianiceras angulatum* (EGOIAN, 1969)**

Text-fig. 4a–f

- 1969 *Colombiceras crassicostatum angulata* EGOIAN, p. 163, pl. XII, figs. 6a, b, v, 7a, b, v, 7a', 8a, b, v, 8a', 9a, b, pl. XXII, fig. 34.
- non 1974 *Colombiceras (Egoianiceras) cf. angulatum* EGOIAN; Avram, p. 5(3), pl. I, figs 3, 4, text-fig. 1 (= ?*Egoianiceras multicostatum*).
- non 1976 *Colombiceras (Egoianiceras) cf. angulatum* EGOIAN; Avram, p. 53(49), pl. VI, figs 2, 3, text-fig. 17 (= Avram 1974, pl. I, figs 3, 4, text-fig. 1).
- non 2004 *Colombiceras cf. angulatum* EGOIAN; Sharikadze et al., p. 389, pl. 50, fig. 2a–c, pl. 54, fig. 2a–c (= *Colombiceras gr. formosum*).

Type. Holotype designated by Egoian (1969: 163, pl. XII, fig. 7a–v) is specimen MEA-157 (coll. Egoian) from upper Aptian of Khokodz River Basin, Russia. Material deposited at All Russia Oil and Gas Scientific-Research Institute.



Text-fig. 4. Roussillon's specimens assigned to *Egoianiceras angulatum* (EGOIAN, 1969).

a: Specimen LGB-ROU.5a. b: Specimen LGB-ROU.5b. c: Specimen LGB-ROU.6. d: Specimen LGB-ROU.11a. e: Specimen LGB-ROU.14. f: Specimen LGB-ROU.4; *Egoianiceras lautum* (GLAZUNOVA, 1953). g: Specimen LGB-ROU.13. h: Specimen LGB-ROU.11b. i: Specimen LGB-ROU.10b. j: Specimen LGB-ROU.3. k: Specimen LGB-ROU.12a. ?*Egoianiceras exiquecostata* (EGOIAN, 1969). l: Specimen LGB-ROU.1; *Acanthohoplites* sp. m: Specimen LGB-ROU.11d; *Parahoplites* sp. n: Specimen LGB-ROU.7. o: Specimen LGB-ROU.8. Scale bar 10 mm.

Material. Ten specimens LGB-ROU.2, LGB-ROU.5a (Text-fig. 4a), LGB-ROU.5b (Text-fig. 4b), LGB-ROU.6 (Text-fig. 4c), LGB-ROU.11a (Text-fig. 4d), LGB-ROU.14 (Text-fig. 4e), LGB-ROU.4 (Text-fig. 4f), LGB-ROU.11e, and doubtfully LGB-ROU.10a and LGB-ROU.11c.

Description. Specimens LGB-ROU.4, LGB-ROU.5a, LGB-ROU.5b, LGB-ROU.11e, and LGB-ROU.14 are small, nearly complete, evolute ammonites. The body chamber occupies almost half of the outer whorl. The first visible whorls of specimen LGB-ROU.5b develop the ammonitella, and then a short Royerianum stage. This is followed by a densely ribbed Gargasense juvenile stage over one and a half whorls in other specimens. This progressively changes into a short Crassicostatum sub-adult stage over one whorl, with the rapid decrease of atuberculate secondaries between enlarged primaries. As growth increases, the ribs become much more spaced and cuneiform on the body chamber (= Tobleri stage), somewhat flat topped over the venter in specimen LGB-ROU.5a.

Specimen LGB.ROU.11a is a moderate-sized, evolute ammonite with an incomplete body chamber occupying half of the last whorl. The first visible whorls of the shell develop the Gargasense juvenile stage along nearly one and half whorls, changing into the Crassicostatum sub-adult stage over one whorl. Primary ribs are distinctly inflated, dominantly bifurcate, bearing strong thickenings on the posterior branches. Secondary ribs pass from four to two as growth increases. Ribbing changes abruptly into the Tobleri adult stage over three-quarters of the outer whorl. The peristome is not preserved. Specimens LGB.ROU.6 and LGB.ROU.12b are similar, but incomplete or badly crushed.

Specimen LGB-ROU.11c is a body chamber fragment of moderate size, showing a Tobleri stage, marked by the alternation of strong, slightly flexuous, primary ribs, with a slight retrocurvature at the umbilical margin and a single secondary starting at mid-flank. All ribs seem to be flat-topped over the venter.

Discussion. The type series of *Egoianiceras angulatum* (EGOIAN, 1969) shows a limited range of variability affecting the adult size, the robustness of the primary ribs during the Gargasense juvenile stage, and the strength of thickening at the point of furcation (Egoian 1969). Ventral ribs are about 35 over the last whorl, and this does not vary much in the type series. Most of the material from Roussillon falls within the range of variability of *Egoianiceras angulatum* (EGOIAN, 1969), with the exception of specimens LGB-ROU.6, 11a, and 12a. These three specimens are fairly close to the paratype MEA-310 figured by Egoian (1969: pl. XII, fig. 6), but they have inflated primary ribs during the Crassicostatum stage, bearing strong thickenings on the posterior branches. Then, the later growth stages conform with typical *Egoianiceras angulatum* (EGOIAN, 1969). These three specimens likely represent robust representatives of the variation series, and they should not be kept separate in a palaeobiological perspective. These strongly ribbed *Egoianiceras angulatum* (EGOIAN, 1969) seem to also be present in the *Parahoplites melchioris* Zone of the Kopet Dag (e.g., Glazunova 1953: pl. VIII, fig. 3a–b) and Turkmenia (e.g., Tovbina 1982: pl. I, fig. 3a, b), where they have been mixed up with *Acanthohoplites aschiltaensis*

(ANTHULA, 1900) and its junior synonym *Protacanthoplites abichi* (ANTHULA, 1900). A revision is needed.

Occurrence. The type series of *Egoianiceras angulatum* (EGOIAN, 1969) comes from the ‘zone with *Parahoplites melchioris* and *Colombiceras tobleri*’ of western Caucasus (Egoian 1969). These two latter taxa are widespread in the Mediterranean Tethys, and usually found in a rock interval between the upper *Epicheloniceras martini* Zone and the lower *Parahoplites melchioris* Zone of the SMAZ (Dauphin 2002). Elsewhere, *Egoianiceras angulatum* (EGOIAN, 1969), or allied forms, come from the *Parahoplites melchioris* Zone of the former soviet authors (Glazunova 1953, Tovbina 1982). Our record from Roussillon is the first reliable occurrence of *Egoianiceras angulatum* (EGOIAN, 1969) outside the Trans-Caspian regions, as the Romanian specimens better correspond to juveniles of *Egoianiceras multicostatum* (AVRAM, 1974), while those from Colombia better match the group of *Colombiceras formosum* SHARIKADZE, KAKABADZE et HOEDEMAEKER, 2004. In the Vocontian Basin of SE France, Dauphin (2002) reported the occurrence of *Egoianiceras angulatum* (EGOIAN, 1969) below the first black shale horizon (FA1) of the Falot episodes, which is a marker of the base of her *Colombiceras tobleri* Zone. Unfortunately, the material remains unfigured for confirmation.

Egoianiceras lautum (GLAZUNOVA, 1953)

Text-fig. 4g–k

- 1913 *Acanthohoplites aschiltaensis* (ANTHULA) var. *aplanata* SINZOW; Sinzow, p. 111, pl. 6, fig. 4.
1953 *Acanthohoplites lautus* GLAZUNOVA, p. 37, pl. V, figs 9a, b, 10, 11a, b, text-fig. 13.
1953 *Acanthohoplites lautum* var. *laxa* GLAZUNOVA, p. 38, pl. V, figs 12a–c, 13, 14, 15, text-fig. 14.
1953 *Acanthohoplites bigoti* var. *incivilis* var. nov. GLAZUNOVA, p. 36, pl. V, fig. 7a–v.
1953 *Acanthohoplites bigoti* SEUNES; Glazunova, p. 35, pl. V, figs 3, 4, 5a, b, 6, text-fig. 11.
1967 *Gargasicerias lautum lautum* (GLAZUNOVA); Dimitrova, p. 189, pl. LXXXIX, fig. 10.
1967 *Gargasicerias lautum laxa* (GLAZUNOVA); Dimitrova, p. 189, pl. XC, fig. 9.
?1967 *Gargasicerias aptiense* (ROCH); Dimitrova, p. 189, pl. 90, fig. 10.
?1987 *Acanthohoplites lautus* (GLAZUNOVA); Leshchukh, p. 129, pl. 15, figs 6, 7.
2008 “*Protacanthoplites*” aff. *lautus* (GLAZUNOVA); Moreno-Bedmar et al., fig. 1.

Type. There is no typification made in the literature, but Dimitrova (1967) and Leshchukh (1987) made repeated reference to Glazunova’s specimen (Glazunova 1953: pl. V, fig. 9a–v) from the upper Aptian of the western Kopet Dag, Turkmenistan. It is designated here as a lectotype, in agreement with Article 72 of the ICZN.

Material. Five specimens LGB-ROU.13 (Text-fig. 4g), LGB-ROU.11b (Text-fig. 4h), LGB-ROU.10b (Text-fig. 4i), LGB-ROU.3 (Text-fig. 4j), and LGB-ROU.12a (Text-fig. 4k).

Description. Specimens LGB-ROU.3 and LGB-ROU.12a are small, nearly complete, evolute ammonites. The body chamber occupies half of the outer whorl in the

former specimen. The ontogeny starts with a densely ribbed Gargasensis juvenile stage over one whorl. The transition with the Crassicostatum sub-adult stage is worn, followed by a typical Tobleri stage on the body chamber in specimen LGB-ROU.3.

Specimen LGB-ROU.10b is a very small, complete, evolute ammonite, with a body chamber occupying half of the outer whorl. The inner whorls are worn, followed by moderately dense Gargasensis juvenile stage over one and a half whorls. This changes progressively into a short Crassicostatum sub-adult. Bifurcate primary ribs bear discrete points of furcation high on the flank. The transition toward the Tobleri stage is worn. The latter is somewhat erratic, marked by dominant simple ribs, irregular in thickness, and irregularly disposed. The peristome seems to be present and composed of two smooth interspaces separated by distant single atuberculate ribs.

Specimen LGB-ROU.11b is a slightly distorted ammonite showing a dense Tobleri stage over its body chamber, occupying half of the outer whorl.

Discussion. The plexus *Gargasicerias lautum lautum* (GLAZUNOVA, 1953) and *Gargasicerias lautum laxa* (GLAZUNOVA, 1953) from the upper Aptian of Mangyshlak were tentatively re-assigned to *Egoianicerias* by Frau et al. (2020). Indeed, they show close ornamental affinities with the juveniles of *Egoianicerias angulatum* (EGOIAN, 1969) (compare with Glazunova 1953: pl. V, fig. 13 for example), but differ in a smaller adult size ($D \sim 30$ mm), an early acquisition of a rounded whorl section, and a more densely ribbed Gargasensis and Crassicostatum stage, in which primary ribs are discrete or erased. Differences between these two subspecies are found in rib density and its extent in the adult. Since both subspecies co-occur in Kopet Dag (Glazunova 1953), Bulgaria (Dimitrova 1967), SE France (this work), and possibly in Spain (Moreno-Bedmar et al. 2008), it is tempting to consider that they belong to the same variation series, and are here gathered into *Egoianicerias lautum* (GLAZUNOVA, 1953). The Tobleri stage is more often irregular than in *E. angulatum*. Here we identify a few specimens from the Kopet Dag (e.g., Glazunova 1953: pl. V, fig. 7) that are intermediate in ribbing between *Egoianicerias lautum* (GLAZUNOVA, 1953) and *Egoianicerias angulatum* (EGOIAN, 1969). Similar forms are found at Roussillon (e.g., Text-fig. 4g), reinforcing the view that both taxa may correspond to two extreme morphotypes of the same species.

Occurrence. The type material of *Egoianicerias lautum* (GLAZUNOVA, 1953) comes from the *Parahoplites melchioris* Subzone of western Kopet Dag (Glazunova 1953), and was later reported from the same zone in Bulgaria (Dimitrova 1967), SE Spain (Moreno-Bedmar et al. 2008), and doubtfully in Crimea (Leshchukh 1987).

?*Egoianicerias exiuecostatum* (EGOIAN, 1969)

Text-fig. 4l

?1960 *Acanthohoplites nolani* (SEUNES); Kudryavtsev, pl. XIII, fig. 4, text-fig. 117.

non 1968 *Acanthohoplites nolani* (SEUNES); Wiedmann and Dieni, p. 88, pl. IX, figs 10a–c, 17a, b, text-fig. 63a–c.

1969 *Acanthohoplites nolani exiuecostata* EGOIAN, p. 160, pl. XI, fig. 2a–v.

non 1979 *Acanthohoplites nolani exiuecostatus* EGOIAN; Vašíček, p. 331, pl. 1, fig. 1.

non 1983 *Acanthohoplites nolani exiuecostatus* EGOIAN; Menčík, pl. XLIII, fig. 2 (= Vašíček, 1979, pl. 1, fig. 1).

?1990 *Acanthohoplites nolani exiuecostatus* EGOIAN; Ivanov and Stoykova, pl. I, fig. 1.

non 2002 *Acanthohoplites nolani exiuecostatus* EGOIAN; Skupien and Vašíček, fig. 7.10 (= Vašíček, 1979, pl. 1, fig. 1).

Type. The holotype by monotypy is specimen MEA-243 (Egoian coll.) of Egoian (1969: 160 pl. XI, fig. 2a–v), from the upper Aptian of the Khokodz River Basin, Russia.

Material. A single specimen LGB-ROU.1 (Text-fig. 4l).

Description. The specimen corresponds to a small cast of an almost complete acanthohoplite ammonite. The body chamber occupies half of the outer whorl. The peristome is not preserved. Shell shape is characterised by a very evolute coiling. The first visible whorls develop an apparent compressed, subrectangular whorl section. The ornaments first consist of irregular, fine, simple primary and secondary ribs. Then, the primary ribs strengthen, thicken in the upper flank, and are separated by one or two secondary ribs of variable length and strength. The latter can be coalescent on the primaries at varying heights. This abruptly changes for an alternation of sharp, slightly flexuous primary ribs, and generally one fine secondary rib, starting at varying heights. Primary ribs develop a slight retrocurvature at the umbilical margin. Ribbing progressively changes into a Tobleri adult stage, comprising an alternation of spaced, slightly flexuous flat-topped primary rib, with a clear retrocurvature at the umbilical margin, and generally one secondary rib starting at a variable height on the flank.

Discussion. Based on the description of Egoian (1969), *Acanthohoplites nolani exiuecostata* EGOIAN, 1969 corresponds to a small acanthohoplite ammonite with an extremely discoidal ($Ww/D \sim 0.32$), strongly depressed ($Ww/Wh \sim 0.32$), very evolute ($U/Wh \sim 0.77$) subdiscocone coiling ($U/D \sim 0.31$). The whorl section is compressed and subquadrate, with a flattened venter in the juvenile, becoming suboval with convex flanks in the adult, and a flattened venter. There is no evidence of a ventral furrow. Although crushed, the specimen at our disposal very closely matches *Acanthohoplites nolani exiuecostata* EGOIAN, 1969. Other reports in the literature are either doubtful or outright incorrect, and need a revision.

The shell parameters and the character of the sculpture of *Acanthohoplites nolani exiuecostata* EGOIAN, 1969 strongly deviate from the type species *Nolanicerias nolani* SEUNES, 1887 as revised by Bulot et al. (2014). The species broadly conforms to the diagnosis of *Egoianicerias* given above, except that it has a continued flat venter over the outer whorl and a slender juvenile stage lacking strong primary ribs. Also, there is a lower number of secondary ribs than the type species *Egoianicerias angulatum*. *Acanthohoplites nolani exiuecostata* EGOIAN, 1969 is tentatively referred to as ?*Egoianicerias*, pending more material to be collected. Finally, it should be noted that the subspecies *Acanthohoplites nolani nolani* EGOIAN, 1969 non Seunes, 1887, and *Acanthohoplites nolani nodosa* EGOIAN, 1969 are

fairly close to *?Egoianiceras exiquecostata* (EGOIAN, 1969), differing only in a denser ribbing and strengthening of the peri-umbilical retrocurvatures of the primary ribs in the adult. A revision is needed.

Occurrence. The species *?Egoianiceras exiquecostatum* (EGOIAN, 1969) and the closely-allied forms from western Caucasus were reported from the *Acanthohoplites nolani* Zone of Egoian (1969). Correlation with the SMAZ is almost impossible, because the affinities and ranges of Caucasian “*Nolaniceras nolani* (SEUNES, 1887)” remain largely unclear with their west-European counterpart (Bulot et al. 2014).

Genus *Acanthohoplites* TOVBINA, 1970
(= *Protacanthoplites* TOVBINA, 1970)

Type species. *Parahoplites aschiltaensis* ANTHULA, 1900, by subsequent designation of Roman (1938).

Diagnosis. See details in Frau (2023).

Remarks. Frau (2023) recently confirmed that the genera *Protacanthoplites* and *Acanthohoplites* are synonyms, and the latter genus should be kept due to its publication date priority.

***Acanthohoplites* sp.**
Text-fig. 4m

Material. Specimen LGB-ROU.11d (Text-fig. 4m).

Description. Specimen LGB-ROU.11d is a small, incomplete ammonite. Ribbing of its body chamber, occupying one quarter of the outer whorl, consists of the alternation of strong primary ribs with distinctive elongated tubercles, and few, commonly two, atuberculate secondaries irregularly arranged. The tubercles of the primary ribs divide into two, rarely three, branches over the venter. Primary ribs can be followed by an approximated secondary rib, so that they mimic a constriction. All ribs cross the venter.

Discussion. Specimen is tentatively assigned to the genus *Acanthohoplites*, since its ribbing closely matches the Abichi stage of the type species *Acanthohoplites aschiltaensis* (ANTHULA, 1900) sensu Frau (2023).

Occurrence. In the Vocontian Basin of SE France, *Acanthohoplites* has its lowest occurrence datum between the first (FA1) and second (FA2) black shale levels of the Fallot episodes (Dauphin 2002). This falls in the lower part of her *Colombiceras tobleri* Zone, which is the lower part of the upper *Epicheloniceras martini* Zone of Dutour (2005).

Superfamily Parahoplitoidea SPATH, 1922
Family Parahoplitidae SPATH, 1922
Genus *Parahoplites* ANTHULA, 1900

***Parahoplites* sp.**
Text-fig. 4n, o

Material. Two specimens LGB-ROU.7 (Text-fig. 4n) and LGB-ROU.8 (Text-fig. 4o).

Description. Specimen LGB-ROU.7 is a moderate-size septated fragment. Ribbing is an alternation of dense,

sharp slightly flexuous, simple primary ribs and one or two secondary ribs, starting low on the flanks. All ribs pass over the venter rather straight. The umbilical wall is steep, almost recurved internally.

Specimen LGB-ROU.8 is a moderate-size incomplete ammonite. Ribbing of the inner whorls is an alternation of strong, slightly flexuous, simple primary and secondary ribs. Secondaries start at mid-flank. On the remaining body chamber, the ribbing is progressively less pronounced, eventually disappearing altogether. There remains a strong, regular peri-umbilical bullae with a slight retrocurvature, and uniform ribs over the upper flank and venter. The umbilical wall is steep, almost recurved internally.

Discussion. The Parahoplitidae *Parahoplites* is considered a cosmopolitan upper Aptian ammonite (Lehmann et al. 2015). The genus unfortunately suffered from extreme taxonomic splitting (Klein and Bogdanova 2013), and homeomorphy has led to erroneous taxonomic interpretations, in particular with the New World faunas (Ovando-Figueroa et al. 2018?). *Parahoplites* should be limited to the various Boreal-Atlantic species, for which the taxonomy needs simplification. The material at our disposal is not identified to the species level, due to defective preservation, but the greatest affinities are found with the species *Parahoplites grossouvrei* (JACOB, 1905) and *Parahoplites campichii* (PICTET et RENEVIER, 1854) for specimen LGB-ROU.8, while specimen LGB-ROU.7 is closer to *Parahoplites nutfieldensis* (SOWERBY, 1815).

Occurrence. The distribution of a *Parahoplites* assemblage has long been recognized in the Boreal-Atlantic Subrealm, and is identified to the *Parahoplites melchioris* Zone in the Caucasus and the *Parahoplites nutfieldensis* Zone in UK (Bogdanova and Mikhailova 2016, and references therein). Only rare occurrences are found in the adjacent areas, such as in the Vocontian Basin of SE France, where the genus is reported within (Dauphin 2002) or above (Joly and Delamette 2008) the Fallot black shale episodes.

Significance of the Roussillon ammonite fauna

The Roussillon ammonite fauna is a mixture of taxa usually found in a rock interval between the upper *Epicheloniceras martini* Zone and the *Parahoplites melchioris* Zone of the SMAZ, with the exception of *?Egoianiceras exiquecostata* (EGOIAN, 1969). This rock interval is known to include organic matter peak enrichments in the Vocontian Basin, defining the Fallot black shales (Bréhéret 1997). Those black shales result from intermittent oxygen-deficient bottom water conditions (Caillaud et al. 2022), and are associated with a deep renewal in ammonite assemblages (Dauphin 2002, Dutour 2005), including the entries of various Acanthohoplitidae and Parahoplitidae, viz. *Colombiceras tobleri* (JACOB et TOBLER, 1906) and *Egoianiceras* spp. below FA1, followed by *Acanthohoplites aschiltaensis* (ANTHULA, 1900) between FA1 and FA2, and *Parahoplites* spp. in FA4, and the disappearance of the Douvilleiceratidae *Epicheloniceras* spp. in FA2”. To better highlight this suite of bioevents, Dauphin (2002) amended the SMAZ and erected the *Colombiceras tobleri* Zone,

whose base is fixed at the entry of the nominative index species. A comparison between the Dauphin's and Dutour's zonation of the upper Aptian is provided, using a composite Vocontian-type sedimentary column (Text-fig. 2b).

Co-occurrence of *Egoianiceras* spp. and *Acanthohoplites* sp. at Roussillon matches well the faunal association from the lower part of the *Colombiceras tobleri* Zone of Dauphin (2002). The additional record of *Parahoplites* sp. at Roussillon further supports the recognition of the lower *Colombiceras tobleri* Zone. We do not find any evidence of *Diadochoceras* or *Nolaniceras* in the studied material, and a younger age for the fifth unit (i.e., *Nolaniceras nolani* Zone) suggested by Moullade (1965) and Dutour (2005) is not supported by the available material.

Comparison with planktonic foraminifera from the fifth unit reinforces our dating. It has been documented by Moullade et al. (2017), that the base of the *Globigerinelloides algerianus* Zone falls in the top of the fifth unit, based on the sampling performed at Gargas. The same event is recorded just above second Fallot black shales (FA2^o) in the Vocontian Basin (Dauphin 2002). The glauconitic sands of the fifth unit, including the studied phosphatized ammonites, can be thus confidently interpreted as the local sedimentary expression of the Fallot episodes.

Conclusion

Both ammonites and planktonic foraminifera from the Apt area support a correlation between the Fallot black shales and the glauconitic sands of the fifth unit of the Aptian-type series. We here confirm the spread in acanthohoplitid and parahoplitid ammonites at the transition between the *Epicheloniceras martini* Zone and the *Parahoplites melchioris* Zone of the SMAZ. This is dominated by relatives of the Acanthohoplitidae *Egoianiceras*, which show a large spectrum of variation, encompassing the group of species *E. angulatum* (EGOIAN, 1969) and *E. lautum* (GLAZUNOVA, 1953).

Acknowledgments

The author is grateful to Luc G. Bulot (1963–2022) for the donation of his Roussillon ammonites. Warm thanks are also due to Zuzana Heřmanová, Executive Editor of Fossil Imprint, Zdeněk Vašíček (Ostrava-Poruba), and an anonymous person for providing useful reviews.

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