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Review

On the Rarity and Peculiarity of the Early Toarcian (Lower Jurassic) Leukadiellinae Ammonites—Systematic Review and Insights on the Interplay of Environmental Stress, Evolution and Biodiversity †

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Abstract: The subfamily Leukadiellinae Macchioni and Venturi, 2000 includes the two rare genera *Leukadiella* Renz, 1913 and *Renziceras* Arkell, 1953. Genus *Leukadiella* is characterised by ornamental and structural features unusual to the family Hildoceratidae Hyatt, 1867; for this reason, it has been occasionally grouped with other "odd" representatives of this family, as, for instance, *Frechiella* Prinz, 1904 and *Paroniceras* Bonarelli, 1893. While *Renziceras* comprises only one species, the eleven species currently recognised within *Leukadiella* show a noticeably discontinuous variability field; together with rarity of findings, the interpretation of this variability represents a renowned obstacle to their classification and phylogenetic reconstruction. Following an analysis of the morphological characters commonly used for defining *Leukadiella* species, a revised taxonomic scheme is herein proposed. Two clusters of characters are defined, based on which two morphologically distinct groups of species are distinguished, referred to as Helenae Group and Ionica Group. The genus name *Leukadiella* is maintained for species of the Helenae Group, which are restricted via synonymy to *Leukadiella helenae* Renz, 1913 and *Leukadiella jeanneti* Renz, 1927. The new genus name *Neoleukadiella* gen. nov. is proposed for species of the Ionica Group, which, by analogous limitation, are *Neoleukadiella ionica* Renz and Renz, 1946 and *Neoleukadiella gallitellii* Pinna, 1965. The reduction in the number of species from eleven to four is consistent with their rarity and limited paleogeographic distribution. The closely related *Renziceras* is considered the direct progenitor of *Leukadiella*; in turn, the Apennine genus *Cingolites* Sassaroli and Venturi, 2010 is proposed as transitional between *Hildaites* Buckman, 1921 and *Renziceras*. Conversely, the progenitor of *Neoleukadiella* remains uncertain, although a possible relationship between *Leukadiella* and *Neoleukadiella* species is tentatively traced. Finally, some challenging assumptions are made by emphasizing the role of environmental stress in controlling developmental dynamics that may drive striking phenotypic modification, of the kind observed in the Leukadiellinae species.

Keywords: Rosso Ammonitico; *Leukadiella*; *Neoleukadiella*; paleopathology; epigenetics

Citation: Ridente, D. On the Rarity and Peculiarity of the Early Toarcian (Lower Jurassic) Leukadiellinae Ammonites—Systematic Review and Insights on the Interplay of Environmental Stress, Evolution and Biodiversity. *Geosciences* **2022**, *12*, 411. https://doi.org/10.3390/geosciences12110411

Academic Editors: Jesus Martinez-Frias, Pierre Pellenard, Emanuela Mattioli and Guillaume Dera

Received: 26 July 2022
Accepted: 4 November 2022
Published: 9 November 2022

1. Introduction

Ammonites are among the most known fossils, due to their abundant and global fossil record. They uncover a multiform evolutionary history spanning a time interval exceeding 300 Ma, from the middle Palaeozoic to the end of the Mesozoic Era. In many localities, ammonites form exceptionally rich fossil assemblages, locally forming "lumachella" rocks. For instance, several fossil-rich beds occur in the Rosso Ammonitico Formation of the Apennines, an alternation of marly limestones and clayey marls marking the basal part (Toarcian-Aalenian) of the Umbria-Marche Basin fill [1–3]. This is a several hundred meters thick carbonate-to-siliclastic succession, recording the Lower Jurassic-Oligocene evolution of the Tethys Ocean [4–13].

Hildoceratids are decidedly the most representative group in the Toarcian Rosso Ammonitico, in some intervals overwhelmed in abundance only by phylloceratids. The majority of hildoceratid species is typically described based on rich collections, reaching up to hundreds of exemplars in the case of the utmost representative genus *Hildoceras* Hyatt, 1867 [14]. Therefore, what should one conclude if a screening of the literature would reveal that less than 30 specimens of *Leukadiella* Renz, 1913 [15] have been documented from all the known Italian localities? *Renziceras* Arkell, 1953 [16], the other genus within the subfamily Leukadiellinae Macchioni and Venturi, 2000 [17], is also infrequent, counting even less findings than *Leukadiella* (only 9 worldwide based on literature data). Moreover, *Leukadiella* and *Renziceras* show morphological peculiarities (e.g., coarse clavate ribs, ventral tubercles, nodes, and spines) by which the phylogenetic relationships with other representatives of the Hildoceratidae remain puzzling. However, whereas *Renziceras* is represented only by *Renziceras nausikaae* (Renz, 1913) [15], *Leukadiella* includes up to eleven species, some displaying marked morphological differences (Figure 1).

Altogether, rarity and peculiarity of *Leukadiella* and *Renziceras* have, on one hand, hampered the understanding of the evolutionary mechanisms and pathways by which this group arose from earlier hildoceratids; on the other, they offer an intriguing playground for emphasizing the riddle of the evolutionary or paleo-environmental meaning of rare and morphologically peculiar species in the fossil record; although, given the limited findings, many assumptions remain speculative.

Based on the review of existing data, a new classification of *Leukadiella* species is proposed, along with an attempt at reconstructing possible evolutionary scenarios consistent with the limited morphological and stratigraphical record of *Leukadiella* and related genera. In particular, the peculiarity and variability of morphological characters are analysed in the light of the main phylogenetic and evolutionary hypotheses proposed in the literature, according to which *Leukadiella* descends directly from *Bouleiceras* Thévenin, 1906 [18] or, alternatively, from *Hildaites* Buckman, 1921 [19], *Mercaticeras* Buckman, 1913 [20] or *Orthildaites* Buckman, 1923 [21], either directly or via *Renziceras* [17,22–25]. Finally, the Apennine genus *Cingolites* Sassaroli and Venturi, 2010 [26] also from the early Toarcian, is herein added to the list as a possible precursor of *Renziceras* and *Leukadiella*. Among the diverse processes by which any of the possible evolutionary scenarios may have been accomplished, authors have proposed a combination of anagenetic and heterochronic trends [17,23,24]. In addition, some developmental morphogenetic effects are herein tentatively explored on the background of the local to regional uprising of environmental crises and the distressing of ecosystems.

In the most general sense, environmental stress is conceived as a marked change in physical and chemical parameters which, in the case of marine ecosystems, may include sea level, currents, temperature, salinity, oxygenation, and pollution [27,28]. Significant periods of relatively rapid environmental change have been detected in the stratigraphic record as geochemical/sedimentological signals [29–36] and put in relation with major extinction events [27,37]. Among others, ammonites suffered the late Pliensbachian-early Toarcian crisis associated with the Karoo magmatic event [38,39], during which sea level oscillations and black shale deposition were recorded [40–45].

Environmental deterioration is supposedly capable of destabilizing populations by reducing their size or even modifying developmental processes and phenotypic variability; if not lethal, these effects may significantly influence evolutionary processes [46–48].

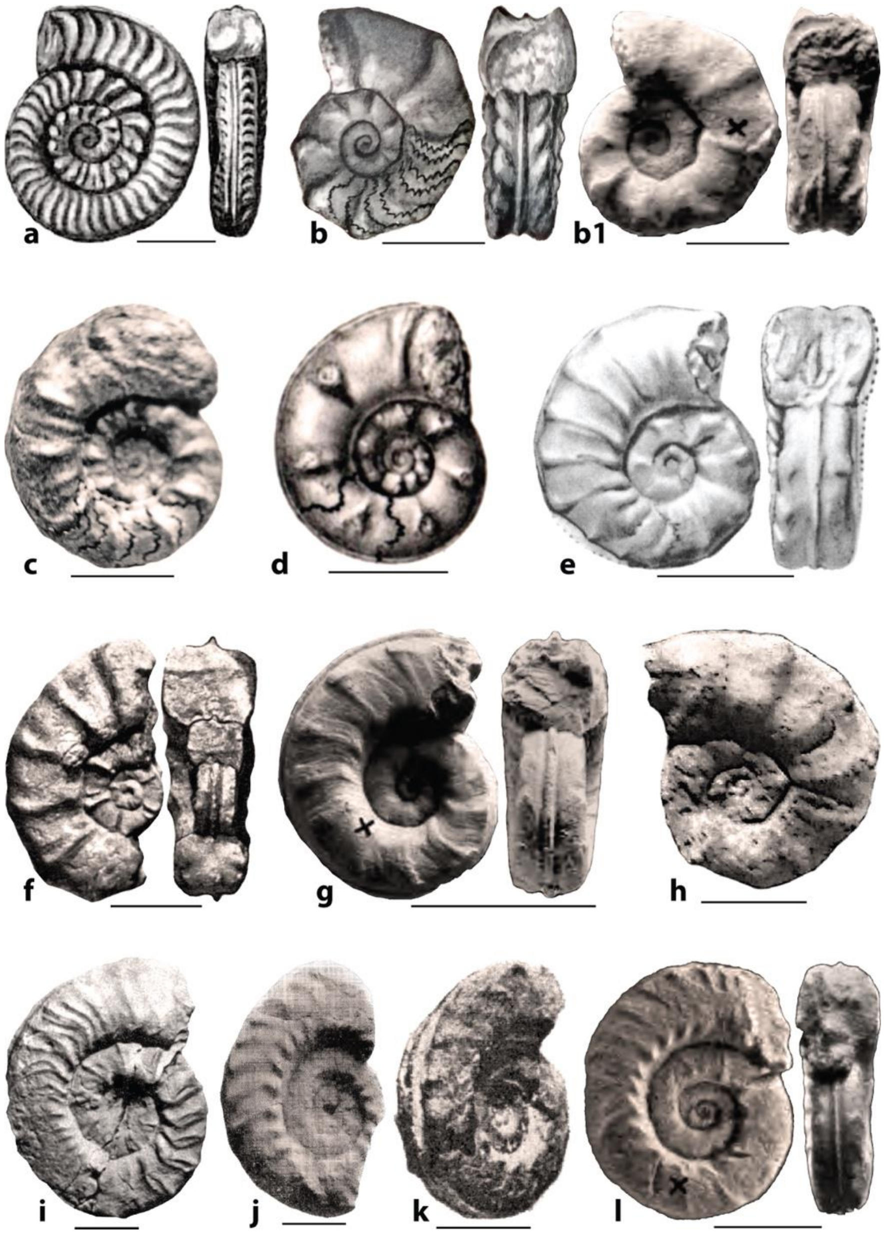


Figure 1. Original illustrations of the holotypes of *Renziceras* and *Leukadiella* species (scale bar = 10 mm). (**a**) = *R. nausikaae* [15]; (**b**) = *L. helenae* Renz, 1913 [15]; (**b1**) = same holotype of *L. helenae* refigured by Wendt [23]; (**c**) = *L. ticinensis* Renz, 1922 [49] (emended by Renz and Renz [50]); (**d**) = *L. reisi* Renz, 1925 [51]; (**e**) = *L. jeanneti* Renz, 1927 [52]; (**f**) = *L. amuratica* Renz and Renz, 1946 [50]; (**g**) = *L. attenuata* Wendt, 1966 [23]; (**h**) = *L. morettinii* Macchioni and Venturi, 2000 [17]; (**i**) = *L. ionica* Renz and Renz, 1946 [50]; (**j**) = *L. gallitellii* Pinna, 1965 [53]; (**k**) = *L. lombardica* Pinna, 1965 [53]; (**l**) = *L. sima* Kottek, 1966 [22]. Note that the coarse ornamentation with ventral clavi retained in the inner whorls of *R. nausikaae* is comparable with the ornamental pattern of *Leukadiella* species from (**b**) to (**h**), but not with that of species from (**i**) to (**l**).

These scenarios may be key for understanding the occurrence of rare and "strange" species in the fossil record, as in the case of *Leukadiella* and other early Toarcian groups. Because phenotypic novelties stemming during events of environmental stress may be significant [54], the post-crisis biodiversity is also affected, creating the premise for compensating (on the long term) the reduction in biodiversity caused by extinctions during the crisis acme. The late Pliensbachian-early Toarcian crisis is of interest for the subsequent renewal of ammonite species in greater part stemming from the *Hildaites* group [26,55], which coincides with the emergence of *Leukadiella* or of its closest precursor.

2. Historical Background

Despite being considered typical of Italy and Greece, *Leukadiella* species are rare in the Toarcian fauna of the Apennines, Southern Alps, and Greek area. The closest related genus *Renziceras*, with its only species *R. nausikaae*, is even less frequent than *Leukadiella*, with only 9 specimens reported in the literature: 7 specimens from the Apennines have been reported by Macchioni and Venturi [17]; one dubious fragment from Spain was described as *Leukadiella* sp. by Braga et al. [56], and later re-interpreted as *R. nausikaae* by Macchioni and Venturi [17]. Whereas *Renziceras* is unknown outside the Mediterranean region, other findings of *Leukadiella* are known only from Canada [25]; in addition, one ambiguous designation is also reported from South America [57]. The specimens from Canada differ significantly from the Mediterranean ones because of their larger growth size, with average diameter of 80 mm and a maximum diameter of 155 mm [25].

Historically, the classification of genera *Leukadiella* and *Renziceras* has been approached as a two-fold problem, one dealing with the subfamily in which to group them, and the other concerning their direct or closest ancestor [16,17,23,24]. In the case of *Leukadiella*, a third problem concerns the relationships between the different species, largely centred on some marked and apparently discontinuous morphological differences. Both *Leukadiella* and *Renziceras* have been often related to *Frechiella* Prinz, 1904 [58], *Paroniceras* Bonarelli, 1893 [59], *Oxyparoniceras* Guex, 1974 [24], *Bouleiceras* and *Nejdia* Arkell, 1952 [60]. These genera are also relatively rare in the Mediterranean or worldwide [61–64]; as a whole, they have been alternatively conceived as forming a unique subfamily Bouleiceratinae [24] or Hildoceratinae [25]; two separate subfamilies Paroniceratinae and Leukadiellinae [25,65]; or even three distinct subfamilies Bouleiceratinae, Paroniceratinae and Leukadiellinae [66].

The Leukadiellinae subfamily was established by Macchioni and Venturi [17] to group *Leukadiella* and *Renziceras* while separating them from other peculiar hildoceratids. In this view, *R. nausikaae* was interpreted as the founder and most likely ancestor of *Leukadiella*. *Renziceras* is represented by only one species based on a specimen from the Toarcian of Greece (Epirus). This was described as *Hildoceras nausikaae* by Renz [15] (p. 607, pl. 14, figure 4, and text figures 25, 25a) (herein refigured in Figure 1a), later assigned to genus *Bouleiceras* [52] (p. 486), and finally designated as the new genus *Renziceras* by Arkell [16] (p. 36). Both Renz [15] and Arkell [16] were impressed by the “dimorphic” morphology of *Renziceras*, consisting of a markedly different ornamentation between the early and adult stage whorls. The inner whorls appear coronate, with strong spaced-out ribs terminated on the ventral edge by prominent tubercles, whereas ornamentation on the last whorl abruptly changes into less thick, gently sinuous ribs without tubercles (Figure 1a). The pre-adult stage morphology of *Renziceras* is overall similar to that displayed by *L. helenae* and other similar species (Figure 1b–h); on the other hand, it is significantly different from the basic morphological pattern of *L. ionica* and similar species with thinner ribs and both periumbilical and ventral nodes or tubercles (Figure 1i–l). This posed the problem of the meaning of such neat differences among *Leukadiella* species [17].

In accordance with the presence of periumbilical and ventral nodes and tubercles in some *Leukadiella* species, Guex [24] interpreted *Leukadiella* as a lateral branch stemming from *Bouleiceras*, considered the ancestor of *Nejdia* and of the Paroniceratinae (Figure 2a). In this view, the thin ribs paired along umbilical nodes (or even with ventral tubercles) typical of *Bouleiceras* (Figure 2b) are considered the precursor of the ornamental pattern displayed by *L. ionica* (Figure 1i). Apart from *Bouleiceras* [23,24,67], also *Hildaites* [22,23,25] (Guex, personal communication) and *Orthildaites* [17] have been credited as possible progenitors.

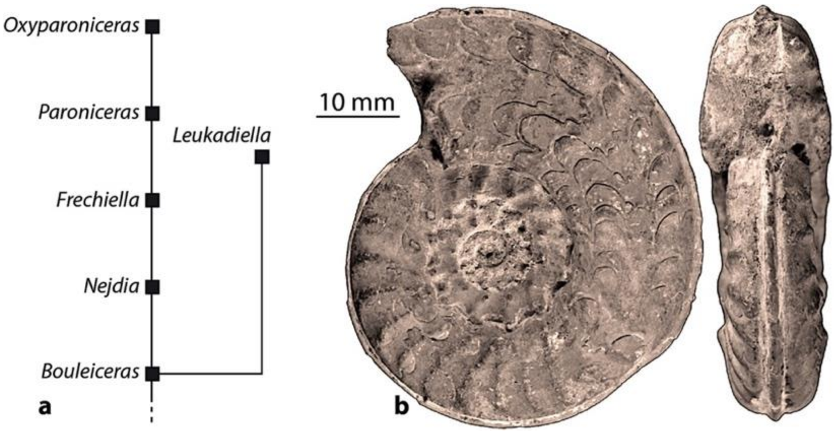


Figure 2. (**a**) = Phylogenetic scheme proposed by Guex [24]. (**b**) = *Bouleiceras nitescens* Thévenin, 1906 [18] (syntype, from Muséum National d'Histoire Naturelle, Paris, http://coldb.mnhn.fr/catalognumber/mnhn/f/r01517). Note the double (umbilical and ventral) row of tubercles in the inner whorls of *Bouleiceras*. Some authors consider these as precursors of the umbilical and ventral nodes in *L. ionica* (see Figure 1i).

As in the case of *Bouleiceras*, the hypothesis of a direct derivation from the "tubercled" *Hildaites* is rooted in the supposed homology between the paired-sigmoidal ribs in *Hildaites propeserpentinus* [19] (Figure 3a) and in *L. ionica* (Figure 1i), thus conceived as the founder of the genus. Alternatively, authors assuming a coarse-clavate ribbed species as the founder of the genus [17] have proposed as indirect ancestors (via *Renziceras*) some coarse-ribbed *Hildaites* and *Orthildaites* (Figure 3b); even earlier, also genera with a markedly sulcated-carenated venter-like *Mercaticeras* have been considered as possible ancestors [2,16].

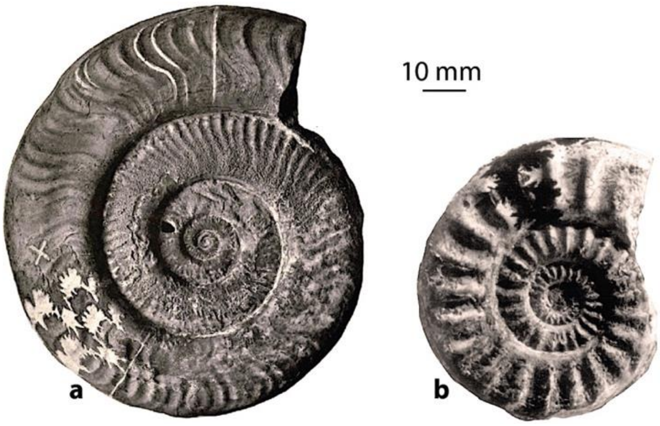


Figure 3. Hildoceratinae usually proposed as ancestral to *Leukadiella*: (**a**) = *H. propeserpentinus* (holotype, from Buckman [19]), considered the ancestor of *L. ionica*; (**b**) = *Orthildaites douvillei* Haug, 1884 [68] (holotype, from Gabilly [69]), considered a possible ancestor of *L. helenae* via *R. nausikaae*. Note that *H. propeserpentinus* is characterised by coupled ribs and umbilical nodes interpreted as precursors of the ornamental pattern in *L. ionica* (Figure 1i); however, it lacks the ventral nodes. Also note that in *O. douvillei* the ontogenetic stages are reversed compared to *R. nausikaae* (Figure 1a), with the thicker ribbed stage in the outer whorls of *Orthildaites* and in the inner ones of *Renziceras*. Moreover, the thicker ribs of *Orthildaites* attenuate towards the venter instead of further thickening into a clavi, as in *Renziceras* and *Leukadiella*.

According to Wendt [23], two branches stem from the founder species *L. helenae* (Figure 4a): one leading to *L. attenuata* (Figure 1g) and one along which species developed coupled ribs through "proterogenesis". This second branch is represented by the sequence: *L. amuratica*–*L. ionica*–*L. sima* (Figure 1f,i,l, respectively), the latter characterized by the simplification of ornamentation and the reoccurrence of single ribs only (Figure 1l). Macchioni and Venturi [17] interpret their new species *L. morettinii* (Figure 1h) as the founder species, from which later separate two main branches (Figure 4b), one conducive to *L. helenae* (Figure 1b,b1), and one to *L. ionica* and *L. gallitellii* (Figure 1i,j).

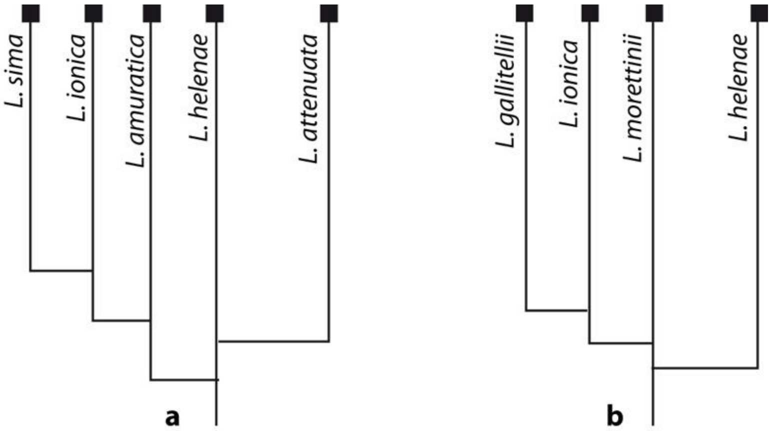


Figure 4. (**a**) = phylogenetic scheme according to Wendt (1966): *L. attenuata* (Figure 1g) and *L. amuratica* (Figure 1f) both derive from *L. helenae* (Figure 1b,b1); *L. amuratica* then gives rise to *L. ionica* (Figure 1i), from which finally descends *L. sima* (Figure 1l). (**b**) = phylogenetic relationships according to Macchioni and Venturi (2000): *L. helenae* (Figure 1b,b1) and *L. ionica* (Figure 1i) both derive from *L. morettinii* (Figure 1h); from *L. ionica* then derives *L. gallitellii* (Figure 1j). Note that *L. gallitellii* is characterised by simple ribs with marked and elongated umbilical tubercles, an ornamental pattern shared by *L. lombardica* and *L. sima* (Figure 1k,l).

It is worth noticing that the coarse-ribbed *Hildaites* stock is also ancestral to the Apennine genus *Cingolites*, which, according to Sassaroli and Venturi [26] (p. 114), likely stemmed from *Hildaites crassus* Guex, 1973 [70]. *Cingolites* differs from *Hildaites* because of the overall clavate ribs producing the broad coronate venter with wide sulci (distinctive also with respect to *Orthildaites*), and the trapezoidal-quadrate whorl section (Figure 5).

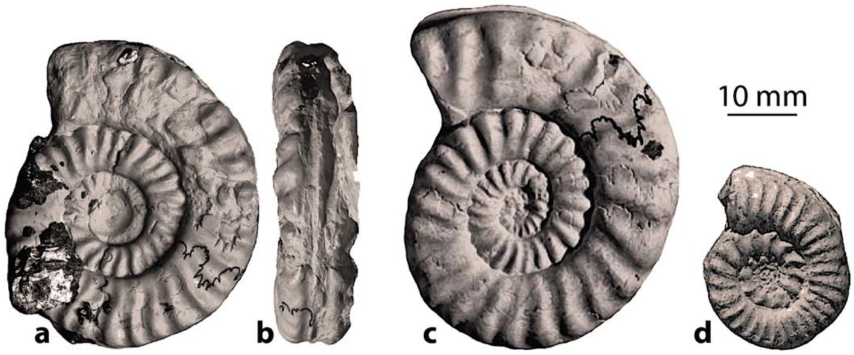


Figure 5. Comparison of the ornamental pattern of *C. clavatus* ((**a**–**c**); (**a**,**b**) = holotype; from Sassaroli and Venturi [26]) and *R. nausikaae* ((**d**), from Macchioni and Venturi [17]).

On this basis, *Cingolites* is herein proposed (in addition to *Bouleiceras*, *Hildaites*, *Orthildaites* or even *Mercaticeras*) as a credible progenitor bridging *Hildaites* with the *Renziceras*-*L. helenae* line. This interpretation further reduces the morphological gap between the *Hildaites* and the clavate-ribbed *Leukadiella* species. Instead, the origin of non-clavate species, as for instance *L. ionica*, remains more problematic, essentially because: (a) the transition *amuratica-ionica* proposed by Wendt [23] is based on very few specimens, and (b) the differences between the ornamentation of *L. ionica* and that of any other lower Toarcian species, including *H. propeserpentinus*, are even more striking and discontinuous.

3. Material and Methods

3.1. Available Data

At present, literature data indicate that the worldwide representatives of *Leukadiella* amount to 70 specimens, assigned to 11 different species (Table 1). Of these, only *L. helenae* and *L. ionica* are represented by more than three specimens (including the holotype).

Table 1. List of *Leukadiella* specimens and species figured or described in the literature. Only specimens figured by each author are included in the total count of known specimens; for instance, Wendt [22] includes three *L. ionica* in the list of the available material without figuring them. When a specimen is refigured by diverse authors it is counted only once. For instance, Wendt [23] reviews and refigures specimens already figured by Renz [15,49,51,52,71], Renz and Renz [50] and Kottek [22]; Pinna [53] establishes *L. gallitellii* on a specimen already figured by Gallitelli [72]; Gallitelli-Wendt [73] figures a specimen of *L. ionica* already figured by Wendt [23].

Author(s)	Number of Specimens	Number of Species	Findings from Italian Localities
Renz [13]	1	1 *L. helenae* n. sp.	
Renz [49]	1	1 *L. helenae* n. v. *ticinensis*	
Renz [71]	1	1 *L. helenae*	
Renz [51]	2	1 *L. reisi* n. sp.; 1 *L. helenae* var.	
Renz [52]	2	1 *L. helenae* v. *ticinensis;* 1 *L. jeanneti* n. sp.	
Renz and Renz [50]	5	1 *L. amuratica* n. sp.; 3 *L. ionica* n. sp.; 1 *L. ionica* n.v. *paganiensis*	
Deleau [74] (*fide* Wendt [23])	1	1 *L. ionica*	
Schindewolf [75] (*fide* Wendt [23] (p.142,145))	2	1 *L. ionica;* 1 *L.* sp.	
Pinna [53]	2	1 *L. gallitellii* n. sp.; 1 *L. lombardica*	1 *L. gallitellii* (Central Apennines) 1 *L. lombardica* (Southern Alps)
Kottek [22]	5	1 *L. amuratica;* 1 *L. ionica;* 1 *L. sima* n. sp.; 1 *L. paganiensis;* 1 *L. ionica* subsp.	
Wendt [23]	6	2 *L. helenae;* 1 *L. ionica;* 2 *L. attenuata* n. sp.; 1 *L.* sp.; 3 *L. ionica* (not figured, not counted herein)	1 *L. ionica* (Central Apennines) 2 *L. helenae* (Sicily) 1 *L. attenuata* n. sp. (Sicily)
Gallitelli-Wendt [73]	1	1 *L. ionica* (same specimen figured by Wendt [23]; counted therein)	
Levi Setti [76]	4	1 *L. helenae*, 1 *L. ionica*, 1 *L. lombardica*, 1 *L.* sp.	1 *L. ionica* (Central Apennines) 1 *L. helenae* (Central Apennines) 1 *L.* sp. (Central Apennines) 1 *L. lombardica* (Southern Alps)
Hillebrandt [57] (*fide* Jakobs [25])	1 (doubtful)	1?	
Howarth [77]	1	1 *L.* aff. *ionica* (doubtful)	
Jakobs [25]	14	8 *L. ionica;* 2 *L.* aff. *ionica;* 2 *L. amuratica;* 1 *L.* aff. *helenae;* 1 *L.* sp.	
Pettinelli et al. [78]	1	1 *L. ionica*	
Macchioni and Venturi [17]	17	3 *L. helenae;* 3 *L.* cfr. *helenae;* 2 *L. morettinii* n. sp.; 1 *L.* aff. *morettinii;* 3 *L. ionica;* 3 *L. gallitellii;* 1 *L.* aff. *jeanneti;* 1 *L.* n. sp.	All from the Central Apennines
Géczy and Szente [79]	1	1 *L. jeanneti*	
Géczy et. al. [80]	1	1 *L. helenae*	
Ridente, this work	2	2 *L. helenae*	Both from the Central Apennines

In addition to literature data, only 2 specimens of *L. helenae* are the result of more than three decades of sampling of the Rosso Ammonitico of the Central Apennines conducted by the author and other research groups at Sapienza University. Both specimens are from the same locality, near the town of Polino (Figure 6).

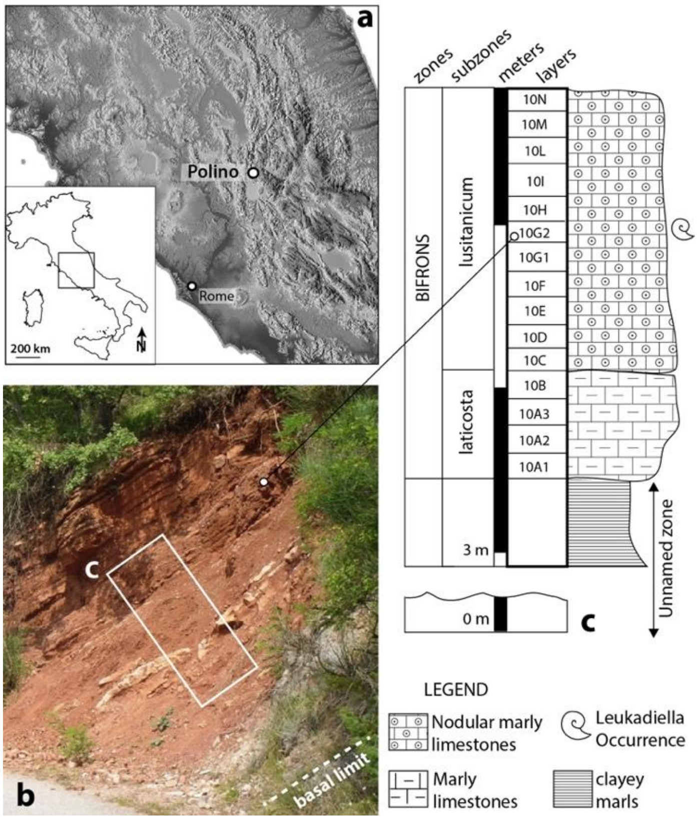


Figure 6. (**a**) = location of the Polino Rosso Ammonitico section (Central Apennines) where two specimens of *L. helenae* were found (one from the detritus). (**b**) = basal part of the Rosso Ammonitoco and position of layer 10G2 yielding specimen PO_LE10G2 (Figure 7a–d). (**c**) = lithological and biostratigraphic scheme. Below the Bifrons zone, a sterile interval ("unnamed zone") extends to the base of the section, encompassing the stratigraphic interval usually assigned to the Serpentinum and Tenuicostatum zones [43,81].

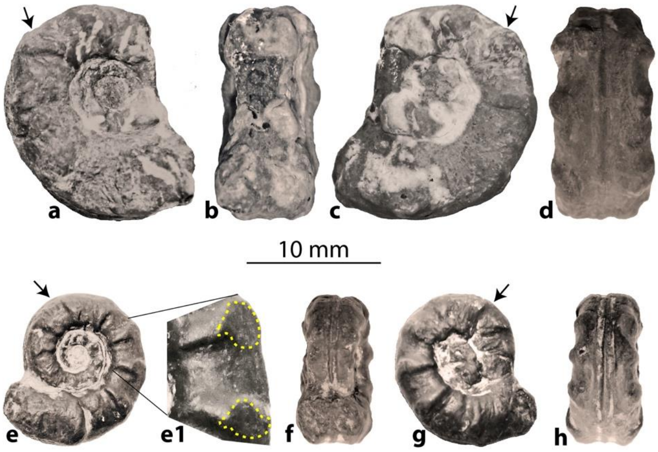


Figure 7. Two specimens of *L. helenae* from the Polino Rosso Ammonitico section (Figure 6): (**a**–**d**) = PO_LE10G2, from the Lusitanicum subzone; (**e**–**h**) = PO_LEd1, juvenile specimen from the detritus. Arrows indicate the onset of the living chamber; (**e1**) = closeup of the neat fracture left by broken spines (yellow dashed line).

Specimen PO_LE10G2 is a broken phragmocone with part of the body chamber, ca. 26 mm in diameter and severely eroded on both sides; specimen PO_LEd1 is a well-preserved individual only 18 mm in diameter, including greater part of the body chamber (Figure 7). Therefore, the main data on which this review is based are the original illustration of holotypes and diagnosis by the designating author, or even later revisions of the original diagnosis [17,23]. It is worth noting that 29 among the 70 specimens documented in the literature (41% of the total) are from Italian localities; of these, 17 specimens have been described by Macchioni and Venturi [17], all collected in the Central Apennines and grouped within 6 different species (Table 1).

Of the other 10 specimens (representing 5 species) reported in the literature from Italian localities, 5 are from the Central Apennines, 2 from the Southern Alps, and 3 from Rocca Busambra, in Sicily (Table 1). As to the biostratigraphical distribution, all but one of the occurrences of *Leukadiella* reported in the literature are from the Bifrons zone (50, 53, 23, 73, 76, 25, 17, 79, 80, Ridente, this work). Specimens PO_LE10G2 (Figure 7a–d) was found in layer 10G2 of the Rosso Ammonitico section near Polino (Figure 6), together with an abundant fauna of *Hildoceras lusitanicum* Meister, 1913 [82]. The exception to a bio-stratigraphic distribution limited to the Bifrons zone is one specimen that Macchioni and Venturi [17] assign to the final part of the Serpentinum Zone, in the same interval where they record the occurrence of *R. nausikaae*.

3.2. Classification Methods

Taxonomic characters and criteria for the classification of *Leukadiella* species and the reconstruction of their phylogenetic relationships are revised essentially based on literature data. The list of taxonomic characters most frequently used in the literature for the definition of *Leukadiella* species and their variability can be summarized as follows:

- whorl embracement: from evolute to moderately involute;
- whorl section shape: sub-quadrate or sub-trapezoidal or sub-rectangular;
- shape of the flanks: more or less rounded;
- shape of the umbilical wall and ventri-lateral shoulder: rounded or sloping;
- ventral keel and sulci: variably pronounced and variably carved, respectively;
- type and shape of the ribs: either simple or paired; paired ribs may merge only at umbilical nodes or even at ventral nodes (forming fibulae), with couplets sometimes formed by a more raised primary rib and an attenuated secondary one. The shape of the ribs is either thick-clavate and overall straight or thin and sinuous, at times also concave backward;
- number of ribs: less than 10–12 when coarse-clavate, up to more than 20 when thinner and sinuous;
- umbilical and/or ventro-lateral tubercles and nodes: variably pronounced and overall elongated;
- suture line: variably simplified, particularly the lobes.

A comparison of the classification schemes proposed by diverse authors indicates that the ornamental pattern provides the most noticeable taxonomic characters for the distinction of species. Based on the variability of ornamental characters described above, two main ornamental patterns can be distinguished, consisting in clavate ribs variably thick and well spaced-out throughout the whorl; or non-clavate ribs, overall thin and closely spaced. Other characters (e.g., whorl section shape; whorl embracement), as well as other aspects of the ornamentation (e.g., paired ribs, presence of umbilical and/or ventral tubercles and nodes) are subdued to the principal clavate/non-clavate ornamental pattern (Figure 8).

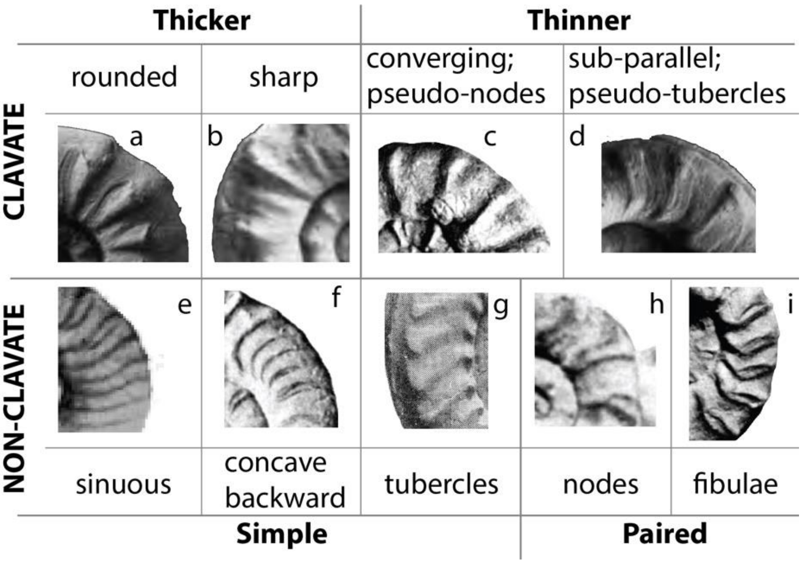
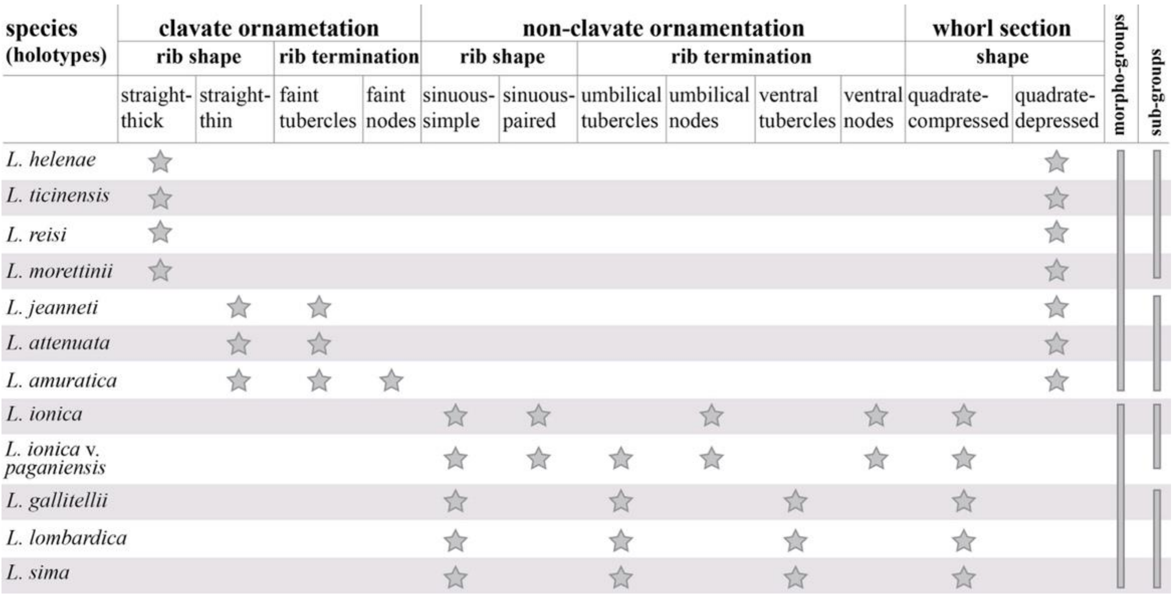


Figure 8. Ornamental patterns and variability of rib type and shape: the two basic patterns are the clavate and spaced-out ribs or the non-clavate and denser ribs. Clavate ribs are variably thick, simple and straight, and more or less rounded (**a**,**b**). The occasional occurrence of periumbilical reliefs and intercalated secondary ribs may simulate paring ribs (**c**,**d**). Non-clavate ribs are simple or truly paired, either sinuous (**e**) or more backward concave (**f**). Simple ribs show both periumbilical and ventral tubercles (**g**); paired ribs show periumbilical nodes only (**h**) or both periumbilical and ventral nodes, forming fibulae (**i**).

This variability and its relationship with the currently accepted species of *Leukadiella* is summarized in Figure 9, with reference to the holotypes of each species and variety proposed by diverse authors (compare with Table 1).



species (holotypes)	clavate ornametation				non-clavate ornamentation						whorl section		morpho-groups	sub-groups
	rib shape		rib termination		rib shape		rib termination				shape			
	straight-thick	straight-thin	faint tubercles	faint nodes	sinuous-simple	sinuous-paired	umbilical tubercles	umbilical nodes	ventral tubercles	ventral nodes	quadrate-compressed	quadrate-depressed		
L. helenae	☆											☆		
L. ticinensis	☆											☆		
L. reisi	☆											☆		
L. morettinii	☆											☆		
L. jeanneti		☆	☆									☆		
L. attenuata		☆	☆									☆		
L. amuratica		☆	☆	☆								☆		
L. ionica					☆	☆		☆		☆	☆			
L. ionica v. *paganiensis*					☆	☆	☆	☆		☆	☆			
L. gallitellii					☆		☆		☆		☆			
L. lombardica					☆		☆		☆		☆			
L. sima					☆		☆		☆		☆			

Figure 9. Distribution among the currently accepted *Leukadiella* species (see Table 1) of the main taxonomic characters (see Figure 8). Besides the ornamental features, also whorl section shape is represented, roughly based on the width/height ratio (w/h ≤ 1 = compressed; w/h ≥ 1 = depressed). Note that species can be separated into two main morpho-groups: (1) clavate/depressed and (2) non-clavate compressed. In addition, two sub-groups can be recognized within each main group, namely: with thick or thin clavate ribs (the latter with faint umbilical tubercles or nodes); and with simple or paired non-clavate ribs (the latter also with ventral nodes).

4. Systematic Palaeontology

4.1. Morphological Variability of Leukadiella Species and Classification Problems

A comparison of the currently accepted species of *Leukadiella* indicates that the main morphological characters and their variants (particularly those concerning the shape of ribs and the occurrence of nodes and tubercles) combine in order that two morphological groups can be defined:

Morphological Group 1 (MG1): structural features such as moderately involute whorls and quadrate-depressed section are coupled with single, coarse-clavate, straight and spaced-out ribs (usually no more than 10–12 per whorl) ending with ventral clavi (Figure 8a–d); periumbilical nodes and paired ribs, or even neat periumbilical tubercles, are absent (Figure 9). Overall, this set of characters is typical of the following species (see Figure 1): *L. helenae*, *L. ticinensis*, *L. reisi*, *L. jeanneti*, *L. amuratica*, *L. attenuata* and *L. morettinii*.

Morphological Group 2 (MG2): overall evolute and quadrate-compressed whorls are associated with thin and denser (up to >20 per whorl) sigmoidal or backward concave ribs, ended by periumbilical and ventri-lateral tubercles or even welded at both ends by nodes to form fibulae (Figure 8e–i; see also Figure 9); overall, rib shape is inconstant (diverse patterns may be present in the same specimen) and irregular (ribs of the same type may differ in thickness and overall shape). This morphological pattern is shared by the following species (see Figure 1): *L. ionica*, *L. gallitellii*, *L. lombardica* and *L. sima*; it is also typical of *L. ionica* var. *paganiensis*, which, according to Wendt [23], is a junior synonymous of *L. ionica*.

The two distinct morphological groups corresponding to MG1 and MG2 are respectively referred to as Helenae Group and Ionica Group, with reference to the most representative species in each group; if and how these two groups can be bridged remains an open question. It is worth noting that the ventral clavi in *L. helenae* (and likely in other species within MG1) are remnants of protruding spines that rarely preserve [17] (pl. 4 figures 1, 2); therefore, the shape and prominence of the ventral clavi (as well as the degree of rib projection) may reflect differential preservation of spine remnants rather than interspecific morphological variants (see Figure 7e).

Three species within the Helenae Group share a peculiarity by which they subtly differ from the basic pattern of *L. helenae*; these are: *L. jeanneti*, *L. amuratica* and *L. attenuata* (Figure 1e–g, respectively; see also Figure 9). These are peculiar because of the occasional occurrence of a periumbilical relief on some ribs or because ribs tend to thin on the middle flank, as they stem from a thicker umbilical segment, somewhat resembling a periumbilical tubercle (particularly in the holotypes of *L. jeanneti* and *L. attenuata*; Figure 1e,g). Overall, *L. jeanneti*, *L. amuratica* and *L. attenuata* pose the following problem: on one hand, they appear similar to a point that they may be variants of the same species (in which case *L. amuratica* and *L. attenuata* would be junior synonymous of *L. jeanneti*); on the other, their morphological peculiarities (tendency towards rib thinning and paring, or even development of a periumbilical relief) recall features more clearly expressed in species of MG2 (e.g., compare the ornamental pattern in Figure 8c with that in Figure 8h; and that in Figure 8d with that in Figure 8g).

This twofold problem can be solved by considering the *jeanneti-amuratica-attenuata* morphotypes as bridging the two groups, although morphologically closer to the MG1 pattern (Figure 9). This interpretation is consistent with the phylogenetic trend proposed by Wendt [23], according to which a sequence can be traced from *L. helenae* to *L. ionica* via *L. amuratica* (Figure 4a), along with a heterochronic process leading to the development of coupled ribs in the final species. In this view, the transition proposed by Wendt [23] can be supported by also involving *L. attenuata* and *L. jeanneti* (Figure 10; compare with Figure 4a), either as distinct species or (more likely) as variants of the same species, which by priority would be *L. jeanneti* (Figure 1e).

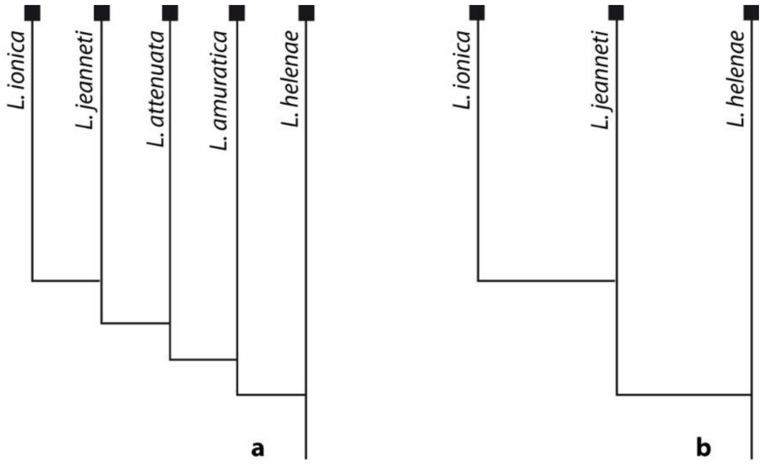


Figure 10. (**a**) = Possible phylogenetic relationships between species of MG1 (*L. helenae, L. jeanneti, L. amuratica, L. attenuata*) and MG2 (*L. ionica*) based on the observed ornamental pattern. (**b**) = alternatively, *L. jeanneti L. amuratica* and *L. attenuata* may be variants of the same species (see data summarized in Figure 9), in which case they would merge into only one branch (*L. jeanneti*) separating *L. helenae* from *L. ionica*.

Notwithstanding whether morphological data support the occurrence of the heterochronic process invoked by Wendt [23], this transition is key for bridging MG1 and MG2; alternatively, MG1 and MG2 can be considered as two distinct groups stemming separately from two different (though related) ancestors. Both the MG1 and MG2 groups are present in the Apennines and Mediterranean region, whereas the specimens from North America described by Jakobs [25] can be referred to MG2 only. In fact, the specimens that Jakobs assigns to *L. amuratica* [25] (figures 6.11, 6.15, 6.16) and *L.* aff. *helenae* [25] (figures 6.13, 6.14) do show a coarser ribbing pattern; yet the shape of the ribs and their pairing in umbilical and ventral nodes is typical of the Ionica Group. These specimens thus evidence a coarsening of the ribs in species of the Ionica Group, rather than the presence of the "*helenae*" ornament type (MG1) in the *Leukadiella* from North America.

The coarseness of the ornamentation in specimens from North America may depend on their larger growth size, reaching values (average diameter of 80 mm and a maximum diameter of 155 mm; Jakobs [25]) unusual to *Leukadiella* from the Apennines. Therefore, species of the Helenae and Ionica groups are markedly different not only in their basic morphology, but also because of their geographical distribution, with the Helenae Group exclusive of the Mediterranean area and the Ionica Group present also in North America, though with "giant" morphotypes if compared with those from the Mediterranean.

4.2. Restriction of the Number of Accepted Species

The eleven species of *Leukadiella* currently accepted have been originally defined mainly based on differences in the ornamental features. However, the low number of findings for each species does not afford confident determination of the variability field of taxonomic characters; moreover, the coarseness of ribs and tubercles or clavi is significantly biased by preservation. This is particularly relevant for species of the Helenae Group, in which the shape and largeness of the ventral clavi reflect the degree of preservation of the root of the spines after they break off [17]. An implication of this reasoning is that the difficulty of defining the variability field of taxonomic characters and the overlooking of preservation bias may have determined an overestimation of the number of species.

With these considerations in mind, the morphological pattern displayed by *L. helenae, L. ticinensis*, *L. reisi*, and *L. morettinii* (Figure 1b–d,h) appears similar, and the differences on which their distinction has been based become less remarkable (Figure 9). Only in the case of *L. jeanneti, L. amuratica* and *L. attenuata* (Figure 1e–g), the presence of subtle periumbilical bumps or relative thinning of the ribs on the middle flank may represent some distinguishing features (Figure 9). Nevertheless, even in this case the lack of a proper number of specimens is an obstacle to the confident evaluation of the taxonomic relevance of these features (herein evaluated only basing on the figure of the holotypes). With all the above considered, species of the Helenae Group such as *L. ticinensis*, *L. reisi* and *L. morettinii* (Figure 1c,d,h) are interpreted as junior synonymous of the senior *L. helenae* (Figure 1b,b1); similarly, *L. amuratica* and *L. attenuata* (Figure 1f,g) may be interpreted as junior synonymous of *L. jeanneti* (Figure 1e). In this view, the *amuratica-attenuata-jeanneti* ornamental pattern (described above) allows tentatively to separate *L. jeanneti* (Figure 1e) from *L. helenae* (Figure 1b,b1). The number of species of the Helenae Group would thus be reduced via synonymy to only two species: *L. helenae* and *L. jeanneti*.

With reference to the Ionica Group, the number of species as well seems overwhelming compared to the variety of taxonomic characters and their understanding in terms of ontogenetic/intraspecific variability. *L. ionica* (Figure 1i) apparently differs from the other species of the group (Figure 1j–l) because of the occasional occurrence of ribs paired by periumbilical and ventral nodes, forming fibulae (Figure 9); these alternate with ribs pairing only at the periumbilical node, or even with simple ribs bending backward from an elongated umbilical tubercle. In contrast, fibulae are absent in *L. gallitellii*, *L. lombardica* and *L. sima* (Figure 1j–l), which are all comparable in showing only simple ribs, though retaining umbilical and ventral tubercles (Figure 9). For this reason, *L. gallitellii, L. lombardica* and *L. sima* are likely the same species, as also remarked by Macchioni and Venturi [17]; accordingly, and by priority, this species should be named *L. gallitellii*. Considering that, apart from the holotype of *L. ionica* var. *paganiensis* [50], only one rather ambiguous exemplar has been figured [22] (see Table 1), this variety is herein considered synonymous to *L. ionica,* in accordance with Wendt [23]; therefore, the Ionica Group as well reduces to two species: *L. ionica* and *L. gallitellii.*

4.3. Revised Classification Scheme

The above results indicate that the combination of ornamental and structural features by which the Helenae Group and Ionica Group have been separated define a taxonomic rank above the species level. Accordingly, the differences between species of these two groups are interpreted as reflecting two distinct genera. Consequently, the name *Leukadiella* is maintained exclusively for the senior species *L. helenae* and the closely related species *L. jeanneti*. The new genus name *Neoleukadiella* gen. nov. is proposed for the only two species herein considered plausible among those listed in the Ionica Group: *N. ionica* and *N. gallitellii,* which thus result as a *combinatio nova*. Based on this taxonomic approach, the following genera and species are herein recognised within the stock of former *Leukadiella* species: *L. helenae, L. jeanneti, N. ionica* comb. nov. and *N. gallitellii* comb. nov. (Figure 1b,b1,e,i,j, respectively).

Regarding the higher rank classification, the former genus *Leukadiella* has been frequently grouped at subfamily rank with *Frechiella* and *Paroniceras,* essentially due to sharing a neat departure from the basic morphological pattern of the Hildoceratinae, rather than because of sharing any significant common character. Indeed, there is no morphological character by which any species of *Leukadiella* and *Neoleukadiella* gen. nov. can be grouped with species of *Frechiella* and *Paroniceras* below the family rank. The Leukadiellinae subfamily proposed by Macchioni and Venturi [17] is thus the more suitable option in which to place *Leukadiella* and *Neoleukadiella* gen. nov., together with *Renziceras*. In this view, *Cingolites*, a possible direct ancestor of *Renziceras* characterised by clavate ribs and a coronate ventral area, could be also included in the Leukadiellinae Subfamily. All the above considered, a revised classification scheme is herein proposed.

Subclass **Ammonoidea** Zittel, 1884 [83]
Order **Ammonitida** Hyatt, 1889 [84]
Suborder **Ammonitina** Hyatt, 1889 [84]
Superfamily **Hildoceratoidea** Hyatt, 1867 [14]
Family **Hildoceratidae** Hyatt, 1867 [14]
Subfamily **Leukadiellinae** Macchioni and Venturi, 2000 [17]
Genus *Leukadiella* Renz, 1913 [15]

Diagnosis (emended). Genus *Leukadiella*, as herein redefined, is characterized by moderately embracing whorls with quadrate-depressed section and a deep umbilicus; ribs are simple, straight, coarse-clavate, well spaced-out (about 7–10 per whorl) and terminate with a variably pronounced ventral clavi (Figure 1b–h, Figures 7 and 8a–d). Neat periumbilical tubercles or nodes are lacking, although in some specimens there is subtle evidence of occasional thickening or converging of ribs near the umbilicus. The venter is variably wide, also depending on the shape of the whorl, which in turn varies with size. The height of the central and lateral keels is also variable, as well as the depth/width of the sulci; the lateral keels are affected by the different preservation of the ventral clavi along the ribs, which are the inception of large spines that rarely preserve. All known specimens are small, the two largest ones reported in the literature reaching the diameter of 30 [17] and 31.5 mm [23]. The suture line shows elements (number and shape of saddles and lobes) comparable with the general pattern of the Hildoceratitic line, though simplified (see Macchioni and Venturi [17] for a detailed description of the suture line based on a relatively large data set).

Type species. *Leukadiella helenae* Renz, 1913 [15] (by original designation, pp. 587–590, pl. 14, figures 1–3).

Occurrence. Lower Toarcian, Bifrons Zone.

Leukadiella helenae Renz, 1913
(Figure 1b,b1, Figure 7a–h; Figure 1c,d,h by synonymy)

1913 *Leukadiella helenae*; Renz, pl. 14, figures 1–3; text figure 17.
1922 *Leukadiella helenae* var. *ticinensis*; Renz, pl. 7, figure 1.
1923 *Leukadiella helenae*; Renz, pl. 12, figure 3.
1925 *Leukadiella reisi*; Renz, pl. 5, figure 4a.
1927 *Leukadiella helenae* var. *ticinensis*; Renz, pl. 13, figure 8a.
1966 *Leukadiella amuratica*; Kottek, pl. 13, figure 7.
1966 *Leukadiella helenae*; Wendt, pl. 13, figures 1a–d, 2a–c, 3a–c, 4a–d.
1972 *Leukadiella helenae*; Levi Setti, text figure III: 2a–d.
?1972 *Leukadiella* sp.; Levi Setti, text figure III: 4a–d.
2000 *Leukadiella helenae*; Macchioni and Venturi, pl. 1, figures 17 and 18; pl. 2, figures 14, 19, 20; pl. 3, figures 14, 20; pl. 4, figures 1, 2.
2000 *Leukadiella* cfr. *helenae*; Macchioni and Venturi, pl. 1, figures 14–16; pl. 2, figures 11–13; pl. 3, figures 6, 7, 22.
2000 *Leukadiella morettinii*; Macchioni and Venturi, pl. 1, figure 3; pl. 2, figure 10; pl. 3, figures 10, 12–13, 17; text figure 3.
2000 *Leukadiella* aff. *morettinii*; Macchioni and Venturi, pl. 1, figure 2; pl. 2, figure 15; pl. 3, figure 19.
? 2000 *Leukadiella* aff. *jeanneti*; Macchioni and Venturi, pl. 1, figure 20; pl. 2, figure 16; pl. 3, figure 15.
2008 *Leukadiella helenae*; Géczy et al., pl. 2, figures 5, 6.

Description. Moderately involute whorls and quadrate-depressed section, which becomes trapezoidal in correspondence of the ventral coarsening of ribs. Ribs are few and well-spaced, usually up to 10 per whorl or less. They are straight with a rounded or sharp axial crest (e.g., Figure 8a,b), and thicken regularly and rapidly on the middle flank, before culminating in broad clavi on the ventral margin. The clavi are the inception of unpreserved large spines; the umbilical segment of the ribs is instead narrow and deprived of tubercles, although in some ribs it may be thicker than in others (Figure 8c,d). The venter is bisulcate-tricarenate, variably wide depending on the shape and size of the whorl. In some cases, the ventral clavi fade into a continuous (“*Mercaticeras*-like”) lateral keel and both the two sulci and the ventral area appear narrowed; alternatively, the ventral clavi and the interspace between them drop into a broader lateral sulcus without forming an evident lateral keel, and the ventral area appears typically sunk.

Material and provenance. Two specimens from the Rosso Ammonitico section of Polino (Central Apennines). Specimen PO_LE10G2 (Figure 7a–d) is from the Lusitanicum subzone (Figure 6); specimen PO_LEd1 (Figure 7e–h) is from an unknown bed.

Remarks. Specimen PO_LE10G2 is badly preserved and consists of a broken phragmocone (D = 26 mm) with a half-whorl body chamber eroded on both sides (Figure 7a,c). The fracture that cuts the terminal part of the body chamber has removed part of the internal phragmoconic whorls; the remaining is a 12 mm segment just preceding the onset of the body chamber (arrows in Figure 7a,c). The phragmoconic segment is better preserved than the body chamber and shows five closely spaced suture lines and three clavate ribs; the ventral area is poorly preserved, with the sulci and the central keel intensely eroded (Figure 7d).

Specimen PO_LEd1 (Figure 7e–h) is 18 mm in diameter, the whorl section is depressed (w/h = 8/6 = 1.3), and suture lines are not visible at eye or with eye lent, but they can be detected with an optical microscope, appearing very simplified (possibly a juvenile feature) and revealing that more than half of the preserved last whorl is part of the body chamber (arrows in Figure 7e,g). Ribs on the final whorl are 9 or 10, and some thickening (like thick striae) near the umbilicus is also observed in some of the interspace between ribs. The ventral clavi are evident and appear neatly cut along the break-off of the spine; the cut has left an oblique-flat surface that may mimic a forward projection of the clavi (Figure 7e). The ventral area is bisulcate-tricarenate.

Comparative description. The distinction between *L. helenae* and *L. jeanneti* is subtle and largely based on the narrower and less clavate ribs shown by the holotype of *L. jeanneti* (and also by the junior synonymous *L. amuratica* and *L. attenuata*; Figure 1e–g). In particular, the ribs in the final whorl of *L. jeanneti* show a periumbilical bump from which they extend straight or bend slightly backward and without significant thickening along the middle flank; an abrupt coarsening occurs on the ventral edge, producing a tubercle or clavi (Figure 1e,g). Also intercalated secondary ribs seem present in the holotype of the junior synonymous *L. amuratica*, which appear to fade out on the middle-inner flank, somewhat simulating their pairing with the preceding and more pronounced rib (Figure 1f).

Genus Neoleukadiella gen. nov.

Diagnosis. *Neoleukadiella* gen. nov. is characterized by overall evolute and quadrate-compressed whorls with sinuous ribs ended by periumbilical and ventral tubercles, either simple or paired, or even welded at both ends by nodes to form fibulae. The ventral area is narrow and bisulcate-tricarenate, relatively wider in less compressed specimens. When present, paired ribs (merged by single or double nodes) irregularly alternate with simple ones, although the latter may be clearly prevalent or even the only present. Independently of being only simple or alternating with paired ribs, their number can be up to more than 20.

Remarks. *Neoleukadiella* gen. nov. is different from *Leukadiella* essentially in the ornamental pattern, the former being characterized by thinner and denser sinuous ribs (up to 20 per whorl or more), which are never clavate and are either simple or paired by periumbilical nodes, or even welded into fibulae when also ventral nodes are present. In *Leukadiella*, instead, clearly merging ribs and periumbilical tubercles are absent, and the thicker single ribs (rarely more than 10–12 per whorl) are ended by a ventral clavi.

The “giant” specimens from Canada described by Jakobs [25] are herein all interpreted as belonging to *Neoleukadiella* gen. nov., according to their ornamental pattern. This consists of coarse ribs that, however, differ from the typical ornamentation of *Leukadiella* because of their sinuous shape, the presence of an elongated umbilical tubercle instead of ventral clavi, and the frequent pairing into umbilical and ventral nodes.

Type species. *Neoleukadiella ionica* comb. nov. (Renz and Renz, 1946) [50] (by original designation, pp. 174–175, pl. 12, figures 5, 7, 7b, 9).

Occurrence. Lower Toarcian, Bifrons Zone.

Diagnosis. *N. ionica* comb. nov. is characterized by sinuous paired ribs, randomly alternating with simple ribs; the paired ribs may form fibulae and show an elongated umbilical node and a more rounded ventral node (Figure 1i). The simple ribs may become thinner and tend to lose tubercles in the mature stage (Figure 1i). The pattern of alternation between simple and paired ribs, as well as the occurrence of fibulae, appears overall random from the inner to the outer whorls, although simple ribs occur more frequently in the final whorl. In the holotype (herein refigured in Figure 1i) the whorl section is slightly compressed (w/h = 0.90) in the last whorl, at a diameter of 41 mm [50].

Comparative diagnosis. *N. ionica* comb. nov. and *N. gallitellii* comb. nov. (Pinna, 1965) [53] (by original designation, pp. 269–270, pl. 1, figures 1a−c, 3b) differ because, in the latter, the ribs are simple and never paired along the umbilical or ventral margin, though they as well depart from an elongated, forward-projected umbilical tubercle, and terminate in a well-marked, forward-projected ventral tubercle (Figure 1j; Figure 1k,l by synonymy). In the holotype of *N. gallitellii* comb. nov. (refigured in Figure 1j) the whorl section is quadrate (w/h = 1) in the last whorl, at a diameter of 38 mm [53].

5. Discussion

5.1. Taxonomic Review and Phylogenetic Implications

The comparative analysis of morphological characters traditionally used to define *Leukadiella* species suggests that different rib patterns and shell structure are mutually associated and exclusive of some species only. On this basis, two distinct clusters of taxonomic characters can be defined, herein used to separate two morpho-groups: the Helenae Group and the Ionica Group. The marked diversity of these two groups could be bridged by the supposed (though not obvious) transition from the *amuratica-attenuata-jeanneti* ornamental pattern (herein considered as representing one species, namely *L. jeanneti*) to that of species of the Ionica Group (Figure 10); alternatively, the lack of any phylogenetic link between the two groups would point towards their separate origin. In any case, the Helenae and Ionica groups are interpreted as representing two distinct genera. The name *Leukadiella* is maintained for the Helenae Group, whereas the new name *Neoleukadiella* gen. nov. is proposed for the Ionica Group; each genus includes two of the four species herein maintained valid: *L. helenae*, *L. jeanneti*, *N. ionica* comb. nov. and *N. gallitellii* comb. nov.

This revised taxonomy avoids the problem of accounting for a remarkable peculiarity in the systematics of hildoceratids: the inclusion in the same genus of species with straight-clavate simple ribs, or thin-sinuous simple ribs with or without umbilical and ventral tubercles; or even paired ribs with umbilical nodes, or both umbilical and ventral nodes forming fibulae. Indeed, the differences in ornamental and structural patterns used to separate *Leukadiella* and *Neoleukadiella* gen. nov. appear consistent when compared with differences among other genera within hildoceratids or other groups; some examples are provided by *Hildaites* and *Orthildaites*; *Mercaticeras*, *Pseudomercaticeras* Merla, 1933 [85] and *Merlaites* Gabilly, 1974 [86]; *Phymatoceras* Hyatt, 1867 [14] and *Chartronia* Buckman, 1898 [87]; *Paroniceras* and *Frechiella*; and even *Renziceras* and *Leukadiella*.

The problem of the founder species of the Leukadiellinae is an unsolved question. *H. propeserpentinus* (Figure 3a) is frequently considered the most likely direct progenitor of *L. ionica* [25], whereas some coarse-ribbed *Hildaites* (e.g., *H. forte* Buckman, 1921 [19]) or even *Orthildaites* (Figure 3b) are usually assumed as ancestral to *L. helenae*, either directly or via *Renziceras* [17,22–24]. Only the genus herein referred to as *Leukadiella* appears closely related and in morphological continuity with *Renziceras*, from which it can be derived by heterochronic truncation of the adult stage, characterised by evolute coiling and "*Arieticeras*-like" ornamentation (Figures 1a and 5d). Conversely, there is limited evidence for extending heterochrony also to the arising of *N. ionica* comb. nov. from *Renziceras* or even from *L. amuratica* (as proposed by Wendt [23]) or *L. helenae* (as proposed by Macchioni and Venturi [17]). As for the ancestor of the *Renziceras*-*Leukadiella* lineage, the basic morphological features displayed by *Cingolites* (Figure 5a–c) represent a liable prototype from which the *Renziceras* morphological pattern can be derived. In particular, the clavate ornamentation and the broad-coronate venter of *Cingolites* may bridge the *Renziceras-Leukadiella* stock with the strong-ornamented *Hildaites* or *Orthildaites*.

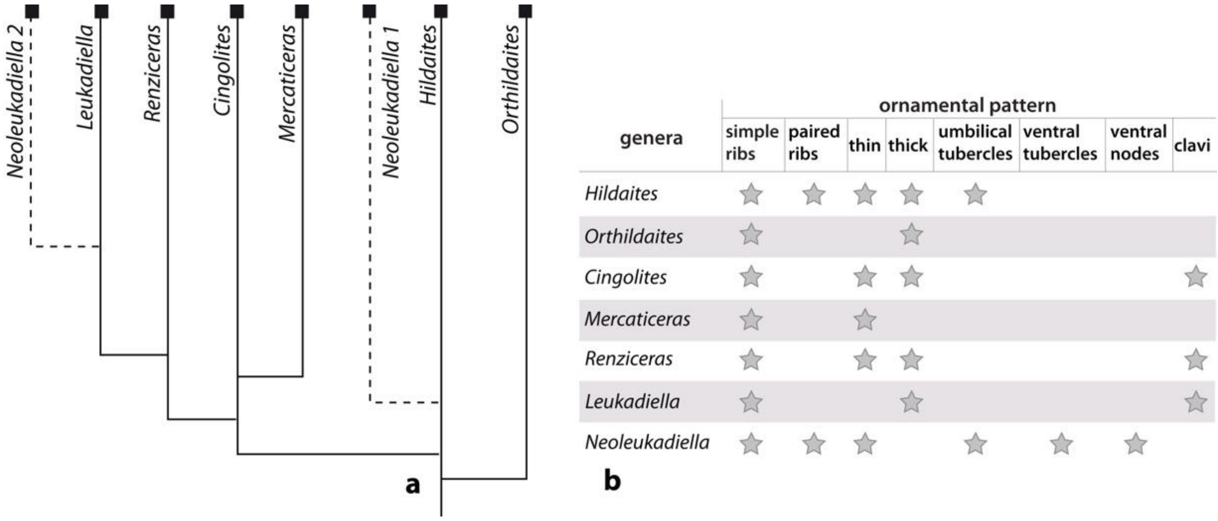
The ornamental pattern displayed by *Cingolites* is similar to the hildaitic coarse-ribbed pattern to a point that Howarth [65] considers this genus as synonymous of *Hildaites*. However, the distinguishing structural and ornamental features described by Sassaroli and Venturi [26] are noteworthy and justify a taxonomic distinction between *Cingolites* and *Hildaites*. In particular, the main features by which *Cingolites* differs from the coarse-ribbed *Hildaites* and *Orthildaites* (i.e., overall clavate ribs and broad coronate venter with wide sulci) are the same by which it appears comparable with *Renziceras*, and thus close to the Leukadiellinae. Despite this evidence, Sassaroli and Venturi [26] accommodate *Cingolites* in the subfamily Hildoceratinae. Furthermore, because both *Renziceras* and *Cingolites* have been recurrently acknowledged as morphologically and phylogenetically comparable either with *Hildaites* and *Mercaticeras*, it is surprising that Sassaroli and Venturi [26] avoided outlining any phylogenetic affinity between their new genus *Cingolites* and *Renziceras*.

The filling of the gap between *Renziceras-Leukadiella* and the *Hildaites* stock significantly attenuates the morphological peculiarity by which the arising of *Leukadiella* has been historically connoted. In addition, the ornamental pattern and the broad sulcated-tricarenated ventral area of *Cingolites* also suggest a possible relationship between this genus and *Mercaticeras*. In this view, the affinity remarked by diverse authors between *Mercaticeras* and *Leukadiella* reflects the sharing of an origin from a common group, rather than an ancestor-descendant relationship.

Tracing the origin of *Neoleukadiella* gen. nov. is instead more difficult, and available data point towards the two possible hypotheses outlined above: one based on the direct derivation from the Helenae Group [17,23] (see Figure 4) and one considering a distinct origin from an earlier hildaitic ancestor (Figure 11). The latter hypothesis relies essentially on the assumption that the paired ribs link *N. ionica* comb. nov. directly to *H. propeserpentinus* [22,25]. However, the double nodes forming fibulae along the ribs of *N. ionica* comb. nov. are markedly different from the nodes and ribbing pattern of *H. propeserpentinus* (as well as from that of any other *Hildaites* species). This observation is not meant to exclude *Hildaites* as a possible ancestor but rather to remark that other alternatives can be considered, including that of a simple ribbed descent, either within the *Hildaites* group or a different one. It is worth noting that nodes and rib-pairing are features that may arise in species stemming from a simple-ribbed morphotype; as, for instance, in the case of *Pseudomercaticeras, Phymatoceras* and *Merlaites*, all with random nodes and coupled ribs though likely descending from the simple-ribbed *Mercaticeras*. As an implication of this reasoning, other alternatives deserve consideration, including that of a less coarsely ornamented variant of *Leukadiella* as a possible precursor of the *Neoleukadiella* (i.e., the *Neoleukadiella* 2 hypothesis in Figure 11)*;* indeed, *L. jeanneti* with its broader ornamental variability, as herein interpreted (Figure 10), may likely be this precursor.

5.2. Internal Clocks and "Unconventional" Evolutionary Mechanisms

The origin of the Leukadiellinae seems consistent with the renowned role of *Hildaites* as a "prolific" founder of early-middle Toarcian groups [17,26,55,77]; a question therefore arises on the reasons why *Hildaites* becomes prolific. Furthermore, remains unclear how paired ribs with nodes and fibulae arise abruptly, manifesting together with simple ribs and in an overall irregular and inconstant pattern. Based on the above results, heterochrony and anagenetic trends only partly account for the diversification of the Leukadiellinae from the Hildoceratinae morphotype. Therefore, other "unconventional" mechanisms may have determined the stemming of new phenotypic variants. The speculation herein put forward is that both the prolificity of the *Hildaites* stock and the abrupt arising of "peculiar" ornamental patterns can be put in relation with some kind of "morphogenetic susceptibility" triggered by environmental perturbation [44,88–91]. In this view, the abrupt arising of morphological novelties may reflect alteration, under unfavourable environmental conditions, of "internal clocks" controlling developmental processes or even silent gene re-activation mechanisms [48].



genera	ornamental pattern							
	simple ribs	paired ribs	thin	thick	umbilical tubercles	ventral tubercles	ventral nodes	clavi
Hildaites	★	★	★	★	★			
Orthildaites	★			★				
Cingolites	★		★	★				★
Mercaticeras	★		★					
Renziceras	★		★	★				★
Leukadiella	★			★				★
Neoleukadiella	★	★	★		★	★	★	

Figure 11. (**a**) = Phylogenetic reconstruction tentatively accounting for the origin of *Renziceras*, *Leukadiella* and *Neoleukadiella*, and their possible relationships with *Hildaites*, *Orthildaites*, *Cingolites* and *Mercaticeras*. *Neoleukadiella* 1 and 2 represent two alternative hypotheses for the uncertain origin of *Neoleukadiella*: in case 1, *Leukadiella* and *Neoleukadiella* are not in direct relationship but share a common origin from the *Hildaites* group (via *Cingolites* and *Renziceras* in the case of *Leukadiella*, from an unknown morphotype in the case of *Neoleukadiella*); in case 2, *Neoleukadiella* arises from *Leukadiella* (possibly via *L. jeanneti*; compare with Figure 10). (**b**) = basic ornamental patterns of genera in (**a**).

One such mechanism is described by Guex [44] based on cases of ammonite lineages which, concomitantly with a deterioration of environmental conditions, tend towards a simplification of their morphology by recalling ancestral patterns (i.e., proteromorphosis). The reappearance of ancestral ornamental features introduces new (though "recycled") phenotypic patterns at the end of a lineage, mimicking a reiterative evolutionary trend starting and ending with comparably simplified morphotypes (i.e., homeomorphism). The ending homeomorph with its simplified morphology often preludes to the arising of a new lineage or even to an evolutionary radiation [44]. This phenomenon has been correlated with the effect of environmental stress and referred to as "reinitialization of evolutionary clocks" [44] (hereinafter REC).

Whatever the mechanism by which the archaic genetic information is maintained and reactivated, the frequently observed re-occurrence of archaic morphologies, also in pathological or injured ammonites [92], is an indication that genetic information relative to ancestral structures is not (completely) lost during phylogenesis [93]. In addition, experimental evidence indicates that environmental stress (thermal or chemical) during the early developmental stages of organisms may alter the ontogenetic expression of phenotypes [88,94,95]; these developmental effects may be key to the understanding of how archaic morphologies are preserved and resumed. In this view, it is likely that, although different, heterochrony and REC may share a mechanism based on the susceptibility of internal (developmental and evolutionary) clocks to external triggering causes (altered/distressed environmental conditions); such mechanisms may be more varied than heterochrony and REC, and manifest diversely in the fossil record.

Differently from REC processes, the relevance of heterochrony in fossil-documented evolutionary events has been poorly considered in the light of its affinity with environmental triggering. Nevertheless, these processes have relevant implications for evolutionary mechanisms because the onset and persisting of ecologically induced phenotypic/developmental changes can be conceived as an epigenetic-like mechanism. In a similar scenario, some interesting implications disclose by assuming that, at least in some cases, the lethal consequences of perturbed developmental processes may be attenuated by the emerging, via REC-like processes, of a "coherent phenotypic anomaly". Coherent phenotypic anomaly is referred to any "abnormal" feature that reproduces a morphological pattern normally displayed by other (usually ancestral) groups. It is thus possible that these stress-induced morpho-genetic changes determine tolerable (though abnormal) phenotypic variants within populations; these are subject to Darwinian selection as any other variant, resulting in their elimination or diffusion. Once screened by selective processes, the uprising phenotypic pattern would be maintained throughout the recession of the external pressure, leading to the ensuing of a morphologically diversified population.

Because environmental stress also results in the overall restriction of favourable living conditions, the size of the ensuing modified populations is influenced and subject to restraining in terms of number of individuals and geographical distribution. At their stemming, the new morphotypes may have a low frequency, ranging between that of pathological individuals and that of small populations struggling to persist a bottle neck-like phase. In this view, the interplay of environmental stress and developmental processes can be considered as an unconventional morphogenetic mechanism that, in addition to classical mutation events (as well as frequently conducive to lethal consequences), prompts Darwinian selection by expanding phenotypic variability. Moreover, because developmental alteration may cause apparently abrupt morphological changes, marked by the reoccurrence of "pre-evolved" structures, phenotypic variation is broadened in a non-gradualist way. Indeed, "monstrous" phenotypes (in the form of coherent phenotypic anomaly) that persist through the stressful conditions by which they spur provide material for selective pressure to burst speciation and marked (macro?) diversification.

5.3. Pathological Morphotypes and "Coherent Phenotypic Anomaly"

The above scenario, although speculative, well describes phenomena recorded in the fossil record and interpreted within the frame of heterochrony, atavism, and REC [28,44]. In addition, pathological specimens documented in the literature show, apart from cripple-like anomalies affecting ornamental features [92], also abnormal morphology of the kind herein referred to as coherent phenotypic anomaly. A typical case is that in which the two sides of an ammonite are different, one reproducing the exact pattern of a related species [93]. However, the limits between "cripple" and "coherent" morphological anomalies are not always obvious. In this respect, an interesting example is provided by two abnormal specimens of *Hildoceras*, one figured by Renz [49] (pl.7, figure 4) and one by Buckman [96] (p. DCCLXXIIIA, figures 1–4). Buckman's "dysmorph" is a specimen of *Hildoceras bifrons* Bruguière, 1789 [97] displaying on one side an abnormal morphology perfectly coherent with the ornamental pattern of its ancestor *Hildoceras laticosta* Bellini, 1900 [98] (Figure 12a,b); Renz's "pathological form" shows ribs on the last whorl that tend to merge along the ventral margin, by this recalling the ornamental pattern typical of *N. ionica* comb. nov. (Figure 12c). Although different in many respects from those developed by *Neoleukadiella* gen. nov., the ventral "pseudonodes" of this abnormal *Hildoceras* provide evidence for the possible occurrence of such morphological features as a consequence of some kind of dysfunction.

The assumption herein made is that the abrupt arising of peculiar ornamental patterns, such as those displayed by the Leukadiellinae (in particular by *Neoleukadiella* gen. nov.), can be foreseen as one among other cases of stress-induced altered development and/or re-occurrence of ancestral-like morphological features, rather than representing inheritance from a direct ancestor retaining similar characters (i.e., *Hildaites* species or others retaining a precursor homology in their ornamental pattern). Coarse ribs with tubercles, nodes and spines are indeed frequently displayed in diverse ammonite groups, some of which within lineages ancestral to the Hildoceratinae (as for instance *Bouleiceras*, among others).

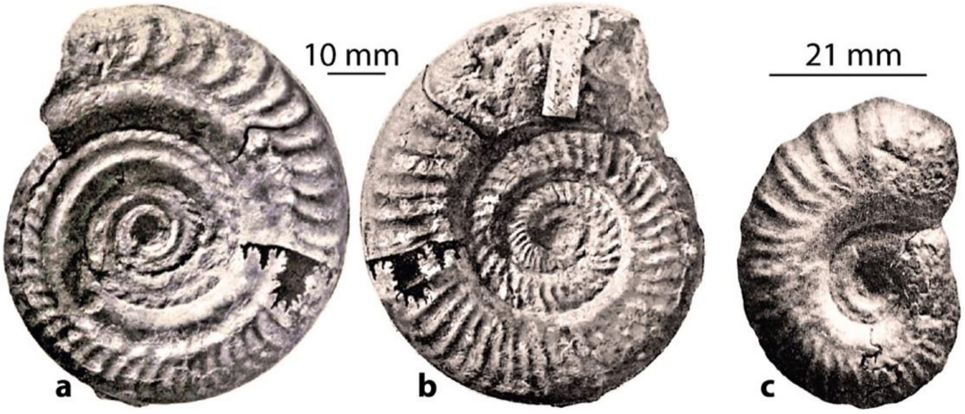


Figure 12. (**a**,**b**) = pathological specimen of *H. bifrons* with an abnormal side (**b**) perfectly resembling the ancestral species *H. laticosta* (from Buckman [96]). (**c**) = pathological specimen of *H. bifrons* with abnormal ribs merging at the umbilical and ventral margin of the final whorl (from Renz [49]), similar to the fibulae occasionally occurring in *N. ionica* comb. nov.

Although it is not possible to unambiguously link any of such mechanisms to the emerging of the specific morphological changes displayed in the fossil record by species of the Leukadiellinae, they are a valid alternative to supposed (though stratigraphically not evident) continuous and gradual anagenetic trends originating from species of *Bouleiceras* or *Hildaites*. Moreover, their possible relationship with environmental stress accounts for the reduced areal and stratigraphic distribution of the ensuing species, as well as for the poor number of findings and small size of individuals, which are all features that one would expect from populations that are struggling to survive under unfavourable conditions. The migration to different (and possibly more favourable) environments may account for the increasing of average growth size, as in the case of the North American representatives (herein interpreted as representatives of *Neoleukadiella* gen. nov.).

5.4. Environmental Stress, Species Resilience and Biodiversity Recovery

One of the most invoked causes of protracted environmental perturbation with evolutionary implications is the giant volcanism and the resulting effects on water/atmosphere chemistry and global climate [27,38,39]. Some major extinctions appear correlated with these events and also with regional-global marine regressions, in some cases associated with negative trends in $\delta^{13}C$ [44]. Among these there is the late Pliensbachian-early Toarcian crisis, triggered by the Karoo magmatic event and recorded by marine transgression-regression events and black shale deposition [40,41,43,45]. The spreading of the Hildoceratinae is commonly interpreted in terms of an evolutionary radiation following this environmental crisis and the subsequent extinctions [42,44,99].

According to the available biostratigraphic data, the *Leukadiella*-*Neoleukadiella* stock occurs in the Bifrons Zone (Lusitanicum Subzone at the Polino section; Figure 6). This interval post-dates the early Toarcian crisis and recovery of the Hildoceratinae, when *Cingolites* and *Renziceras* (or even an unknown direct ancestor of *Neoleukadiella* gen. nov.) are supposed to appear. Notwithstanding the uncertainties on the origin of *Neoleukadiella* gen. nov., even in the case of the origin of *Leukadiella* there is a noticeable stratigraphic gap separating it from *Renziceras.* This stratigraphic gap may be a consequence of the amplification of the low frequency of *Leukadiella* in the lower Toarcian, an interval where also other groups become infrequent [24]. In the Apennines, this interval corresponds to a sterile or poorly fossiliferous part of the Rosso Ammonitico Formation (Figure 6), known as “unnamed zone” because of the lack of biostratigraphic markers [1,100]; sediments of this interval are often affected by anoxic events [55].

In this view, the restriction to the Bifrons Zone of the occurrence of *Leukadiella* may reflect a biased first appearance datum; indeed, one finding of *Leukadiella* below the

Bifrons Zone is reported in the literature [17]. This may indicate that earlier populations of *Leukadiella*, if ever existed, were even smaller than during the Bifrons Zone, when they grew somewhat larger though never reaching the wealth of other coeval groups (e.g., *Hildoceras* and *Mercaticeras*, among others). Possibly, pulses of resurging environmental stress during the Bifrons Zone may have impacted on these striving populations of *Leukadiella*, determining their final extinction or even enhancing the arising of the abnormal and somewhat atavistic morphological features (e.g., thin-sinuous simple ribs and paired ribs with umbilical and ventral nodes) displayed by *Neoleukadiella* species (in accordance with the "*Neoleukadiella* 2" hypothesis; Figure 11).

More in general, the sterile or poorly fossiliferous intervals in the lower Toarcian Rosso Ammonitico may record a period of recovery and resilience of the few species that survived the late Pliensbachian-early Toarcian extinction events; locally, restrained populations gave rise to new morphotypes, only some of which persisted until the next extinction or the next evolutionary radiation. The evolutionary radiations following extinctions are traditionally correlated with the simplification of morphological patterns at the end of the surviving lineage [44]; this simplification is interpreted as a way for the survivals to regain "adaptation potential" and evolvability towards new complexity. However, it is also likely that the "peculiar" phenotypes emerging during these periods of environmental and biological crisis are as well prime to the stemming of morphologically new evolutionary lineages, by which biodiversity loss is partly healed (or even increased).

As an example, despite their overall simple morphology, the *Hildaites* species spreading immediately after the crisis display a number of different (sometimes contrasting) ornamental variants, as for instance: rib thinning and increasing in number or thickening and spacing out; trends towards more sinuous or strait ribs; umbilical tubercles and nodes grouping ribs or fading of the umbilical termination of ribs; this latter trend leading to the complete disappearance of the umbilical segment and the forming of the umbilical wall and smooth band preluding to the *Hildoceras* morphotype [101,102]. Following this early Toarcian radiation, while the *Cingolites-Renziceras-Leukadiella-Neoleukadiella* branch was not particularly successful, most of the ornamental and structural novelties introduced (or re-introduced) by the early Hildoceratinae persisted in other groups such as *Mercaticeras*, *Pseudomercaticeras*, *Merlaites* and *Phymatoceras*, significantly contributing to the middle Toarcian differentiation of diverse ammonite lineages.

6. Conclusions

The rarity of specimens of *Leukadiella* (only 70 findings worldwide documented in the literature) is a renowned obstacle to their understanding and classification, an issue further complicated by the peculiar morphology of this taxon compared to that of other Hildoceratidae. It is not simple to define distinctive morphological traits for tracing the limits and defining the relationships between most of the historically established species, or for reconstructing their phylogeny with respect to other groups. Moreover, the supposedly related genera as well are infrequent in the stratigraphic record. *Renziceras*, for instance, is even less common than *Leukadiella*, with only seven findings in the Apennines and a total of nine documented worldwide.

The comparative analysis of taxonomic characters (largely based on figures) indicates that the morphological differences that authors have referred to for distinguishing up to eleven species smooth to a point that their number reduces to only four; these are parted in the two genera *Leukadiella* and *Neoleukadiella* gen. nov. as follows: *L. helenae*, *L. jeanneti*, *N. ionica* comb. nov. and *N. gallitellii* comb. nov. Only genus *Leukadiella* appears closely related and in morphological continuity with *Renziceras*; the origin of *Neoleukadiella* gen. nov. remains dubious and may be tentatively derived either from *Leukadiella* or from an unknown early Toarcian progenitor. Both the *Renziceras-Leukadiella* branch or the putative unknown progenitor of an independent *Neoleukadiella* gen. nov. likely descend from the *Hildaites* stock. In the case of *Renziceras-Leukadiella*, an intermediate morphotype has been identified in *Cingolites,* an Apennine genus morphologically bridging the coarse-ornamented *Hildaites* and the clavate-ribbed *Renziceras*. In addition, some ornamental and structural features of *Cingolites* also suggest a possible relationship with *Meracaticeras* (likely the progenitor of other species with paired ribs and nodes, such as *Pseudomercaticeras*, *Merlaites* and *Phymatoceras*).

The simple ribs with double tubercles of *N. gallitellii* comb. nov. and, even more, the fibulate ribs of *N. ionica* comb. nov., represent brand-new ornamental patterns within the Hildoceratidae that cannot be directly derived from any pre-existing ornamental pattern within *Hildaites*, *Orthildaites, Renziceras* or other lower Toarcian Hildoceratinae; therefore, linking *Neoleukadiella* with other taxa requires a morphological jump. In the light of this unavoidable discontinuity, also a parental relationship with *Leukadiella* deserves consideration. For instance, *Leukadiella* and *Neoleukadiella* gen. nov. may be bridged based on some "peculiar" features by which *L. jeanneti* is distinguished with respect to *L. helenae*; these may include the tendency towards less thick ribs and fading of the umbilical segment of secondary ribs, altogether resembling (and perhaps being precursor of) ribs paired by umbilical nodes.

As a conceptual exercise, the origin of the straight-clavate ribs in *Cingolites* (later accentuating in *Renziceras-Leukadiella*) and the arising of the sigmoidal-fibulate ribs in *Neoleukadiella* gen. nov. may be interpreted in the frame of developmental distressing, instead of a direct inheritance via anagenetic trends from an ancestor already possessing similar characters. Altered development may result in abnormal (i.e., pathological) individuals or in phenotypic effects comparable to those emerging during heterochrony and REC-like processes. These include the reactivation of silenced developmental schemes by which ancestral structures are resumed. The resumed characters may retain a "coherent morphology" by which they may not result lethal, although being the expression of a pathological or disease-like induction effect. The ensuing modification may be conceived as any other mutation-driven morphological change, and thus reveal neutral, advantageous or disadvantageous under selective pressure. Therefore, the unconventional evolutionary processes herein invoked are not meant as in contrast with Darwinian selection, but rather as a morphogenetic mechanism complementary to punctual gene mutation, potentially capable of expanding in a non-gradualist way the phenotypic variability on which selective processes operate.

From an evolutionary perspective, the problem arising concerns the mechanism by which ecologically induced developmental (regulatory) changes become "genetically fixed" in order to persist on the long-term and give rise to a new phyletic lineage, rather than resulting in an abnormal phenotype that would be wiped out within one generation or in the next few ones. The existence of a similar mechanism has implications as to the meaning and impact of epigenetic-like processes during evolution. It is worth noticing that the abrupt emerging of new morphologies under the control of this overall epigenetic-like mechanism is not viewed as a direct adaptive response to environmental pressure, but rather as a consequence of a stress-induced dysfunction that casually reintroduces pre-existing morphological patterns. As a paradox, the main impact of epigenetic-like processes in determining marked morphological modifications during evolutionary events would result from the resuming of "preformed" structures. While the above hypotheses are evidently speculative, they are conceptually intriguing in the light of exploring evolutionary pathways from a paleontological perspective, specifically by relying on the reading of the "*Leukadiella* event" as it appears from the stratigraphic record.

Funding: This research received no external funding.

Data Availability Statement: Specimens PO_LE10G2 and PO_LEd1 (the only collected material used in this study) are available at the Paleontological Museum of the Earth Science Department, Sapienza University of Rome.

Acknowledgments: I am grateful to J. Sandoval and two anonymous reviewers for contributing significantly to the improvement of the manuscript with constructive comments and suggestions. I also wish to thank the Guest Editors P. Pellenard, E. Mattioli and G. Dera for their assistance and support.

Conflicts of Interest: The authors declare no conflict of interest.

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