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Itierella melognensis n.gen., n.sp., and Paradicostella hautevillelompnesensis n.gen., n.sp. (Ammonoidea, Neocomitidae, Neocomitinae), two new upper Valanginian trituberculated ammonoids from the Jura Mountains, eastern France

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Abstract: Several ammonoid specimens from the upper Valanginian (Lower Cretaceous) sedimentary succession of Hauteville-Lompnes, Department of Ain, eastern France, are assigned to the new genera and species *Itierella melognensis* n.gen., n.sp., and *Paradicostella hautevillelompnesensis* n.gen., n.sp. Specimens collected in the past were misidentified as *Acanthodiscus* UHLIG, 1905, and erroneously assigned to the lowermost part of the Hauterivian stage. The revision of the Marnes de Mélogne, along with the collection of a rich associated ammonite fauna, allows *Itierella* to be recognized as a latest Valanginian homeomorphic form of the genus *Acanthodiscus*, and *Paradicostella* as closely related to the genus *Dicostella* Busnardo, 1966. The Marnes de Mélogne are revised as mostly belonging to the upper *Saynoceras verrucosum* to *Criosarasinella furcillata* ammonite zones (uppermost Valanginian), while their uppermost metre is assigned to the *Acanthodiscus radiatus* Zone (lowermost Hauterivian).

Keywords:

- Lower Cretaceous;
- ammonite systematics;
- biostratigraphy;
- homeomorphism;
- lithostratigraphy

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Résumé: Itierella melognensis n.gen., n.sp., et Paradicostella hautevillelompnesensis n.gen., n.sp. (Ammonoidea, Neocomitidae, Neocomitinae), deux nouveaux ammonoïdes trituberculés du Valanginien des montagnes du Jura, Est de la France. Plusieurs spécimens d'ammonoïdes de la succession sédimentaire du Valanginien supérieur (Crétacé inférieur) de Hauteville-Lompnes, Département de l'Ain, Est de la France, sont attribués aux nouveaux genres et espèces Itierella melognensis n.gen., n.sp., et Paradicostella hautevillelompnesensis n.gen., n.sp. Des spécimens collectés dans le passé avaient été identifiés à tort comme Acanthodiscus UHLIG, 1905 et attribués à l'Hauterivien basal. La révision des Marnes de Mélogne et la récolte d'une riche faune d'ammonites associée permettent d'attribuer Itierella à une forme du Valanginien supérieur, homéomorphe au genre Acanthodiscus, et Paradicostella très proche du genre Dicostella Busnardo, 1966. L'âge des Marnes de Mélogne est révisé comme appartenant à l'intervalle compris entre la partie supérieure de la Zone à Saynoceras verrucosum et la Zone à Criosarasinella furcillata du Valanginien supérieur, tandis que le dernier mètre peut être attribué à la Zone à Acanthodiscus radiatus de l'Hauterivien inférieur.

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Mots-clefs:

- Crétacé inférieur ;
- systématique des ammonites ;
- biostratigraphie;
- homéomorphisme ;
- lithostratigraphie

1. Introduction

A large number of trituberculate ammonite species from the Berriasian to the Hauterivian stages have been historically assigned to the genus Acanthodiscus UHLIG, 1905, which soon became highly polyphyletic. A great deal of effort has later been invested in disentangling numerous homeomorphic forms, with the introduction of the genera Neocosmoceras Blanchet, 1922, Octagoniceras Spath, 1924, Transcaspiites Luppov & MIKHAILOVA, 1985, and Kilianites ÉNAY et al., 1998; for Berriasian forms, and Luppovella NIKOLOV, and Pseudacanthodiscus Baraboshkin, 1997, for lower Valanginian forms. Similarly, RAW-SON (1971) excluded certain northern European forms of the genus Acanthodiscus, which he presented in inverted commas, namely 'Acanthodiscus' ebergensis (Weerth, 1884), 'A.' bivirgatus (WEERTH, 1884), 'A.' confusus Spath, 1924, 'A' n.sp. a and 'A' n.sp. b, which are probably related to the genus Endemoceras THIERMANN, 1964. Consequently, Acanthodiscus is currently regarded as a natural group of forms that is up to now exclusively confined to the basal Hauterivian sedimentary series from Tethys and Boreal-Atlantic Subrealm (MUTTERLOSE et al., 1996, 2021). BUSNARDO and THIEULOY (1989) have provided a comprehensive list of its specific composition.

A set of ammonites with polygonal whorl section and trituberculated ribbing has been collected over the past few decades by several collectors from natural outcrops and from building sites in the vicinity of Hauteville-Lompnes, in the Bugey area, of the meridional Jura Mountains (Ain Department, France; Fig. 1). In general appearance, these ammonites resemble either the Hauterivian genus *Acanthodiscus* or *Dicostella* Busnardo, 1966.

The first occurrence (FO) of the ammonite genus *Acanthodiscus* defines the base of the Hauterivian stage (MUTTERLOSE *et al.*, 1996, 2021), while the faunal association of the Marnes de Mélogne is mostly that of the upper Valanginian *Neocomites peregrinus* and *Criosarasinella furcillata* zones. A detailed examination of the collected specimens reveals significant differences compared to the genus *Acanthodiscus*. These homeomorphic morphotypes are here described as a new genus and a new species *Itierella melognensis* n.gen., n.sp.

Furthermore, an isolated specimen, similar to *Dicostella* but with strong ventro-lateral tubercles, is presently described as a new genus and species *Paradicostella hautevillelompnesensis* n.gen., n.sp.

2. Material and methods

The ammonites described in this contribution were collected by Mr Bruno Hugon (B.H.), who spent several decades investigating the Lower Cretaceous marlstones of the Hauteville-Lompnes area for its fossils. Mr Gustavo Pierangelini (G.P.) contributes to this study with a high-quality specimen used as the holotype of one of the two new genera described. These marlstones, designated here as the Marnes de Mélogne, are situated in the lowermost part of the Grand Essert Formation (Fig. 2) defined by Strasser et al. (2016, 2018). A partial lithological log of the Marnes de Mélogne is provided by Busnardo et al. (1966) at the type locality on the Mélogne stream.

In this study, four natural sections and earthworks (Fig. 3) have been investigated in recent decades by the second author (B.H.): Chomarasse quarry (geographical WGS 84 coordinate system: 46°00'50"N, 5°34'43"E, altitude 805 m), Le Crêt (45°58'42"N, 5°36'02"E, altitude 801 m), Pré Frais (45°59'14"N, 5°35'21"E, altitude 784 m) and Mélogne (45°58'03"N, 5°36'39"E, altitude 830 m). The four sections permit a comprehensive overview of the lithological succession of the Marnes de Mélogne.

The specimens illustrated and measured here are held in the private collections of the second (B.H.) and the third (G.P.) authors. However, plaster casts are deposited in the 'Muséum cantonal des sciences naturelles' at Lausanne, Geology department (MGL), Switzerland.

The photographed specimens were previously whitened with ammonium chloride and photographed using the High Dynamic Range (HDR) method at three different light intensities (underexposed, normal, overexposed).

Morphometric measurements were taken with a caliper and expressed in millimetres, with values assessed to tenths of a millimetre. The estimated values are presented in brackets. All the dimensions of the specimens are given in millimetres. Abbreviations: D = diameter, Wb = whorl breadth, Wh = whorl height, U = umbilical diameter.





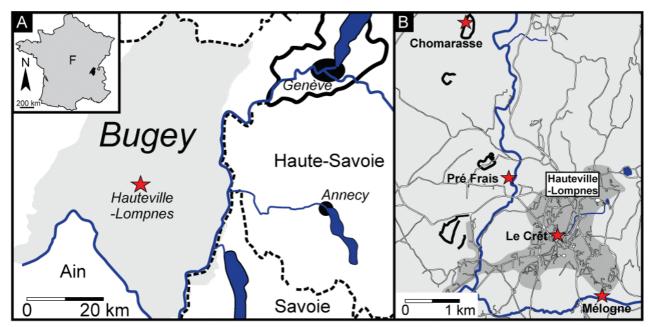


Figure 1: A. Map showing of the city of Hauteville-Lompnes in the Bugey, Ain Department, eastern France. **B.** Location of the four sections (red stars) studied around Hauteville-Lompnes.

3. Description of the sections

3.1 Chomarasse quarry

The Chomarasse quarry (Fig. 4.A-C) is exploited for the extraction of building stone. The lithostratigraphic sequence is composed from bottom to top by:

- Unit 1: Choin d'Hauteville (CH, Fig. 4.A) about ten to fifteen metres of light pinkishwhite to slightly yellow limestone in thick,
 massive and compact beds forming a bar. The
 upper surface is commonly karstified where it
 crops out. The Choin d'Hauteville is the exploited limestone (e.g., ÉNAY, 1989). It contains a fauna of nerineids gastropods, echinoids, and corals. The top is marked by a
 bored hardground coated with an iron crust;
- Unit 2: Calcaire roux (CR, Fig. 4.A) 1.8 metres of cross-bedded, yellow-brown, coarse-bioclastic limestone containing abundant crinoid, bryozoan, and brachiopod remains. The top is marked by a bored hardground coated with an iron crust (Fig. 4.B);
- Unit 3: Marne jaune de Morteau (MJM, Fig. 4.C) - 10 centimetres of yellow, plastic marlstone, extremely fossiliferous, delivering some Olcostephanus sp. and Valanginites nucleus (ROEMER, 1841);
- Unit 4: Marnes de Mélogne (Fig. 4.A) about 7 metres of marlstones divided into three subunits: a lower, 2.5 metres thick sandy marlstone (Lower sandy marlstones), a middle, 2.5 metres thick and less indurated sandy marlstone (Upper sandy marlstones), and an upper, two metres thick marlstone with extremely fossiliferous nodular marly-limestone intercalations (Coquina-rich marlstones), which delivered Karakaschiceras cf. companyi Reboulet, 1996, and Dicostella sp.

3.2 Pré Frais

The Pré Frais section is a natural hillside outcrop, strongly vegetated, which displays the same lithological succession of the Marnes de Mélogne as in the Chomarasse Quarry. The base of the lower sandy marlstones delivered *Karakaschiceras biassalense* (Karakasch, 1889). The exact source location in the section of a specimen assigned to *K. pronecostatum*? (Felix, 1891) is unknown but may also derive from this unit. The Coquina-rich marlstones are characterised by yellow marls, just below the soil, which provided *ex situ K. cf. companyi, Neocomites* sp., *Olcostephanus* sp., *Oosterella* sp. cf. *ondulata* (Reboulet, 1996), and *Himantoceras gigas* (Thieuloy & Bulot, 1993).

3.3 Le Crêt

The Le Crêt section was an ephemeral section excavated during the construction of a building (Carrefour supermarket). This section allowed the observation of the upper half of the Marnes de Mélogne and their transition to a first crinoidal limestone bundle, belonging to the "Pierre jaune de Neuchâtel" facies (yellow bioclastic and oolithic limestone). What appears to be the base of this section was excavated in several places in the village and produced Karakaschiceras cf. companyi, Neolissoceras desmoceratoides (WIEDMANN, 1966), Itierella melognensis n.gen., n.sp., Olcostephanus densicostatus (WEGNER, 1909), and an unidentified ammonite. A specimen of Tescheniceras sp. was collected ex situ. It is likely that this ammonite originated from a higher level within the section, when compared to the nearby Mélogne section. The original stratigraphic position of these ammonites within the coguina-rich marlstone remains uncertain.



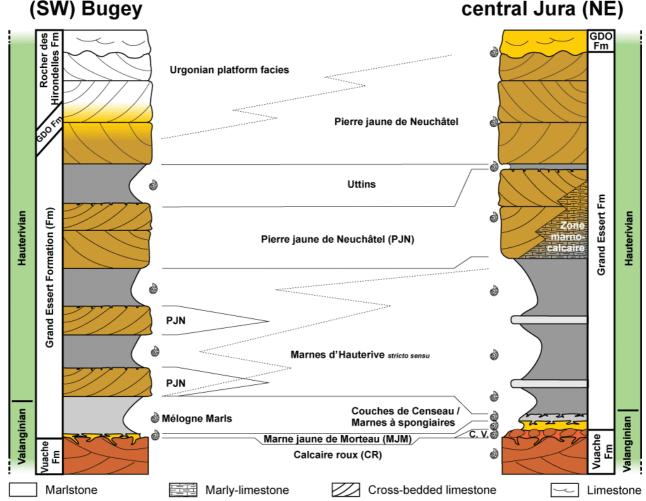


Figure 2: Comparison of the Valanginian and Hauterivian lithological series between the Bugey and central Jura. Lithological log of the central Jura modified after GODET *et al.* (2010).

3.4 Mélogne

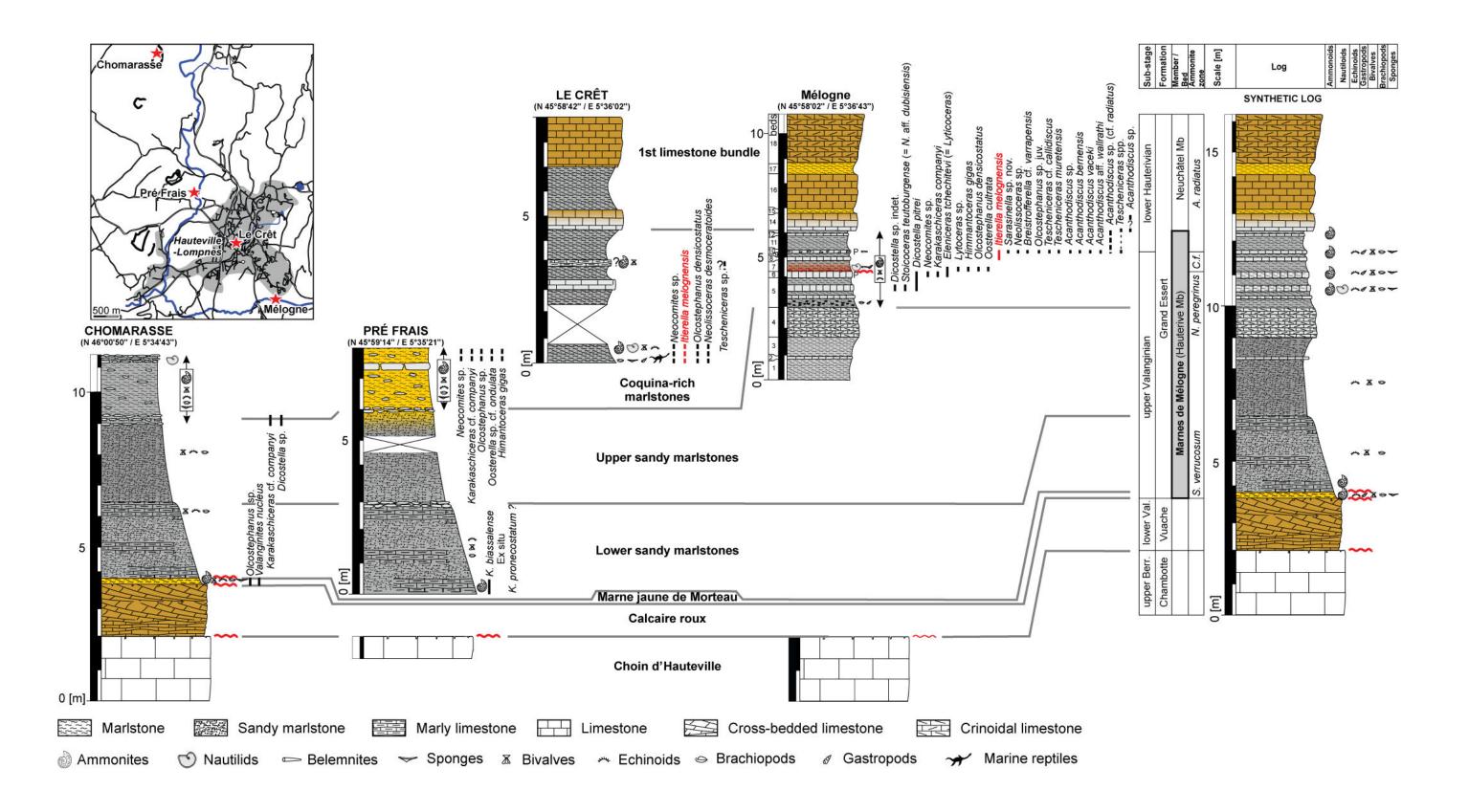
The Mélogne stream section is located between Hauteville and Cormaranche, upstream of the Cascade bridge. The stream is incised into marlstones, which can be observed on the left bank in a succession of small cliffs topped with limestone (Fig. 4.D). Going upstream, the following succession - previously described in detail by BUSNARDO et al. (1966) - can be observed:

- Massive limestones of the Choin d'Hauteville cropping out downstream of the road, at the waterfall;
- The Marnes de Mélogne with around 6 metres of sandy, alternating marlstones and marly limestones. The lower two metres are devoid of fossils, while the 3-metre interval, above a 1-metre-thick crinoidal bed, is very fossiliferous and contains a rich in situ ammonite fauna. The fauna, from bottom to top, includes Dicostella sp., Stoicoceras teutoburgense (WEETH, 1884), Dicostella pitrei BUSNARDO, 1966, Neocomites sp., Karakaschiceras companyi, Eleniceras tchechitevi BRESKOVSKI, 1967, Lytoceras sp., Himantoceras gigas, Olcostephanus sp., Oosterella cultrata (ORBIGNY,
- 1841), Itierella melognensis n.gen., n.sp., Sarasinella n.sp., Neolissoceras sp., Breistrofferella cf. varappensis (BAUMBERGER, 1906), Acanthodiscus sp., A. bernensis (BAUMBERGER, 1906), A. vaceki (NEUMAYR & UHLIG, 1881), A. aff. wallrathi BAUMBERGER, 1906, Olcostephanus sp. juv., Tescheniceras cf. callidiscus THIEULOY, 1971, T. muretensis BREISTROFFER, 1936, and T. spp. Beds 6 to 10 display indications of condensation. Partial phosphatisation of the fossils was observed in bed 6 and especially in bed 10 (P in Fig. 3). A considerable number of ferruginous ooids and bioclasts were observed at the base of bed 7.
- 5 metres of a yellow, crinoidal limestone bundle of "Pierre jaune de Neuchâtel" (PJN) facies, with at its base Acanthodiscus? sp. and Tescheniceras sp.

▶ **Figure 3:** NW to SE correlation of the four sections across the Hauteville-Lompnes syncline.

The occurrence of macrofossils and the stratigraphic distribution of ammonite species are reported on the right side of the logs. A synthetic log of the Marnes de Mélogne lithostratigraphical unit is given to the right.







3.5 Hauteville-Lompnes

In various earthworks in the city of Hauteville-Lompnes, a number of ammonites were discovered. These included *Criosarasinella* cf. *subheterocostata* REBOULET, 1996, *Dicostella pitrei*, *D.* cf. *houdardi* (ROMAN, 1933), *Karakaschiceras* cf. *companyi*, *Neocomites* sp., *Olcostephanus densicostatus*, *Eleniceras tchechitevi*, *Itierella melognensis* n.gen., n.sp., *Paradicostella hautevillelompnesensis* n.gen., n.sp., and other enigmatic neocomitids that remain undetermined.

4. Litho- and biostratigraphy

The upper Valanginian record begins on top of the Calcaire roux with yellow marlstones, which are frequently observed along the Jura Mountain range. These typically comprise coquina-rich marlstones with episodic marly-limestone intercalations and can attain thicknesses of several metres in the Central Jura. In most cases, these deposits are reduced to a few decimetres in thickness and contain a rich fossil content, indicative of sedimentary condensation (Donze & Thieuloy, 1975). In the literature, these marls are frequently designated as "Marnes jaunes à Ammonites Astierianus" (Desor & Gressly, 1859) or "Marne jaune de Morteau" (RENEVIER, 1874). These open-marine marlstone deposits are characterised in particular by the presence of Saynoceras verrucosum (ORBIGNY, 1841) (SAYN, 1889, p. 684), which indicates the lower part of the S. verrucosum Zone (BULOT, 1990). This age is confirmed in the Hauteville syncline by the presence of Valanginites nucleus, which has the same stratigraphic range as Saynoceras verrucosum (see THIEULOY, 1977a; BU-LOT, 1990).

The above Marnes de Mélogne can be considered as lateral equivalents of the eastern Couches de Censeau (French Jura Department; MARCOU, 1859, p. 123) and the Marnes à Bryozoaires / Marnes à Spongiaires (Swiss Vaudois Jura; PICTET & CAMPICHE, 1858 -1860; JACCARD, 1869; SCHARDT, 1895) due to their lithostratigraphic position between the Marnes jaune de Morteau and the Hauterivian series, and also because of their ammonite faunas. Both eastern facies are typically present below the Marne d'Hauterive stricto sensu and show a very reduced thickness, ranging from a few decimetres to a few metres, indicative of condensation in the Central Jura. In the Hauteville syncline, the Marnes de Mélogne are fully developed and show no signs of condensation except at their top. The ammonites present in the Marnes de Mélogne are mostly restricted to the upper part of the formation. Ammonites are typically well preserved, with internal limestone moulds lying horizontally in the strata. Body chambers are not always preserved. This is generally attributed to a bias in the fossilisation process, whereby the phragmocone is more mineralised than the body chamber, which is filled with marlstones. No evidence of reworking or lateral winnowing of the fossils was observed; nor were bioencrusted. The ammonites in beds 8 to 10 from the Mélogne section are less well preserved than those on other beds due to the presence of more bioclastic sediment. From the perspective of biostratigraphy, the most ancient age indices are derived from the Pré Frais section. Karakaschiceras pronecostatum?, collected ex situ, indicates the presence of the K. pronecostatum Subzone, probably from the Lower sandy marlstones. This age attribution is corroborated by Karakaschiceras biassalense, which was collected near the base of the Lower sandy marlstones of the Pré Frais section. Younger age indices are obtained from the Coquina-rich marlstones on the Mélogne section. Dicostella pitrei, found in bed 5, is reported by BULOT in MOJON et al. (2013) from the upper part of the Saynoceras verrucosum Zone (Karakaschiceras pronecostatum Subzone) and the lower part of the Neocomites peregrinus Zone (N. peregrinus Subzone). The associated Stoicoceras teutoburgense is reported from the Dichotomites bidichotomoides and lowermost Stoicoceras tuberculata zones of northwest European Province (= upper Neocomites peregrinus Zone, Olcostephanus nicklesi Subzone and the extreme base of the Criosarasinella furcillata Zone; see Reboulet et al., 2014). According to REBOULET (1996), the sudden appearance of Eleniceras tchechitevi, Himantoceras gigas, Oosterella cultrata, and Karakaschiceras companyi at the base of bed 7, followed by abundant Tescheniceras Vašíček, 2020, in bed 10, indicates the Criosarasinella furcillata Zone. Bed 10 shows a slight overlap of uppermost Valanginian and lowermost Hauterivian faunas. This faunal overlap, together with the slight phosphatisation of the fossils, suggests subtle condensation around the Valanginian - Hauterivian boundary. However, no evidence of reworking was observed. According to REBOULET et al. (1992) and REBOULET (1996), an ammonoid turnover occurred at the boundary of the Valanginian and Hauterivian, and has been interpreted as the response of nektonic organisms to eustatic and climatic changes, probably towards warmer sea-water temperatures. THIEULOY (1977b) defined the base of the Hauterivian stage and the base of the Acanthodiscus radiatus Zone by the first occurrence of the ammonite genus Acanthodiscus, essentially following the opinion of PAQUIER (1900).

▶ Figure 4: A. Overview of the Chomarasse quarry and the lithostratigraphic units composing it. CH = Choin d'Hauteville. CR = Calcaire roux. B. Detail of the bored hardground on top of the Calcaire roux. C. Detail of the Marne jaune de Morteau (MJM) sandwiched between the Calcaire roux and the Lower sandy marlstones (LSM) of the lower Marnes de Mélogne. D. Section through the upper Marnes de Mélogne consisting of the Upper sandy marlstones and the Coquina-rich marlstones, and overlain by the first Pierre jaune de Neuchâtel (PJN) unit.







5. Systematic palaeontology

Superfamily Perisphinctoidea STEINMANN, 1890 Family Neocomitidae SALFELD, 1921 Subfamily Neocomitinae ? SALFELD, 1921 Genus Itierella n.gen.

Type species. *Itierella melognensis* n.gen., n.sp.

Derivatio nominis. A tribute to Jules ITIER (1802-1877), customs inspector for the Ain department and geologist. ITIER is renowned for his pioneering contributions to the study of the Lower Cretaceous of the Bugey region.

Locus typicus. Mélogne section, Hauteville-Lompnes, Ain Department, eastern France.

Stratum typicum. Beds 8 to 10, Coquina-rich marlstones of the Marnes de Mélogne, Hauterive Member, Grand Essert Formation, *Criosarasinella furcillata* to lowermost? *A. radiatus* zones.

Diagnosis. Ammonite morphologically very close to the genus *Acanthodiscus*. Hexagonal whorl section higher than wide. Main ribs bearing prominent tubercles at the umbilical shoulder, lateral at mid-flank, and on the ventro-lateral border. Main ribs regularly bifurcated from the lateral tubercle. Few single intercalated ribs on the outer whorl, starting on the umbilical edge, bearing strong lateral and ventro-lateral tubercles. Flat, smooth, and narrow venter, progressively becoming concave between ventro-lateral tubercles.

Content. The genus is currently monospecific.

Stratigraphic and geographic distribution.Coquina-rich marlstones of the Marnes de Mélogne, Grand Essert Formation, Jura Mountains.

Affinities and differences. The genus *Itierella* is distinguished by its hexagonal whorl section and robust trituberculate ribbing, which closely resemble those of the genera *Distoloceras* HYATT, 1900, *Acanthodiscus* and to a lesser extent to the immature *Dicostella* (Fig. 6).

According to HYATT (1900), the type-species of the genus Distoloceras is Hoplites hystrix (PHIL-LIPS), based on the specimens of NEUMAYR and UHLIG (1881, Pl. XLII, fig. 3; Pl. XLVI, fig. 4), and not that of PHILLIPS. However, the two illustrated specimens do not show bifurcations of the lateral tubercles. Conversely, the lectotype of of NEUMAYR and UHLIG's specimens (NEUMAYR & UHLIG, 1881, Pl. XLVI, fig. 4) exhibits ribs branching from the umbilical tubercle into the ephebetic whorls, whereas at the same diameter Itierella displays single ribs at the umbilical border. In Distoloceras only the main ribs are tuberculated on the siphonal rim, whereas in Itierella the ribs are uniformly tuberculated on the siphonal border. In Distoloceras, the lateral tuberculation appears after the shell reaches a diameter of 30 mm, whereas it is already present at a diameter of less than 10 mm in *Itierella*.

Itierella can be distinguished from Acanthodiscus by its distinctive ornamentation style, which resembles to the internal whorls of the genus Sarasinella UHLIG, 1905. This ornamentation is characterised by trituberculate ribs, which bifurcate from an umbilical and/or mid-flank tubercle and alternate in outer whorls with weaker and less strongly tuberculated single ribs. Acanthodiscus, also present in the Mélogne section (bed 10), appears later, at the base of the Hauterivian. In our species, perisiphonal tubercles are twice as numerous as the median tubercles and in some ribs the ratio is even 1:1 (Fig. 6). In contrast, the number of perisiphonal tubercles in Acanthodiscus is usually triple that of median tubercles (BUSNARDO et al., 1966). This lower number and decreasing ratio of lateral/umbilical tubercles is found only in Acanthodiscus vaceki (NEUMAYR & UHLIG, 1881). In Acanthodiscus, the ventrolateral tubercles are tight and small, sometimes clavate, whereas in Itierella they are prominent, round to clavate on the body chamber, and widely spaced (Fig. 6). The intercalated ribs in Acanthodiscus are relatively short, beginning in the upper third of the flank. In contrast, the ribs in Itierella are considerably longer, beginning at or near the umbilical shoulder. The species Acanthodiscus wallrathi shows similarities with Itierella, in particular, in the rounded and widely spaced tubercles, the presence of intercalated ribs which may extend up to the umbilical shoulder, and the dominance of well-spaced simple ribs on the external whorls. It should be noted that the single-rib stage of the holotype is teratological and may result from damage during shell development. Acanthodiscus wallrathi differs in having an isometric whorl section, whereas in Itierella it clearly becomes higher than wide. Furthermore, the venter is large in Acanthodiscus wallrathi, whereas it is narrow in Itierella. Finally, Acanthodiscus wallrathi was collected in the Marnes d'Hauterive of the Neuchâtel area (Swiss Jura Mountains) and is likely to belong to the lowermost Hauterivian stage. In contrast, Itierella is actually restricted to the uppermost Valanginian stage. The poor preservation of the suture line in Itierella specimens does not allow a comparison with that of Acanthodiscus.

Itierella n.gen. melognensis n.sp. (Fig. 5.A-E)

Synonymy.

? 1908 Acanthodiscus Euthymi.- BAUMBERGER, p. 10, Fig. 102, Pl. 21, fig. 2a, 2b

Holotype. Specimen MGL.110474 (Fig. 5.D-E), collected in the Coquina-rich marlstones of the Marnes de Mélogne, Coll. G. PIERANGELINI.

Derivatio nominis. Species named after the Mélogne stream, where the holotype was collected.

Material. Four calcareous internal moulds from the Coquina-rich marlstones. The holotype MGL.110474 and three paratypes, MGL.110471 from Le Crêt section, MGL.110472 from Mélogne section, and MGL.110473 from Hauteville-Lompnes.



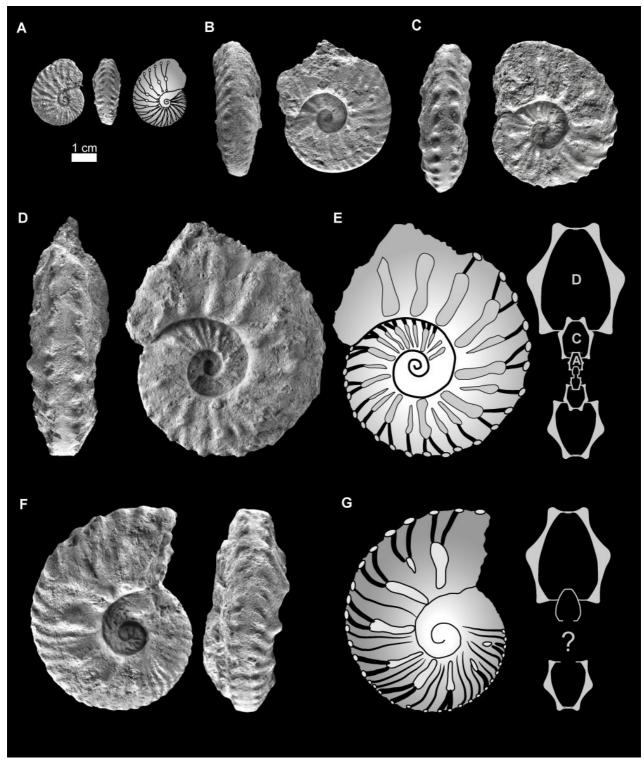


Figure 5: A-C: Itierella melognensis n.gen., n.sp., paratypes, coll. B. Hugon, from the Coquina-rich marlstones subunit. A MGL.110471 from Le Crêt section, B. MGL.110472 from Mélogne section, C. MGL.110473 from Hauteville-Lompnes. D-E. Itierella melognensis n.gen., n.sp., holotype, coll. G. PIERANGELINI, MGL.110474, Coquina-rich marlstones subunit from Mélogne section, unknown position within beds 8 to 10. F-G. Paradicostella hautevillelompnesensis n.gen., n.sp., holotype, coll. B. Hugon, MGL.110475, Coquina-rich marlstones subunit from Hauteville-Lompnes.

Diagnosis. As for the genus.

Description. Specimen MGL.110471 (Fig. 5.A) is a small-sized calcareous mould (D = 27.24 mm) of grey colour. The umbilicus is narrow (U/D = 0.22). The whorl section is subhexagonal in shape, higher than wide (Wb/Wh = 0.73). The

flanks are parallel in the lower half and converge in the upper half. The venter is flat and smooth. The umbilical wall is vertical and joins the flanks at a blunt right angle. Up to a diameter of 20 mm, the ornamentation consists of prorsiradiate, falcoid ribs bifurcating from the umbilical tubercle.



All ribs bifurcate from the lateral tubercle, which is located on the upper third of the flank. The secondary ribs are projected forward and terminate in a ventro-lateral tubercle that is slightly stretched towards the siphon. From 20 mm in diameter, all ribs originate singly from the umbilical tubercle and become more radially arranged, resulting in a perfectly homogeneous ornamentation. The ventro-lateral tubercles gradually lie down on the edge of the ventral band with an oblique orientation. The suture line is not visible due to the small size of the specimen and the nature of the sediment.

Specimen MGL.110472 (Fig. 5.B) is a moderately large calcareous mould (D = 52.00 mm) of grey colour. The umbilicus is narrow to moderately evolute (U/D = 0.30). The whorl section is subhexagonal, higher than wide (Wb/Wh = 0.72). The flanks are slightly divergent in the lower half and then convergent in the upper half. The venter is slightly rounded and smooth. The umbilical wall is convex and moderately high with a rounded umbilical shoulder. From a diameter of 45 mm, simple intercalated ribs are observed with weaker umbilical and lateral tubercles. The ventro-lateral tubercles spread out on the edge of the ventral band with an oblique orientation. The suture line is indistinguishable due to bioclastic nature of the internal mould.

Specimen MGL.110473 (Fig. 5.C) is a moderately large calcareous mould (D = 57.87 mm) of grey colour. The umbilicus is moderately evolute (U/D = 0.32). The whorl section is subhexagonal, and higher than wide (Wb/Wh = 0.69). The flanks are slightly divergent in the lower half and then convergent in the upper half. The venter is slightly rounded and smooth. The umbilical wall is vertical, with a rounded umbilical shoulder. From a diameter of 30 mm, two simple intercalated ribs are visible, with vestigial umbilical and lateral tubercles. All ribs are clearly forward-projecting on the upper third of the flanks and bear a ventrolateral tubercle. All tubercles are prominent. The ventro-lateral tubercles are somewhat obliquely elongated. From a diameter of 50 mm, the venter becomes concave between the ventro-lateral tubercles. The suture line is partially visible but not amenable to study.

Specimen MGL.110474 (Fig. 5.D-E) is a moderately large calcareous mould (D = 81.20 mm) of grey colour. The umbilicus is moderately evolute (U/D = 0.35). The whorl section is subhexagonal, and higher than wide (Wb/Wh = 0.73). The flanks are slightly divergent in the lower half and then convergent in the upper half. The venter is slightly rounded and smooth. The umbilical wall is vertical with a rounded umbilical shoulder. Internal whorls are poorly preserved but we observe rigid prorsiradiate ribs bearing umbilical and lateral tubercles. Some ribs are more robust than others and more strongly tuberculated. On the

outer whorl, we observe that the more robust ribs (main ribs) bifurcate from the lateral tubercle and alternate with one to exceptionally two weaker single ribs with less prominent umbilical and lateral tubercles. The ventro-lateral tubercles are somewhat obliquely elongated and the venter becomes concave between the ventro-lateral tubercles. The suture line is indistinguishable due to bioclastic nature of the internal mould.

Measurements (in mm).

Cat. num.	D	U	Wb	Wh	U/D	Wb/Wh
MGL.110471	27.24	6.10	9.45	13.00	0.22	0.73
MGL.110472	52.00	15.67	15.64	21.81	0.30	0.72
MGL.110473	57.87	18.73	17.48	25.24	0.32	0.69
MGL.110474	81.20	28.27	23.71	32.38	0.35	0.73

Discussion. Specimens show a gradually increasing umbilical width index (U/D) from 0.22 to 0.35, due to an increasing rate of evolution of the coiling. The whorl width index is stable between 0.69 and 0.73.

Stratigraphic and geographic distribution. As for the genus.

Genus Paradicostella n.gen.

Type-species. *Paradicostella hautevillelompne-sensis* n.gen., n.sp.

Derivatio nominis. Genus close (marginally) to the genus *Dicostella* Busnardo, 1966.

Locus typicus. Hauteville-Lompnes, Ain Department, eastern France.

Stratum typicum. Coquina-rich marlstones of the Marnes de Mélogne, Hauterive Member, Grand Essert Formation. Found in earthworks in association with ammonites from the *Neocomites peregrinus* and/or *Criosarasinella furcillata* zones.

Diagnosis. Hexagonal whorl section higher than wide. Main ribs trituberculated, umbilical, lateral at midflank, and ventro-lateral. Ribs regularly bifurcated from the lateral tubercle. Flat, smooth and narrow venter. Two single, sigmoidal, intercalated ribs between each pair of strong ribs on the phragmocone, starting on the umbilical edge and ending on the ventro-lateral edge with a round tubercle. One or no intercalated rib on the outer whorls.

Content. The genus is currently monospecific.

Stratigraphic and geographic distribution. Neocomites peregrinus and/or Criosarasinella furcillata zones from the Coquina-rich marlstones of the Marnes de Mélogne, Grand Essert Formation, of the Jura Mountains. Olcostephanus nicklesi Subzone from bed Be 103, Formation 12, boundary between V5-V6 units, La Bégude, Alpes de Haute-Provence in SE France (THIEULOY et al., 1990). Unknown level in the Troyes region, Paris Basin (GOGUEL, 1940).



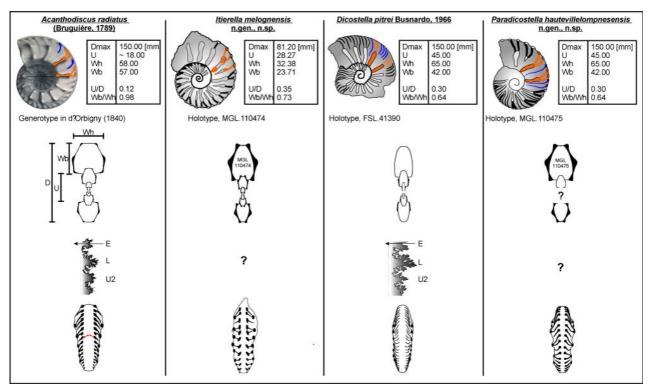


Figure 6: Comparative table of the trituberculated genera present in the Hauteville-Lompnes syncline with *Acanthodiscus* UHLIG, 1905, *Itierella* n.gen., *Dicostella* BUSNARDO, 1966, and *Paradicostella* n.gen. The morphology, ornamentation and suture line are compared.

Affinities and differences. The genus Paradicostella exhibits strong similarities to the genus Dicostella (Fig. 6) and more particularly with D. tuberculatum (ROMAN, 1933) and D. pitrei, with which the similarities in the rate of involution, the shape of the section, and the ornamental style are striking. However, the genus Paradicostella differs from Dicostella essentially in that it exhibits strong ventro-lateral protuberances (Fig. 6). In contrast, Dicostella always has obliquely oriented ribs on the ventro-lateral border, which may be somewhat angular as in the inner whorls of *D. tuberculate* and *D. pitrei*, but never clearly tuberculated. In Paradicostella, the venter can become markedly concave between the tubercles, whereas it is flat to convex in *Dicostella* (Fig. 6). In Paradicostella, one or two secondary ribs extend from the lateral tubercle, whereas in Dicostella they are usually double or triple.

GOGUEL (1940, Pl. III, fig. 4) illustrated an ammonite from the Pietresson de Saint-Aubin collection from near Troyes (Aube, France), which he attributed to *Acanthodiscus radiatus*. This specimen shows very clearly, in the inner whorls, ribs bifurcating in the lower third of the flanks. The last half-whorl exhibits a significant spacing of the main ribs, which bear a pronounced median tubercle that is more developed than the umbilical tubercle. Additionally, there are two intercalated ribs, which are visible towards the umbilical edge and exhibit a pronounced strengthening towards the venter. There is little doubt that this specimen belongs to the new genus and species *Paradicostella hautevillelompnesensis*.

THIEULOY *et al.* (1990) described and illustrated (*op. cit.*, Pl. IV, figs. 5-6) a morphotype, left in open nomenclature, which is distinguished by its well individualised margino-ventral clavi, and coming from their *Olcostephanus nicklesi* Horizon (= current subzone).

Paradicostella n.gen. hautevillelompnesensis n.sp.

(Fig. 5.F-G)

Synonymy.

1940 Acanthodiscus radiatus (BRUGUIÈRE).- GOGUEL, Pl. III, fig. 4.

1990 Dicostella sp. inc. - THIEULOY et al., Pl. IV, figs. 5-6.

Holotype. Specimen MGL.110475, collected in the Coquina-rich marlstones of the Marnes de Mélogne, Coll. B. Hugon.

Derivatio nominis. Species named after the city of Hauteville-Lompnes, Ain Department, eastern France, where the holotype was collected.

Material. One calcareous internal mould.

Diagnosis. As for the genus.

Description. Specimen MGL.110475 (Fig. 5.F-G) is a moderately large calcareous mould (D = 82.43 mm) of grey colour. The umbilicus is moderately evolute (U/D = 0.30). The whorl section is subhexagonal, and higher than wide (Wb/Wh = 0.66). The flanks are slightly divergent in the lower half and then convergent in the upper half. The venter is slightly rounded and smooth, and progressively becomes concave between the ventrolateral tubercles. The umbilical wall is vertical to convex, with a well-rounded umbilical shoulder. Up to a diameter of 65 mm, two to three simple,



sigmoidal, intercalated ribs are visible, with no umbilical or lateral tubercles. All ribs are clearly forward projected on the upper third of the flanks and bear a ventro-lateral tubercle. At a diameter larger than 65 mm, all tubercles are very prominent. The ventro-lateral tubercles are somewhat obliquely elongated. In this specimen, the bifurcation of the primary ribs persists until the end of the shell. The suture line is not visible.

Measurements (in mm).

Cat. num.	D	U	Wb	Wh	U/D	Wb/Wh
MGL.110475	82.43	24.84	23.50	35.76	0.30	0.66

Discussion. A single specimen was collected ex situ during earthworks in the city of Hauteville-Lompnes together with other upper Valanginian ammonites usually observed in the Coquina-rich marlstones.

Stratigraphic and geographic distribution. As for the genus.

6. Phyletic discussion

The morphology of the ammonite shells is favoured trough natural selection, through its environmental and intra- and/or interspecific competitive factors (adaptive selection). It is generally accepted that homeomorphy between two taxa could be the result of a morphofunctional adaptation linked to a similar way of life like the occupation of the same ecological niche. Because of its mode of development and of growth, the ammonites shell has great potential to develop homeomorphies between different taxa that may or may not belong to different lineages and/or at very different times (BERT et al., 2020). Furthermore, some of the homeomorphs discussed here may share a very close genetic heritage as members of a possible evolutionary lineage, as well as homeomorphy by parallel evolution.

6.1. About the phyletic position of *Itierella* n.gen.

Itierella has internal whorls strikingly similar to those of Sarasinella, with trituberculate ribs that bifurcate from an umbilical and/or mid-flank tubercle and alternate in outer whorls with much weaker and less strongly tuberculated single ribs. Itierella n.gen. is moreover found alongside forms attributed to Sarasinella, a genus which is present throughout the Valanginian according to REBOULET (1996). However, Reboulet points out that the upper Valanginian forms are characterised by an acceleration of ontogenetic development, with a shorter trituberculate pattern, less development of the external bullae and a lower frequency of bifurcated ribs on the median tubercle. Indeed, the specimens found at Hauterville-Lompnes closely reflect this phyletic trend. In contrast, Itierella n.gen. shows a completely opposite phyletic trend with the conservation and reinforcement of the initial trituberculate stage throughout the shell, as far as is known from the rare specimens discovered. Furthermore, according to Company (1987), the genus Sarasinella forms a well-characterised and morphologically homogeneous group that develops along the lower Valanginian "Thurmanniceras" pertransiens and Neocomites neocomiensiformis zones. On the contrary, the upper Valanginian and lower Hauterivian forms attributed to Sarasinella appear sporadically and without stratigraphic continuity and probably do not belong to Sarasinella. At the present time, establishing a phyletic link between Itierella and Sarasinella is challenging. However, an origin in upper Valanginian genera with strongly trituberculate inner whorls appears to be the most plausible hypothesis (Fig. 7). Itierella n.gen., shows a homeomorphy by convergence with Paradicostella n.gen. and Acanthodiscus.

6.2. The Neohoploceras - Dicostella - Acanthodiscus plexus

The genus *Dicostella* was introduced by Busnardo *et al.* (1966) to accommodate a fairly heterogeneous group of Neocomitidae from the upper Valanginian of the Tethys and Boreal realms (Kemper *et al.*, 1981; Thieuloy *et al.*, 1990), characterised by strong, most often tuberculated, primary ribs, somehow homeomorphic to the early late Valanginian *Neohoploceras* Spath, 1939, and early Hauterivian *Acanthodiscus*.

COMPANY (1987) had considered a possible phylogenetic relationship between the genera *Karakaschiceras* THIEULOY, 1971, and *Dicostella*. BULOT (1990) proposed an origin of *Dicostella* from the genus *Neohoploceras*, due to the importance of the peri-umbilical fasciculations preceding the establishment of the thickened primary ribs with medio-lateral bulges.

Busnardo et al. (1966) suggested that Dicostella could lead to Acanthodiscus because of their similar ornamentation. THIEULOY (1977b) expressed reservations about the proposed emergence of the genus Acanthodiscus from Dicostella because of the absence of latero-ventral clavi and the suture line, which is more endemoceratid than leopoldiid. Neohoploceras, the parent genus of Dicostella strains, has ventro-lateral tubercles, a feature that is clearly present in primitive forms, and that tends to disappear in more evolved Dicostella species. However, in the internal whorls of evolved Dicostella the ribs clearly form an angulation on the ventro-lateral margin and it is therefore not difficult to imagine that they could return to tubercles. In such case, it would be an example of iterative evolution, which leads to the reappearance of the ancestral phenotype under environmental pressure (selection pressure; BERT et al., 2020). In this sense, the phyletic link between Dicostella and Acanthodiscus is provided by the reappearance of latero-ventral tubercles as in the new genus Paradicostella (Fig. 7). Several tabular representations of the phyletic relationships between elements of the neocomitid fauna of the late Valanginian and early Hauterivian have been proposed for the relationships of Dicostella with related genera (Busnardo et al., 1966; Thieuloy, 1971, 1977b).



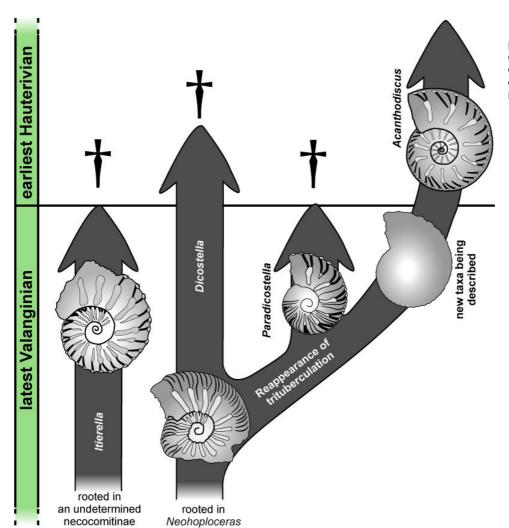


Figure 7: Presumed phylogeny of *Itierella* n. gen. and *Paradicostella* n. gen. in the upper Valanginian to basal Hauterivian interval.

7. Conclusions

A significant number of trituberculate species from the Berriasian to the Hauterivian have been historically attributed to the genus Acanthodiscus, which has subsequently become highly polyphyletic. Extensive research has been conducted to elucidate the relationships between these homeomorphic forms. The individualisation of the latest Valanginian genera Itierella n.gen. and Paradicostella n.gen. represents a further step in the understanding of Early Cretaceous 'Acanthodiscidlike' morphologies. The 'Acanthodiscid-like' phenotype is regularly observed in species with no phyletic relationship, indicating that the process is iterative and could be the result of a morphofunctional adaptation related to similar living conditions on platform-border environments.

Furthermore, the revision of the faunas of the Marnes de Mélogne, including the specimens collected by Busnardo *et al.* (1966), allows for the positioning of the Valanginian-Hauterivian boundary in the Hauteville-Lompnes sector, 1 m below the first units of the Pierre jaune de Neuchâtel, which is consistent with the proposal of Strasser *et al.* (2018, Fig. 10).

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Nomenclatural note:

Life Sciences Identifier (LSID)

https://zoobank.org/References/C449E2D2-2C18-4C61-B51C-0D014BDFF56B

Genus Group

• Itierella PICTET, HUGON & PIERANGELINI, 2025

https://zoobank.org/NomenclaturalActs/2143B922-385E-449C-82B4-82E54CFA43C5

• Paradicostella Pictet, Hugon & Pierangelini, 2025

https://zoobank.org/NomenclaturalActs/9194DB39-D607-4BF1-AB05-E98E0FF489D0

Species Group

• Itierella melognensis Pictet, Hugon & Pierangelini, 2025

https://zoobank.org/NomenclaturalActs/DB6107A6-8945-4E69-B19A-60939961FF3D

• Paradicostella hautevillelompnesensis Pictet, Hugon & Pierangelini, 2025

https://zoobank.org/NomenclaturalActs/3FC44CF4-9697-4296-947F-DCF372FEA74D