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Leukadiellinae, n. subfam. of the Lower and Middle Toarcian. Origin and evolution of the genera *Renziceras* Arkell (1957) and *Leukadiella* Renz (1913)

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ABSTRACT – During the biostratigraphic sampling in the Rosso Ammonitico Umbro-Marchigiano (Toarcian) in the locality of Migiana di M. Malbe (Corciano, PG), a specimen of the genus *Leukadiella* Renz was found with ventro-lateral spines. This find provided the stimulus to reconsider unpublished data from other locations currently under study, and to re-examine the systematic position of the genus *Leukadiella* and, for the first time, of the genus *Renziceras* Arkell. This has been possible in the latter case thanks to the opportunity to examine a fair number of specimens, given that almost 90 years after the species was erected (*H. nausikae*, Renz, 1913), no other find of a specimen of the same had been published. The approach to the investigation took into consideration both the general morphology of the shells and their palaeogeographic and biostratigraphic distribution. The remarkable morphological similarity between *Leukadiella* and *Renziceras* proves that the former developed from the latter by neoteny instead of deriving from *Bouleiceras* Thevenin, as has until now been suggested by many authors. For this reason we believe that the institution of the subfamily *Leukadiellinae* n. subfam. should be considered, in order to set the former two genera in a more appropriate taxonomic entity, separating them distinctly from the subfamily *Bouleiceratinae*.

We also take the opportunity to illustrate two specimens of *Nejdia* Arkell, a genus found for the first time in the Umbria-Marche Apennines, which were discovered in the S. Anna Quarry (Passo del Furlo, PS). Both forms are described both because of the novelty of their discovery and for comparison with the *Leukadiellinae*.

RIASSUNTO – [I *Leukadiellinae*, n. subfam. del Toarciano inferiore e medio. Origine ed evoluzione dei generi *Renziceras* Arkell (1957) e *Leukadiella* Renz (1913)] – Recenti ricerche condotte nei livelli del Toarciano medio ed inferiore del Rosso Ammonitico Umbro-Marchigiano, hanno fornito nuovi dati sulla distribuzione stratigrafica dei generi *Leukadiella* Renz (1913) e *Renziceras* Arkell (1957), spingendoci a riconsiderare la loro posizione sistematica.

I due generi sono piuttosto rari, basti pensare che *Renziceras nausikae* (Renz) dall'anno della sua istituzione nel 1913 non è stata più figurata successivamente. Al contrario, sono facilmente riconoscibili per la loro caratteristica morfologia spinosa.

Il ritrovamento di un discreto numero di esemplari di entrambi i generi ha permesso di definire per la prima volta la loro distribuzione stratigrafica a livello subzonale. Il genere *Renziceras* risulta limitato alla porzione superiore della Zona a *Harpoceras serpentinum* (orizzonte ad *Orthildaites douvillei*), mentre *Leukadiella* si estende dagli stessi livelli del genere anzidetto fino alla parte alta della Zona a *Hildoceras bifrons* [sottozona a *H. semipolatum*].

In base alla distribuzione geografica ed al numero dei ritrovamenti degli esemplari dei generi *Leukadiella* e *Renziceras* risulta che il primo dei due è tipico delle aree Apula ed Appenninica, data la sua relativa abbondanza nell'Appennino Umbro-Marchigiano, in Lombardia e nella Grecia Occidentale. Ritrovamenti sporadici sono stati riportati nella Sicilia Occidentale, in Spagna, Algeria, Sud America e Canada. Quest'ultimo ritrovamento è degno di nota in quanto il ritrovamento di esemplari di *Leukadiella* si associa a quello di *Rarenodia* Venturi, altro tipico genere apulo-appenninico.

Da quanto emerge dai nostri dati e dall'analisi della letteratura la distribuzione paleogeografica del genere *Renziceras* è quasi la stessa di quella di *Leukadiella*. Finora è stato segnalato in Grecia, nell'Appennino Umbro-Marchigiano ed in Algeria. In base alla nostra analisi la sua distribuzione può anche essere estesa alla Spagna (Betico).

La maggior parte degli autori, che si sono occupati dell'origine del genere *Leukadiella*, ha sempre ipotizzato una sua discendenza da *Bouleiceras* Thevenin (1908), sulla base di alcune affinità riguardanti la forma delle coste e la sezione della spira. Quest'ultima è però più larga che alta in *Leukadiella* mentre in *Bouleiceras* risulta il contrario. In *Leukadiella* inoltre, i tubercoli ventrali non sono altro che il punto di inserzione di lunghe spine che si sviluppano parallelamente al piano di simmetria della conchiglia, mentre in *Bouleiceras* le spine sono corte, inserite in prossimità del margine ombelicale e sviluppate perpendicolarmente a detto piano. Anche nelle linee suturali dei due generi vi sono notevoli differenze. Nei *Leukadiella* la porzione ombelicale è ridotta, con lobi ombelicali piccoli e spesso non chiaramente identificabili e le selle sono sempre frastagliate. Al contrario nei *Bouleiceras* lo stile della linea suturale è pseudoceratitico, cioè con selle non frastagliate e lobi sempre ben individuabili.

Negli esemplari più antichi del genere *Leukadiella*, le linee suturali hanno uno stile marcatamente hildoceratino, che suggerisce quindi un legame filogenetico con i *Renziceras*, la cui struttura generale della conchiglia negli stadi più precoci dell'ontogenesi è identica a quella di *Leukadiella*. La mancanza di un elevato numero di esemplari non ci permette di effettuare uno studio biometrico più ampio, tuttavia si ritiene che possa trattarsi di un passaggio di tipo neotenic. Le caratteristiche morfologiche generali, lo stile delle linee suturali e motivazioni biostratigrafiche permettono di escludere un legame filogenetico alternativo di discendenza di *Leukadiella* da *Bouleiceras* attraverso *Renziceras*. Gli stessi elementi invece, suggeriscono un legame con forme grossolanamente costate come il genere *Orthildaites* Buckman o, con le forme di *Hildaites* Buckman a coste poco flussuose.

L'ipotesi di derivazione filogenetica qui proposta, spinge a considerare inadeguate le posizioni sistematiche dei generi *Renziceras* e *Leukadiella* che riteniamo debbano essere inclusi in una nuova sottofamiglia, *Leukadiellinae* (Hildoceratidae), di cui proponiamo l'istituzione.

Il ritrovamento di *L. morettinii* n.sp., al tetto della Zona a *H. serpentinum* ci permette anche di modificare precedenti ipotesi evolutive espresse su questo genere, che prevedevano *L. helenae* come progenitrice del gruppo che si estinguerebbe con *L. sima* Kottek (1966). Quest'ultima specie possiede poi, notevoli affinità morfologiche con *L. lombardica* Pinna, *L. gallitellii* Pinna e *L. attenuata* Wendt. L'esame delle caratteristiche morfologiche di queste specie suggerisce che si possano inquadrare nello stesso taxon.

Si coglie l'occasione per figurare anche due esemplari di *Nejdia* Arkell (1952) ritrovati nel detrito della Zona a *H. bifrons* nella Cava di S. Anna (Passo del Furlo, PS). I due reperti sono stati introdotti nel lavoro sia per l'eccezionalità del rinvenimento, in quanto fino ad ora non erano stati ancora segnalati nell'Appennino Umbro-Marchigiano, sia per confrontare i *Leukadiellinae* con un genere chiaramente appartenente ai *Bouleiceratinae*.

INTRODUCTION

The Bouleiceratinae are one of the most interesting groups in the Toarcian, due to their morphological characteristics and rarity. They can easily be distinguished from other contemporary forms by their suture lines and morphology, and within the context of the Hildoceratidae are considered degenerate because of their suture line (Arkell, 1952) or aberrant (Donovan *et al.*, 1981). Various Authors have concerned themselves with this subfamily, among them Bonarelli (1893, 1895), Thevenin (1908), Renz (1913; 1922; 1925; 1927), Renz & Renz (1946), Deleau (1948), Arkell (1952), Gallitelli Wendt (1963; 1969), Zanzucchi (1963), Geyer (1965), Pinna (1965), Wendt (1966), Pelosio (1968), Levi-Setti (1972), Guex (1973 a, b; 1974), Hillebrandt (1973; 1984), Hillebrandt & Schimdt-Effing, (1981), Braga *et al.* (1985), Venturi (1986), Howarth (1992), Jacobs *et al.* (1994), Jacobs (1995), and Goy & Martínez (1996). We owe the institution of the subfamily to Arkell (1950), who later (Arkell *et al.*, 1952, p. 260) thought it possible that there was a relationship between the genera *Bouleiceras* and *Paroniceras* and between the former and *Nejdia* Arkell (op. cit., p. 266). This hypothesis was only partially concretised with the formalisation of the subfamily, which currently includes the genera *Bouleiceras* Thevenin, *Frechiella* Prinz, *Paroniceras* Bonarelli and *Leukadiella* Renz. Arkell himself (in Arkell *et al.*, 1957) admitted that some morphological similarities between the genera included therein might have been due to evolutionary convergence. The genus *Nejdia* Arkell was not included in the Bouleiceratinae, but instead was placed, albeit tentatively, in the Hammatoceratidae. On the other hand, when Thevenin (1908; p. 12) instituted the species *N. pseudogrumeri*, he stated that *Nejdia* was part of a new group of Harpoceratinae which had greater affinity with the genus *Frechiella*.

Later, Guex (1973 a, 1974) added the genera *Oxyparoniceras* Guex (1974) and *Nejdia* to the Bouleiceratinae, and also proposed a phyletic scheme of the group for the first time, taking up of the opinions expressed by earlier authors. In this phyletic framework, he proposed that *Bouleiceras* succeeded *Tauromeniceras* Fucini of the upper Domerian, keeping the latter in the Arieticeratinae. The group would then have evolved along a main line which includes, in order, *Bouleiceras*→*Nejdia*→*Frechiella*→*Paroniceras*→*Oxyparoniceras*; each of these is supposed to have derived from the preceding one by palingenesis, whilst *Leukadiella* represents the only lateral branch, deriving from *Bouleiceras* by proterogenesis.

Guex's hypothesis, which is still accepted by Howarth (1992), contrasts with Kottek's earlier hypothesis (1966), according to which *Leukadiella* is supposed to have derived from the *Hildaites* gr. *prope-serpentinum* Buckman.

The idea of a close relationship between *Boulei-*

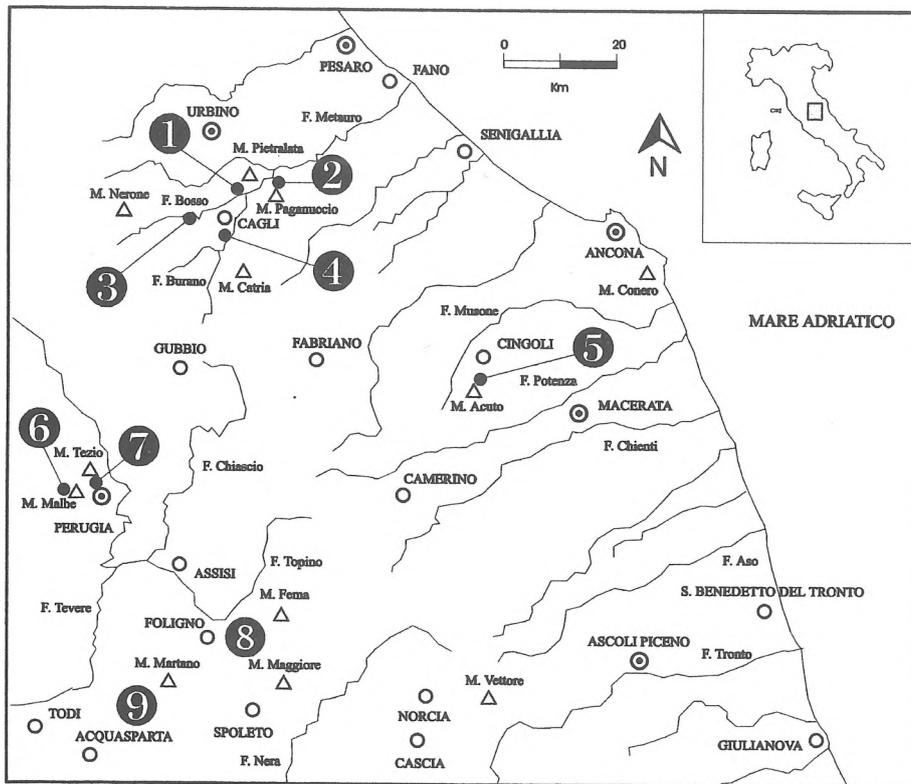
ceras and *Leukadiella* was probably born when Gallitelli (1963) reported the finding of a specimen denominated *Bouleiceras* aff. *marraticum* Arkell. From then on, *Bouleiceras* was generally accepted as the most likely progenitor of *Leukadiella*, as for example did Wendt (1966) and more recently Goy and Martínez (1996). Pinna (1965) renamed Gallitelli's specimen *L. gallitellii* Pinna, and noted that the similarities between *Bouleiceras* and *Leukadiella* are superficial and had led to errors of attribution. Guex (1974), again in order to explain the *Bouleiceras*-*Leukadiella* lineage, held that it was necessary to document the presence of the latter in the *H. serpentinum* Zone; as this evidence was not available, he cited the paucity of fossils in the Greek and Apennine successions of this Zone. According to Braga *et al.* (1985), Guex's phyletic hypothesis (1974) was confirmed by the finding of a specimen of *Leukadiella* sp. in the upper part of the *H. serpentinum* Zone. Lastly, Jacobs (1995) took up Kottek's (1966) idea again, accepting as possible the *Hildaites*-*Leukadiella* derivation, thus including the latter genus in the Hildoceratinae; this with the backing of a private communication from Guex (1992), who no longer supported the idea that the genus *Leukadiella* belonged to the Bouleiceratinae.

In contrast with the genus dealt with above, publications concerning to the genus *Renziceras* Arkell are extremely scarce. It must be emphasised that about eighty-six years have passed since the institution of the type-species (*H. nausikaae* Renz, 1913) and forty-two since the institution of the genus by Arkell (1957). The only note regarding the phylogenetic relationships of *Renziceras* was by Elmi and Rulleau (1995), who believed it possible that *Renziceras* might be a microconch of *Furloceras* Elmi & Rulleau.

The research carried out over the last few years in the Rosso Ammonitico Umbro-Marchigiano has provided a large number of specimens from the *H. serpentinum* Zone, among them being forms attributable both to *Leukadiella* and to *Renziceras*. The similarity between these two genera is remarkable, and is greater than that between *Bouleiceras* and *Leukadiella*. For morphological and biostratigraphic reasons, we therefore believe that *Leukadiella* derives from *Renziceras*, which in turn is not considered to be linked phyletically to *Bouleiceras*.

BIOSTRATIGRAPHY AND PALAEOGEOGRAPHY OF THE GENERA *LEUKADIELLA* E *RENZICERAS*

The genus *Leukadiella* is easily recognisable from its morphology, and is remarkable because of its rarity and its provincialism. It may be considered typical of the Apulian Apennines area, given its relative frequency in Western Sicily, Umbria-Marche Apennines, Lombardy and Western Greece (Renz & Renz, 1946; Arkell *et al.*, 1957; Pinna, 1965; Wendt, 1966; Pelosio, 1968; Ziegler, 1981; Mouterde & Elmi, 1991).



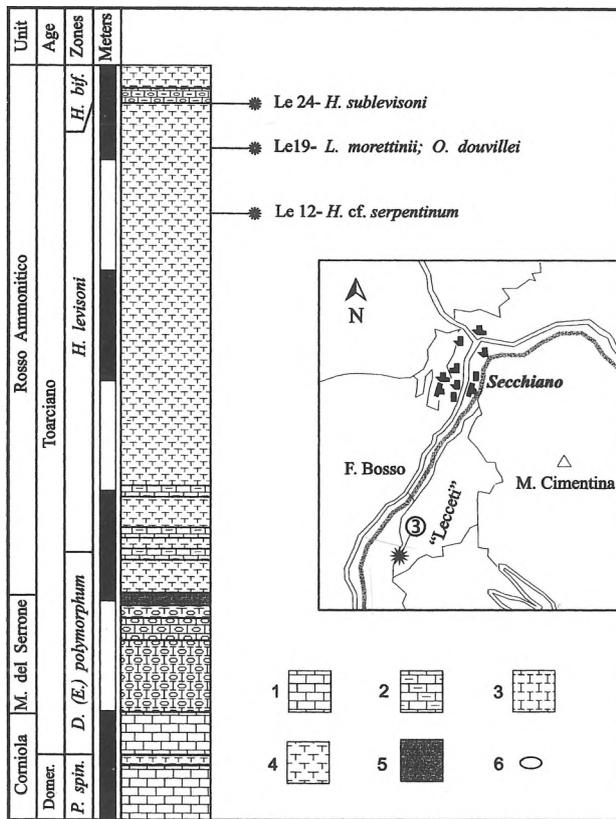
Text-fig. 1 - Location of the stratigraphic sections studied. 1) P.so del Furlo, Grilli Quarry CG; 2) P.so del Furlo, S. Anna Quarry SA; 3) F. Bosso, "Eremita" section, B.ER and "I Lecceti" section, Le; 4) F. Burano, Bu; 5) Cingoli, S.I.E.L.P.A. Quarry, SIE; 6) Migiana di M. Malbe, MM; 7) F.so della Colognola-M. Tezio, FCT; 8) M. di Civitella, MC and Pettino, Pe; 9) Cima Panco, CP and F.so di Pozzale, Po.

Howarth (1992) attributes a specimen found in England (Dorset) to the genus, but this attribution is questionable as it will be explained later. Other finds outside the typical area have been made in Algeria by Deleau (1948) and in South America (Hillebrandt & Schimdt-Effing, 1981; Hillebrandt, 1984); noteworthy for the number and size of specimens are those made by Jacobs *et al.* (1994) and Jacobs (1995) in North America. We would emphasise that in the latter region the genus has been figured together with *Rarenodia* Venturi, another genus typical of the Apulian region (Mouterde & Elmi, 1991). In Spain there are two specimens classified as *Leukadiella* sp.: of these, one has only been mentioned, not figured, and comes from Turmiel (Iberian basin; Goy & Martínez, 1996); the other was found at Sierra de Ricote (Murcia, Subbetic) by Braga *et al.* (1985) and is also reported in Goy *et al.* (1988), Jiménez Jiménez & Rivas Carrera (1992) and Goy & Martínez (1996). According to the respective Authors, the former probably comes from the lower part of the *H. bifrons* Zone, whilst the latter is recorded from the upper part of the *Harpoceras serpentinum* Zone. However, in the Umbria-Marche Apennines, the Lombardy area, Greece and North America, the genus *Leukadiella* has up until now only been found in the *H. bifrons* Zone, as already noted by Renz & Renz (1946), Pinna (1965), Wendt (1966), Gallitelli Wendt (1969), Levi-Setti (1972), Jacobs *et al.* (1994) and Jacobs (1995).

Again, as the literature tells us, the palaeogeographic distribution of the genus *Renziceras* can coincide with that of *Leukadiella*. Until now, though, *Renziceras* has been found in Greece (Renz, 1913; Mouterde & Elmi, 1991), Italy (Venturi, 1986) and Algeria (in Nador; Mouterde & Elmi, 1991). In the Umbria-Marche Apennines its stratigraphic distribution is limited to the upper part of the *H. serpentinum* Zone (Venturi, 1986). More particularly, all the specimens collected *in situ* come from the *Orthildaites douvillei* horizon. We consider that the specimen found by Braga *et al.* (1985) in the *H. serpentinum* Zone, named *Leukadiella* sp., should be attributed to *Renziceras*; this hypothesis is shared by Braga and Jiménez (personal communication, 1998). The palaeogeographic distribution of *Renziceras* must therefore be extended to the Subbetic as well.

TAPHONOMIC CONSIDERATIONS

Although taphonomy is a relatively long-established discipline in the sphere of geological sciences, interest in the subject has been spreading in recent years thanks to a series of theoretical/practical criteria worked out above all by Fernández López (1984; 1986; 1987 a and b). The importance of these studies on the formal and practical levels of biostratigraphic and evolutionary studies can be well understood when one considers, for example, the conclu-



Text-fig. 2 - Stratigraphic section of Lecceti, F. Bosso, Cagli (PS). 1) Limestone; 2) marly limestone; 3) calcareous marl; 4) Marl; 5) Anoxic event; 6) nodules.

sions drawn by Pavia (1994) on the Bayeux succession.

The examples figured come from layers in the Rosso Ammonitico Umbro-Marchigiano, more specifically from the levels of Lithofacies A and B as described in Nini *et al.* (1996), which can be referred to for further information on the lithostratigraphic characteristics.

Most of the specimens collected *in situ* were lying in the parallel plane position relative to the stratification surface. These are preserved in the form of homogeneous and differentiated internal moulds (Macchioni *et al.*, 1996). In the first case, the phragmocone is uniformly filled with micrite, whilst in the second a portion of the phragmocone has the upper half filled with marl and the lower with micrite. According to Macchioni *et al.* (1996), the partial infill has geopetal meaning due to the frequency with which the infilling superposition reflects the polarity of the stratification.

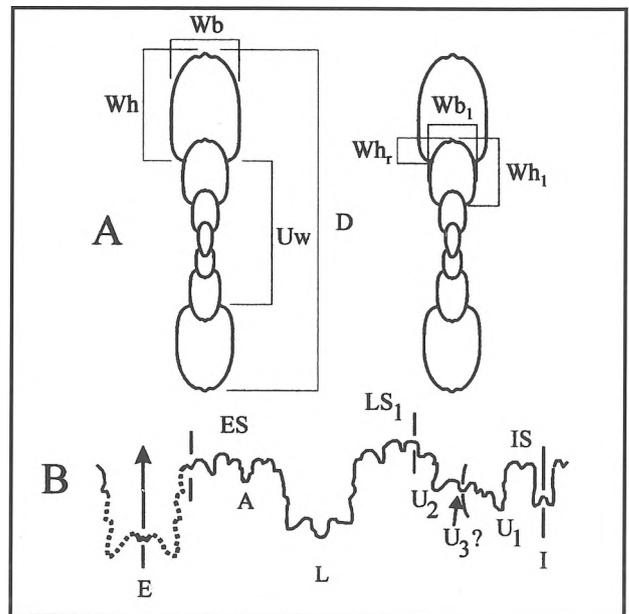
Specimen 434MM6.37 of *L. helenae* was extracted together with the cast and isolated from the latter in the laboratory, a precaution which allowed the spines to be preserved. The extreme rarity with which spines are preserved in this genus seems to indicate

that they were fairly delicate; for this reason the fossil is thought to have been accumulated. This implies that conditions of relative stability of the substratum existed in that level. The same can not be said in the case of specimens 432MM5.21 and 589MM5.15, which have a certain amount of wear on both sides. However, their stratigraphic position coincides with that of other specimens of the same species found both in the same and in other successions studied. The level of taphonomic condensation (Gómez & Fernández López, 1994) is therefore very low.

TERMINOLOGY

For terms relating to ornamentation we would refer to Arkell *et al.*, (1957) as well as to Venturi (1985). The nomenclature of the suture line (Text-fig. 3) has been derived from the works of Schindewolf (1963), Wiedenmann (1973) and Wiedenmann & Kullmann (1981).

Every specimen has an inventory number composed of a code which refers to the succession in which it was found and a progressive location number. The list of codes is shown in the caption to Text-fig. 1. In the case of the specimens found by F. Macchioni, the inventory number comes before the code, which is followed in turn by a number which refers to the stratigraphic position of the specimen (expressed in metres) determined during sampling, or by the code dt. if the specimen came from detritus.



Text-fig. 3 - A) Transversal section of an ammonite: Spiral: Uw/D; flattening: Wb/Wh; growth in height A; growth in width A₁; Wb₁/Wb; overlap: Wh₁/Wh. B) Complete suture line of *L. aff. jeanneti* (Le 18), with the names of the lobes and saddles used in this study.

All the specimens mentioned in the text are deposited at the Dipartimento di Scienze della Terra of the Università degli Studi di Perugia.

SYSTEMATIC SECTION

Order AMMONOIDEA Zittel, 1884
 Suborder AMMONITINA Hyatt, 1889
 Superfamily HILDOCERATACEAE Hyatt, 1867
 Family HILDOCERATIDAE Hyatt, 1867
 Subfamily LEUKADIELLINAE n. subfam.

Type genus – *Leukadiella* Renz, 1913.

Definition of the Subfamily – Evolute to moderately involute forms, with sub-quadrate, sub-rectangular or sub-trapezoidal spiral sections and Wb/Wa ratio greater than or equal to one. Straight or rounded umbilical step. Ventral area ranging from tri-carinate and bisulcate to carinate and non-sulcate. The ribs can be simple or bifurcate, and in the latter case can join together either at the peri-umbilical or at the ventro-lateral margin. They can be prorsiradiate or rursiradiate, or rectiradiate. There are also ventro-lateral and peri-umbilical tubercles and, more rarely, some half-way up the side; the former can be interpreted as being seatings for spines oriented perpendicularly to the spiral axis of the shell. The ornamental style (the design of the ribs, the presence of double or triple ribs and so on) can change during the course of ontogenesis.

The hildoceratitic suture line is sometimes simplified due to the reduction in the number, fringing and depth of the lobes.

Stratigraphic distribution – From the upper part of the *H. serpentinum* Zone, *O. douvillei* horizon, to the *H. bifrons* Zone, subzone *H. semipolitum*.

Genus LEUKADIELLA Renz, 1913

Type species – *Leukadiella helenae* Renz, 1913, pp. 587-590, pl. 14, figs. 1-3, by original designation.

Stratigraphic distribution – Upper part of the *H. serpentinum* Zone, *O. douvillei* horizon, to the *H. bifrons* Zone, subzone *H. semipolitum*.

Earlier descriptions – According to Arkell *et al.* (1957; L 260) the genus is characterised by an “evolute shell decorated with large, separated simple ribs (eight per whorl in the type), which terminate in robust clavi above a keel sunk into a concave venter; the suture line is extremely degenerate”.

In his revision of the genus, in part produced by re-examining the forms collected over various years by Renz, Wendt (1966) provides a more exhaustive diagnosis than that of Arkell (1957), which was more suitable as a description of the type-species only.

Thus, according to Wendt (1966, p. 138), the genus is characterised by a “more or less large umbilicus and the spiral section which can be largely rounded to quadrate. The ornamentation consists of simple rectiradiate ribs, markedly swollen or rursiradiate; these may be double, and may join at marginal or umbilical nodes. Strong keel, often with well-marked siphon grooves. Suture line a little fringed and degenerate, with a maximum of three umbilical lobes. Lobe L wide and simply fringed, I with one point”.

New definition – Based on the analysis of specimens at our disposal and those figured in the literature, we believe that the diagnosis of the genus should be redefined in the following terms:

Evolute to moderately involute (0.33 to 0.49) shell due to variable growth of the coiling, sub-quadrate to sub-trapezoidal whorl section with slightly convex sides, or wide sub-rectangular with largely rounded sides. The keel may be raised and flanked by sulci, the depth of which decreases during growth until they disappear, or remains sunk into a concave ventral area due to the protrusion of marginal-ventral tubercles. Ornamentation comprises clavate ribs which are straight, slightly prorsiradiate and with only slight ventral projection (“L”-shaped), or more or less flexuous ribs projecting markedly into both the umbilical wall and the ventral area (sigmoid). These form tubercles on the ventro-lateral margin, which in some species take on a parabolic pattern. The ribs may be double or single; in the first case primary ribs have generally been seen to be more raised with secondary ribs which may or may not join the former on the ventro-lateral tubercles, or ribs which are fibulated both at the umbilical border and in the ventro-lateral margin with equal relief and width. In reality, these latter are the point of attachment of large spines oriented generally parallel to the shell plane of symmetry, sometimes facing backwards. The design of the ribs can change during the course of ontogenesis, and their number generally increases in the body chamber.

The suture line is more hildoceratitic than bouleiceratitic (also called pseudo-ceratitic) due to the consistently fringed saddles, lobes E, L and U₂ well separated; U₁ and U₂ are often difficult to tell apart; the umbilical portion is usually suspended. Lobe L has two, three or four points, is as wide as, or wider than, LS₁ and shorter than E. Both E and L may be long or short. The inner lobe is mono-bipolar, that is to say that its end is bifid but with short points (see also: Kottek, 1966; p. 120, fig. 60; Levi-Setti, 1972; p. 43, fig. 2 A). External saddle (ES) grooved by one or two accessory lobules, one in LS₁.

Observations on the genus and comparisons – Within the genus we can identify at least two very distinct groups and a third which is morphologically between in. The first group includes *L. helenae* Renz,

L. cf. helenae, *L. morettinii* n. sp. and *L. amuratrica* Renz & Renz, all ranging from moderately evolute to moderately involute. The spiral section goes from sub-quadrate to compressed with convex sides (see also: Pinna, 1965, fig. 3b, pl. 1; Wendt, 1966, p. 144, figs. 7-10; Levi Setti, 1972, p. 39, figs. 1b and 1c.) which gives them their characteristic heart shape. In these species, the ribs are more or less straight and clavate ("L" shaped) and protrude noticeably in the ventral area. The suture line is normally hildoceratine or extremely simplified due to reduced fringing and depth of lobes and saddles.

The second group includes *L. ionica* Renz & Renz, *L. sima* Kottek, *L. gallitellii* Pinna, *L. lombardica* Pinna and *L. attenuata* Wendt. These forms are similar to each other in their evolute spiral, sub-trapezoidal spiral section, the general shape of the ribs, which depending on the species can be single and/or double (in a sigmoid pattern), the presence of parabolic tubercles on the ventro-lateral margin and extended peri-umbilical tubercles. The suture line is moderately fringed and is characterised by the presence of one, two or three umbilical lobes and a lateral lobe which is narrower than LS_1 and almost as long as E (see also: Pinna, 1965, fig. 3b, pl. 1; Wendt, 1966, p. 144, figs. 7-10; Levi Setti, 1972, p. 39, fig. 1b and 1c).

A third group could comprise the extremely rare *Leukadiella* sp. and *L. jeanneti* Renz, which have prorsiradiate ribs and a sub-quadrate section.

As far as the specimen of *Leukadiella ionica* reported by Howarth (1992) is concerned, its attribution to the genus *Leukadiella* is here questioned due to the spiral section being sub-rounded and not sub-quadrate and to the absence of parabolic tubercles,

siphon grooves and, above all, double ribs. Its suture line is also decidedly different both from that of *L. helenae* and from that of *L. ionica* (see Howarth, 1992; p. 159 fig. 39-D; p. 162, lines 1-33 and pl. 30 fig. 2). The uncertainty is further compounded by the small size of this form (12.6 mm diameter).

LEUKADIELLA HELENAE Renz, 1913

Pl. 1, figs. 17-18; pl. 2, figs. 14, 19-20; pl. 3, figs. 14, 20; pl. 4, figs. 1-2

- 1913 *Leukadiella Helenae* (nov. sp. nov. subgen.) RENZ, p. 587, pl. 14, figs. 1-3, fig. 17 in the text.
 1922 *Leukadiella Helenae* var. *ticinensis* nov. var. RENZ, p. 152, pl. 7, fig. 1.
 1927 *Leukadiella Helenae* Renz var. *ticinensis* Renz - RENZ, p. 430, pl. 13, figs. 8, 8a.
 1966 *Leukadiella helenae* Renz - WENDT, p. 138 p.p., text-figs 2-3, pl. 13, figs. 2-3.
 1972 *Leukadiella helenae* Renz - LEVI SETTI, pp. 38-39, fig. 1 a, p. 45, figs. 2 a-d.

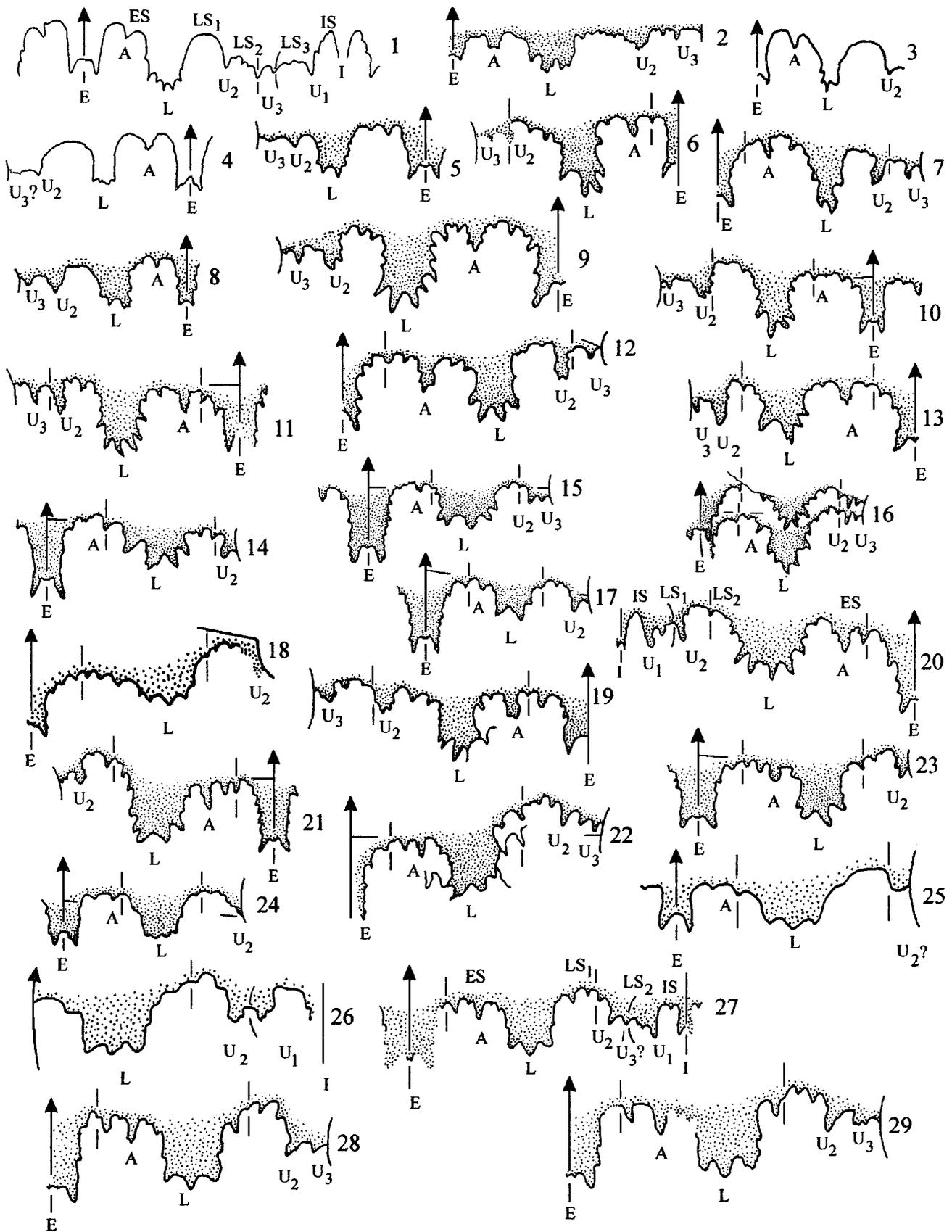
Material – Three specimens: 434MM6.37, found by F. Macchioni, *H. bifrons* Zone, *H. lusitanicum* subzone; Pe35, found by U. Immerigo near Pettino (PG) in the detritus from the *H. bifrons* Zone; MC76, collected in the detritus from the *H. bifrons* Zone by F. Venturi at M. di Civitella, near Foligno (PG).

Description – Moderately evolute shell with whorl section sub-quadrate; the sides are convex with a rounded umbilical margin. The ventral area is not sunken, and has shallow sulci; the keel has a triangular section and is slightly raised, the umbilicus is wide and deep.

In the phragmocone, the ribs are rursiradiate and robust, and are reinforced at the ventro-lateral mar-

EXPLANATION OF PLATE 1

- Fig. 1 - *Bouleiceras nitescens* Thevenin; from Thevenin, 1908; fig. 9.
 Fig. 2 - *Nejdia bramkampii*, Fu 58, Ø 130mm, x 1,5.
 Fig. 3 - *Bouleiceras arabicum* Arkell (1952; fig. 5.3).
 Fig. 4 - *B. marraticum* Arkell (Geyer, 1965; fig. 1d, pag. 28).
 Figs. 5-8 - *Renziceras nausikaae* (Renz); 5) Bu 39, Ø 23mm, x 3; 6) 588MM5.15, Ø 25mm, x 3,3; 7) B.ER32, Ø 20mm x 3; 8) CP61, Ø 16mm, x 4.
 Fig. 9 - *Renziceras* cf. *nausikaae* (Renz), SA52, Ø 38mm x 3.
 Fig. 10 - *Orthildaites* sp., Mo27, Ø 26mm, x 3.
 Fig. 11 - *Renziceras* sp., SIE38, Ø 39mm, x 3.
 Fig. 12 - *Leukadiella* aff. *morettinii* n. sp., Po20, Ø 20mm, x 4.
 Fig. 13 - *Leukadiella morettinii* n. sp. holotype, Le 19, Ø 18,5mm, x 4.
 Figs. 14-16 - *Leukadiella* cf. *helenae* Renz; 14) CP120, Ø 16mm, x 4,6; 15) MC26, Ø 9mm, x 3; 16) 13LCTdt, Ø 18mm, x 3.
 Fig. 17 - *Leukadiella helenae* Renz, Pe 35, Ø 15mm, x 3.
 Fig. 18 - *Leukadiella helenae* Renz, 434MM6.37, Ø 24mm, x 5.
 Fig. 19 - *Leukadiella* n. sp., CG10, Ø 33mm, x 3.
 Fig. 20 - *Leukadiella* aff. *jeanneti* Renz, Le 18, Ø 23mm, x 2.
 Figs. 21-23 - *Leukadiella ionica* Renz & Renz; 21) Pe21, Ø 26mm, x 3; 22) *idem*, Ø 31mm, x 3; 23) MC5 Ø 16mm, x 4. Notes the slight asymmetry of umbilical portion development on the sides of the specimen Pe 21 (fig. 21, 22).
 Figs. 24-29 - *Leukadiella gallitellii* Pinna; 24) Pe25 Ø 16mm, x 4; 25) 435MMdt., Ø 9,5mm, x 7,3; 26) *idem*, Ø 12mm, x 7,3; 27) *idem*, Ø 22,5mm, x 2,7; 28) *idem*, 29mm, x 2,25; 29) *idem*, Ø 33mm, x 1,8.
 Figures by other Authors have been slightly modified to include the names of the lobes and saddles as used in this paper. In order not to overburden the figures, indication of the saddles is limited to two figures only.



gin. Their point of greatest expansion is at about 3/4 of their length, where they get wider while subsiding and protruding from the ventral area.

In the body chamber, about 1/2 a whorl, the five ribs are thinner than those of the phragmocone; in the inner whorls these are robust and spaced out, but moving towards the opening they gradually grow weaker in the umbilical and lateral part, and in the end appear from about 2/3 of the way up the side. Again in the body chamber, there are four intercalary ribs which are even thinner and finer than the main ones, located in front of these latter and slightly more curved. These secondary ribs join the main ones towards the ventral margin where the ventro-lateral widening occurs, whilst they tend only to meet them around the umbilical margin.

The large external tubercles are compressed, and turn out to be in reality the points of attachment for robust, backward-curving spines; where preserved (at least two can be seen in the inner whorls as well), these develop from the ribs without interruption, so that they can be considered a single entity. Initially they are the same width as the ribs, and their section is triangular with slightly concave sides; then they gradually taper and become cylindrical. When seen in the spiral section, they diverge slightly outwards.

Fringed suture line, characterised by a very short, wide L lobe which terminates in three points which are about as wide as the saddle LS_1 ; E with slightly divergent branches, longer than L. The saddle ES is further forward than LS_1 and almost twice as wide as L. A single umbilical lobe in the outer suture, interpreted as U_2 , located on the umbilical margin. The suture line is similar to that of the *L. helenae* holotype both in its general appearance and in having a short, wide lobe L (see Renz, 1922, pl. 7, fig. 1; Wendt, 1966, p. 140, figs. 1-2 and 3).

Observations – This species differs from *L. cf. helenae* in that it is less flattened, has a lesser overlap, is more evolute and has a less marked ventral depression. It should be noted that the last feature has been exaggerated in the original drawing of the holotype

(Renz, 1913; pl. XIV, figs. 1-2), as can be seen by comparing this and the photo of the same specimen in Wendt (1966; pl. 13, figs. 2a, c).

Specimens 434MM6.37 and Pe35 display clear signs of maturity, shown by the interpenetration of the final sutures and the tendency for the spiral to uncoil in the holotype (Callomon, 1981; Howarth, 1992).

LEUKADIELLA cf. HELENAE Renz, 1913
Pl. 1, figs. 14-16; pl. 2, figs. 11-13; pl. 3, figs. 6-7, 22

1966 *Leukadiella helenae* Renz - WENDT, p. 138 p.p., text-figs. 1, 13; pl. 13, fig. 1,4.

Material – Three specimens: MC 26 found by F. Venturi at M. di Civitella, Foligno (PG), from the *H. lusitanicum* sub-zone; 13LCTdt. found by F. Macchioni at Secchiano (Cagli-PS), “Lecce” section, from *H. bifrons* Zone detritus; CP120, collected by G. Basilici in the Cima Panco section (Monti Martani, PG), from *H. bifrons* Zone detritus.

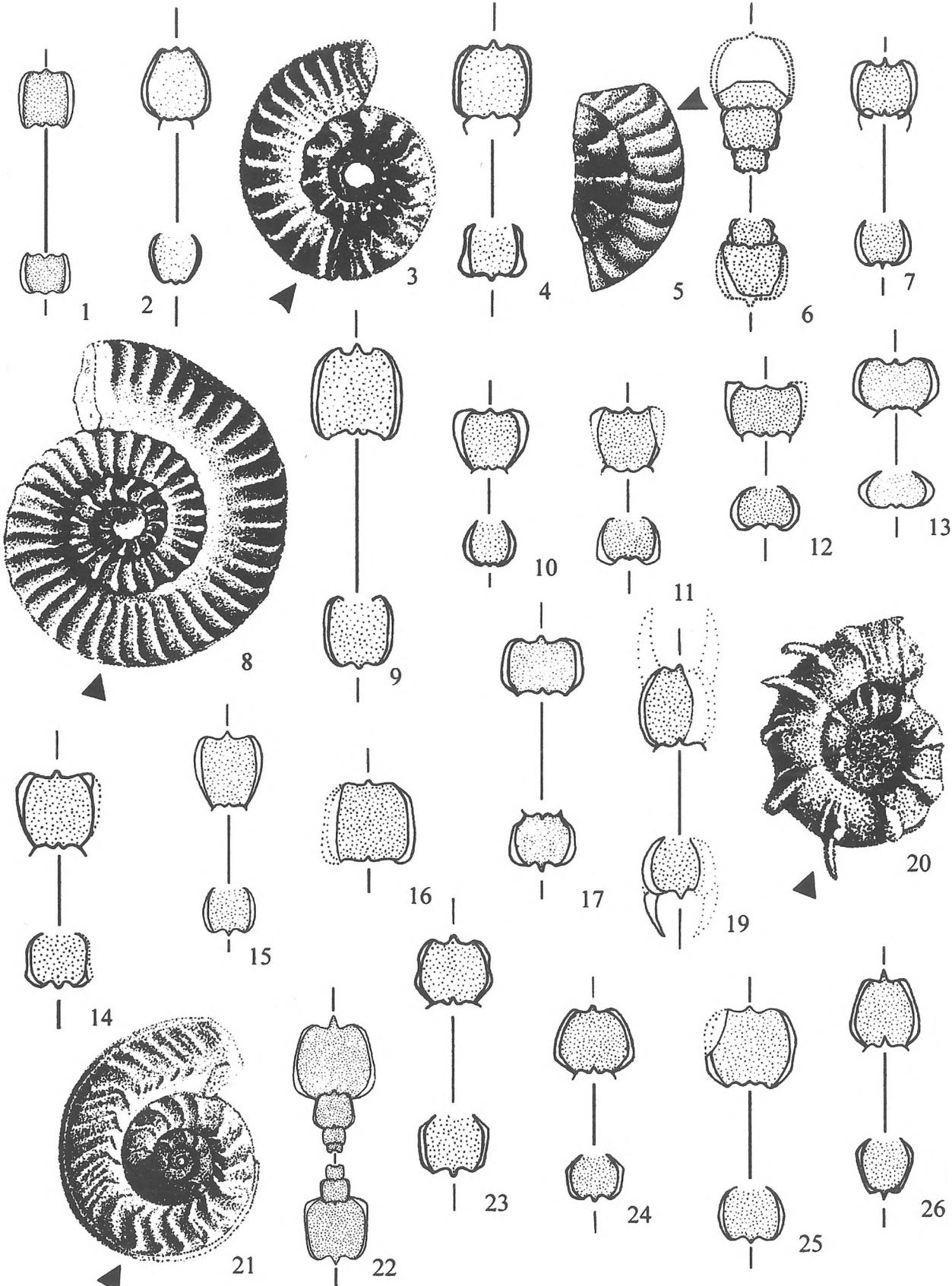
Description – Inflated forms with deep umbilicus. The spiral section is sub-trapezoidal, wider than it is high, with convex sides. The ribs are rectiradiate, strong and clavate, and protrude into the ventral area creating a ventral depression. Here, the keel does not protrude, and is flanked by moderately deep sulci. In MC26 body chamber weak secondary ribs can be seen, intercalated with the main ribs. Again in this specimen, truncated spines can be seen in the last visible rib in the body chamber and the two in the first inner whorl. All the specimens are probably mature, especially 13LCTdt. and CP120.

The suture line is typical of the species: L has four points, and is almost as wide as ES and wider than LS_1 ; the umbilical portion is reduced and suspended, with U_2 and U_3 both dentiform.

Observations – The specimens differ from *L. helenae* in their greater degree of suture line fringing and greater development in length of L. In 13LCTdt. the

EXPLANATION OF PLATE 2

- Figs. 1-6 - *Renziceras nausikaae* (Renz); 1) Bu 39, x 1; 2) 588MM5.15, x 1; 3-4) B.ER32, x2; 5-6) CP61 x 1,5.
 Fig. 7 - *Renziceras* sp., SIE38, x 1.
 Figs. 8, 9 - *Renziceras* cf. *nausikaae*, SA52, x 1.
 Fig. 10 - *Leukadiella morettinii* n. sp., holotype, Le 19, x 1.
 Figs. 11-13 - *Leukadiella* cf. *helenae* Renz; 11) 13LCTdt x 1; 12) MC26 x 1; 13) CP120 x 1.
 Figs. 14, 19-20 - *Leukadiella helenae* Renz, 14) Pe 35, x 1,5; 19-20) 434MM6.37 x 1,5.
 Fig. 15 - *Leukadiella* aff. *morettinii* n. sp., Po20, x 1.
 Fig. 16 - *Leukadiella* aff. *jeanneti* Renz, Le 18, x 1.
 Fig. 17 - *Orthoidaites* sp., Mo 27, x 1.
 Figs. 21-23 - *Leukadiella gallitellii* Pinna; 21-22) 435MMdt., x 1; 23) Pe25, x 1,5.
 Figs. 24, 26 - *Leukadiella tonica* Renz & Renz; 24) MC5, x1; 26) Pe21, x 1.
 Fig. 25 - *Leukadiella* n. sp., CG10, x 1.



last three ribs of the phragmocone have a weak secondary rib in front of them, like those observed in Renz's *L. helenae* var. *ticinensis* (1922) (the ornamentation in the body chamber is not preserved here). In 13LCTdt., a variation in the length of lobe L, influenced by the ornamentation, can be seen. The suture lines located in the rib reliefs show abnormal development of L, whilst those located in the depression between the reliefs show the usual ratio $L < E$. Specimen CP120 differs from *L. helenae* even more than the other two because of the clearly more inflated shell, the absence of the ventral depression and the larger overlap of the whorl, as can be seen in the forms figured by Wendt (1966, pl. 13, figs. 1, 4).

LEUKADIELLA MORETTINII n. sp.

Pl. 1, fig. 3; pl. 2, fig. 10; pl. 3, figs. 10, 12-13, 17;
Text-fig. 3

Derivatio nominis – From the surname of the finder, Elena Morettini.

Holotype – Le19, deposited at the Dipartimento di Scienze della Terra, of the Università degli Studi di Perugia.

Type site – Leccheti section (Cagli, PS), along the right bank of River Bosso.

Type level – The specimen was found at 4.10 metres in the sequence, as previously described by Faraoni *et al.* (1994), in the *O. douvillei* horizon, upper part of the *H. serpentinum* Zone.

Material – In addition to the holotype, we also have specimen 589MM5.15, found in the Migiana section. Both specimens were associated together with some specimens of *O. douvillei* Haug, *Renziceras nausikaae* (Renz) and *Renziceras* sp.

Description of the holotype – Involute shell with sub-quadrate, convex-sided spiral section. Wide ventral area, keeled and slightly grooved. Robust, rectira-

diate ribs, slightly concave, which terminate in tubercles (spine seatings) protruding into the ventral area. There are thin auxiliary ribs, located forward of the main ribs, in the body chamber.

Suture line with L slightly shorter than E, just as observed in the sutures of *Leukadiella ionica-sima* and *L. aff. morettinii* rather than in those of the *L. helenae* group. The umbilical portion shows a certain degree of suspension; U_2 is fairly deep; U_3 (?) is dentiform, and is close to the whorl overlap.

Observations – The species differs from *L. helenae* and *L. cf. helenae* in that it is less flattened, the ventral depression is absent, the rib relief is less marked and the suture line is significantly different. Of all the species known in this genus, this has the most hildoceratine suture line, and similar, therefore, to those of *Renziceras*. However, the ratio $L < E$, the suspension of the umbilical portion and the rather deep and wide of U_2 are all features which enable us to include unambiguously this species in the genus *Leukadiella*.

LEUKADIELLA aff. MORETTINII n. sp.

Pl. 1, fig. 12; pl. 2, fig. 15; pl. 3, fig. 19

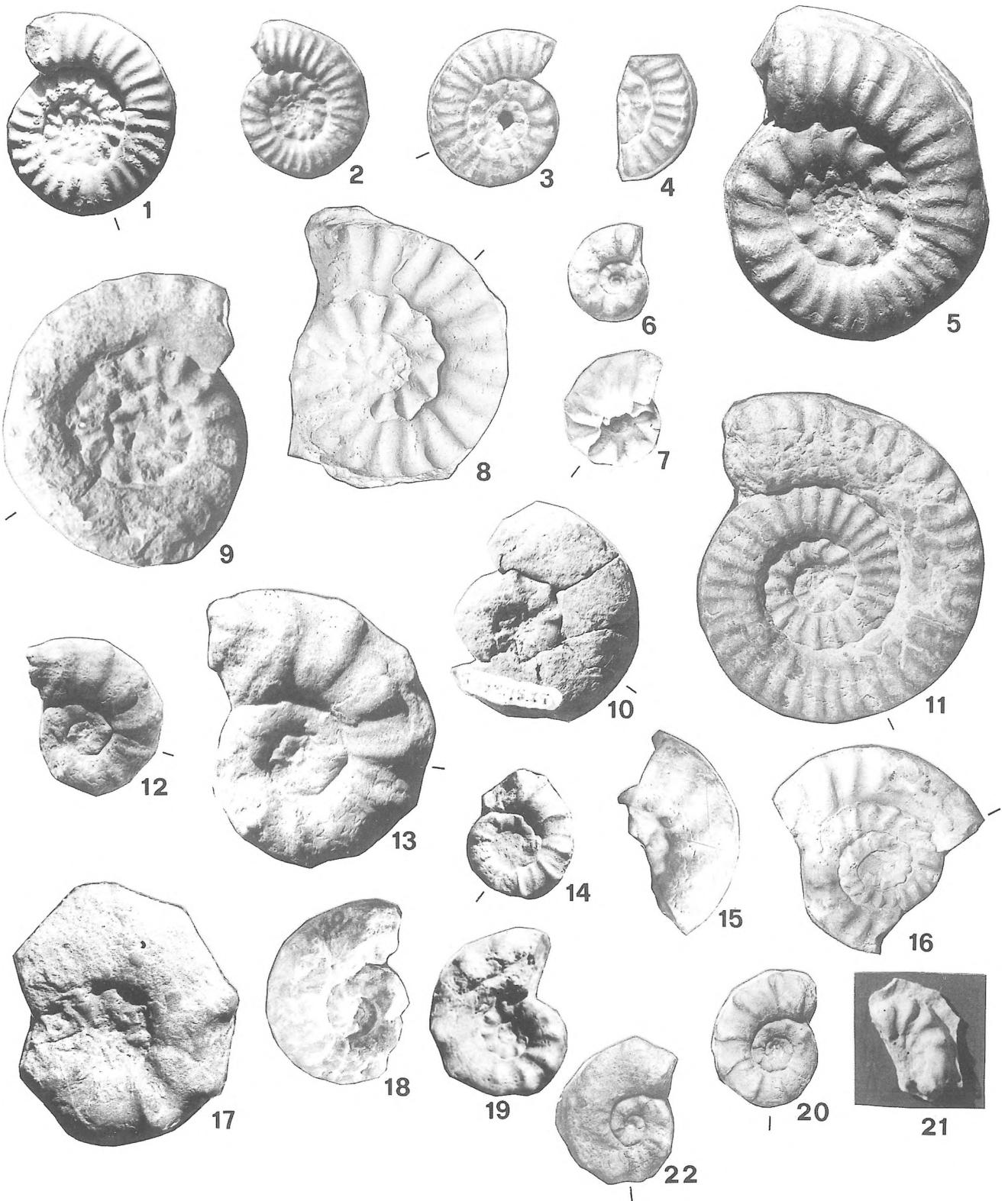
Material – Specimen Po20 found by F. Venturi at Pozzale (Monti Martani-PG), in the *H. lusitanicum* sub-zone.

Description – Moderately evolute shell with only slight overlap of the whorl; in specimen Po20 the section is sub-trapezoidal with convex sides. The ventral area is carinate and bisulcate with shallow sulci. The ribs (12 in the last whorl of the phragmocone) are strong, clavate and tursiradiate (single in the phragmocone and double in the body-chamber) with slight ventral projection.

The suture line is significantly different from that of *L. helenae*: here, L is sub-rectangular and narrower than LS_1 , and U_2 and U_3 are well separated (U_3 becomes external at 13 mm of diameter). The ES accessory has a depth about half of L.

EXPLANATION OF PLATE 3

- Figs. 1-5, 21 - *Renziceras nausikaae* (Renz); 1) Bu 39, x1; 2) 588MM5.15, x 1; 3) B.ER 32, x 1,1; 4) CP61, x 0,95; 5) 588MM5.15, x 2,15; 21) plaster cast of the specimen figured in Braga *et al.* (1985), x1.
Figs. 6-7, 22 - *Leukadiella cf. helenae* Renz; 6) CP120, x 1,05; 7) MC26, x 0,92; 22) 13LCTdt, x 1,05.
Figs. 8-9 - *Renziceras* sp.; 8) SIE38, x 0,9; 9) 432MM5.21, x 1.
Figs. 10, 12-13, 17 - *Leukadiella morettinii* n. sp.; 10) 589MM5.15, x 1; 12) holotype, Le 19, x1; 13) holotype, Le 19, x 1,8; 17) 589MM5.15, x 2,37.
Fig. 11 - *Renziceras cf. nausikaae* (Renz), SA52, x 1.
Figs. 14, 20 - *Leukadiella helenae* Renz, 14) MC 76, x 1; 20) Pe 35, x 1.
Fig. 15 - *Leukadiella aff. jeanneti* Renz, Le 18, x 1.
Fig. 16 - *Orthildaites* sp., Mo27, x1.
Fig. 18 - *Leukadiella* n. sp., CG10, x 0,92.
Fig. 19 - *Leukadiella aff. morettinii* n. sp., Po20, x 1.



Observations – Differs from *L. morettinii* n. sp. in being more evolute, and from *L. helenae* in the greater height of the whorl with respect to the diameter.

LEUKADIELLA IONICA C. Renz, 1946

Pl. 1, figs. 21-23; pl. 2, figs. 24, 26; pl. 4, figs. 5, 8, 10

- 1946 *Leukadiella ionica* n. sp. C. Renz - RENZ & RENZ, p. 174; pl. 12, figs. 5, 7, 7a-b, 9.
 1946 *Leukadiella ionica* var. *paganiensis* nov. var. C. Renz - RENZ & RENZ, p. 175; pl. 12, fig. 8-8a.
 1966 *Leukadiella ionica* Renz - KOTTEK, p. 116; pl. 13, fig. 1.
 1966 *Leukadiella ionica paganiensis* Renz - KOTTEK, p. 117, fig. 62; pl. 13, fig. 2.
 1966 *Leukadiella ionica* subsp. Renz - KOTTEK, p. 117, pl. 13, fig. 3.
 1969 *Leukadiella ionica* Renz - GALLITELLI WENDT, pl. 3, fig. 8.
 1972 *Leukadiella ionica* Renz - LEVI SETTI, p. 39; fig. 1b; pl. III, fig. 1a-c.
 1985 *Leukadiella gallitellii* Pinna - VENTURI, p. 78, fig. 119.
 1995 *Leukadiella ionica* Renz & Renz - JACOBS, p. 90, figs. 5.1-5.5, 6.2-6.6, 6.9-6.10.

Material – Three specimens: Pe21 and MC5 were found by F. Venturi; the former was collected in the detritus of the *H. bifrons* Zone at Pettino (PG), the latter at M. di Civitella (PG), in the *H. lusitanicum* subzone; 068FCT3.70 was found by F. Macchioni in the F.so della Colognola section, in the *H. semipolitum* subzone.

Description – Evolute shell with sub-quadrate section and slightly convex sides. Protruding keel, shallow siphon grooves. Ornamentation consists of double ribs in both the body-chamber and the phragmone, which are L-shaped. These are fibulate both at the peri-umbilical border, on the extended prosiradiate nodes, and at the ventral margin. Immediately after meeting, the ribs curve sharply backwards and then point forwards again in the ventral area, thus forming parabolic tubercles.

In the body-chambers, the first three pairs of ribs have a third auxiliary rib behind them which, being more rursiradiate, tends to meet with the preceding pair.

Characteristic suture line with L sub-rectangular with three points, about half of the ES wide and almost equal to LS; E is slightly deeper than L. Reduced and suspended umbilical portion, with a dentiform U₂. In specimen Pe21 the U₃ is present on one side only.

Observations – All the specimens are perfectly consistent with the characteristics of the species; 068FCT3.70 has the typical ornamentation of *L. ionica paganiensis* Renz, which has simple ribs in the final stages of growth.

LEUKADIELLA GALLITELLII Pinna, 1965

Pl. 1, figs. 24-29; pl. 2, figs. 21-23; pl. 4, figs. 3-4, 9

- 1965 *Leukadiella gallitellii* n. sp. PINNA, p. 5, pl. I, figs. 1a-c, 3b.
 1966 *Leukadiella sima* n. sp. KOTTEK, p. 119, fig. 60; pl. XII, fig. 6.
 1966 *Leukadiella sima* Kottek - WENDT, p. 145, fig. 9; pl. 14, fig. 2a.
 ? 1994 *Leukadiella ionica* Renz & Renz - JACOBS *et al.*, pl. 1, fig. 3.
 ? 1995 *Leukadiella ionica* Renz & Renz - JACOBS, p. 90, figs. 6.1-6.2.

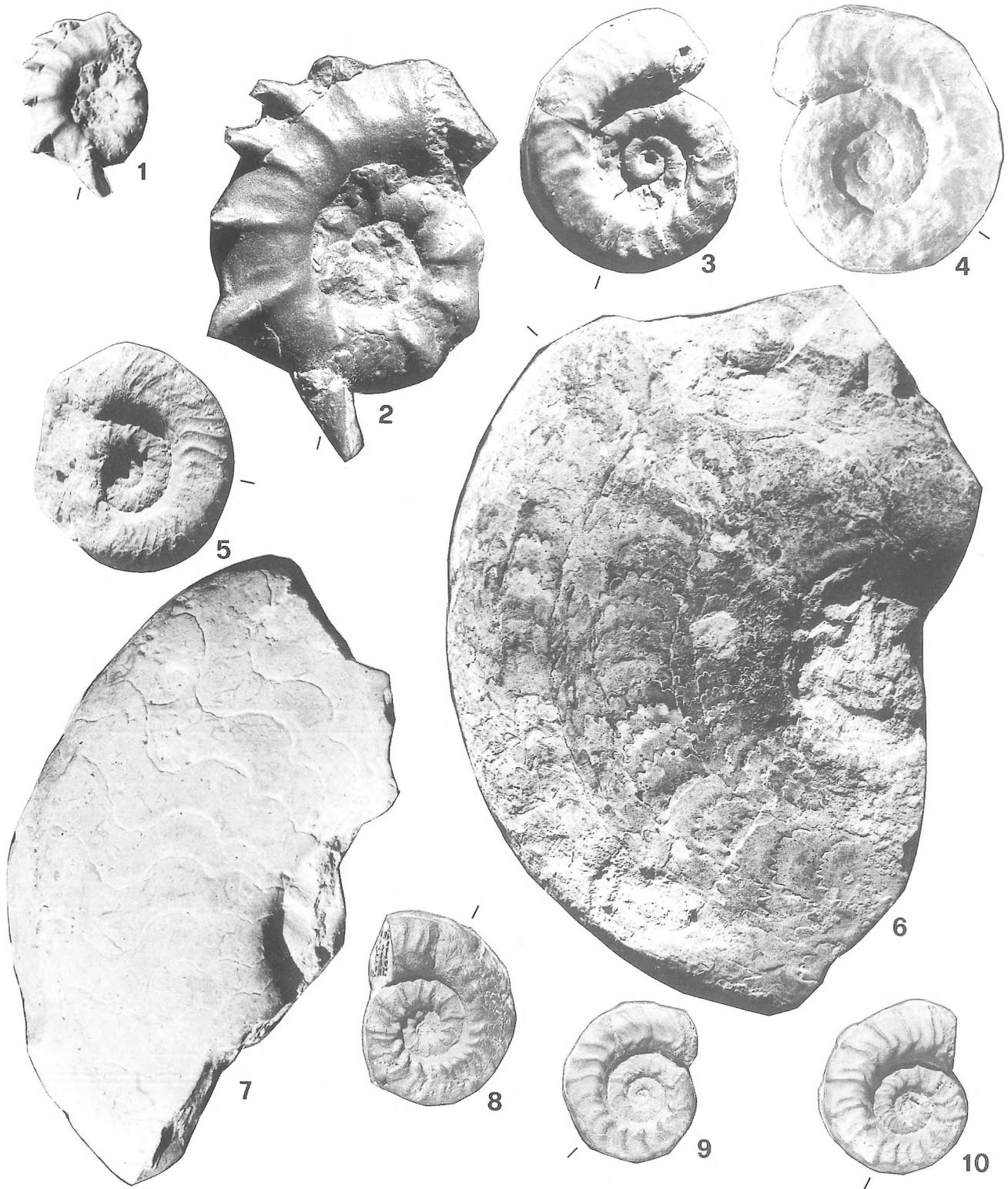
Material – Three specimens: 435MMdt, collected by F. Macchioni, in the *H. bifrons* Zone detritus at Migiana di M. Malbe; Pe25, found by F. Venturi in the *H. bifrons* Zone detritus at Pettino; and 436MM6.65, found by F. Macchioni at Migiana di M. Malbe, *H. bifrons* Zone, *H. semipolitum* subzone.

Description – Evolute shell with sub-rectangular spiral section, slightly wider than its height, up to a diameter of 7 mm (specimen 435MMdt.), and then sub-quadrate, still with straight sides. Sub-acute umbilical borders. Wide, bisulcate ventral area, with wide, relatively deep sulci and strong keel. The stretched, rursiradiate ribs, hardly visible in the first inner whorls, originate from elongate forward-leaning tubercles, forming a characteristic L-shape. On the ventro-lateral border these form a relief bend (with convexity at the apex; parabolic tubercles) and project towards the venter; this type of relief also functioned as seating for spines. At about 20 mm diameter on specimen 435MMdt, there are three successive ribs, larger than the preceding ones, in the middle of which a weak groove divides them into two parts; the more forward of these gradually attenuates and disappears near the peri-ventral relief.

The body-chamber preserves all the ornamental characteristics described except for a general, gradual attenuation of the ribs and, in specimens 435MMdt and 436MM6.65, the presence of double and triple ribs which, in the former, remain distinct beyond the umbilical margin.

EXPLANATION OF PLATE 4

- Figs. 1-2 - *Leukadiella helenae* Renz, 1) 434MM6.37, x 1; 2) 434MM6.37, x 2,37.
 Figs. 3-4, 9 - *Leukadiella gallitellii* Pinna; 3) 436MM6.65, x 1; 4) 435MMdt., x 0,95; 9) Pe25, x 1.
 Figs. 5, 8, 10 - *Leukadiella ionica* Renz & Renz; 5) 068FCT3.70, x 1.; 8) Pe21, x 1; 10) MC5, x 1.
 Fig. 6 - *Nejdia bramkampi* Arkell, Fu58, x 0,9.
 Fig. 7 - *Nejdia pseudogrineri* (Thevenin), Fu 70, x 0,9.



From the figures which illustrate the suture lines on specimen 435MMdt (Pl. 1, figs. 25-29), we can note some features that remain constant during ontogenesis: lobe L sub-rectangular with three points, more or less as wide as saddle LS_1 and about $2/3$ of ES; external saddle (ES) with two accessory lobules, of which A_d is straight, further back and more developed than A_v , which, in turn, is slightly inclined towards the umbilical area; the external lobe (E) is longer than L except in the first figure (fig. 25); inner lobe I is mono-bipolar and ES further back than LS_1 .

The degree of fringing varies, on the other hand; it generally increases, as does the number of accessory lobules to LS_1 , where the main accessory is displaced towards lobe L. It should be noted that the umbilical portion is initially made up of a suture lobe, and then of dentiform U_1 and U_2 (fig. 26), and finally (fig. 29) U_3 , as already outlined in previous figures.

Observations – As already mentioned during discussion of the affinities within the genus, the general morphology of the shell and the ornamental style are identical in the species *L. gallitellii*, *L. lombardica* and *L. sima*. As Pinna (1965) himself accepts, the first two are very close and there are no appreciable differences as far as the spiral is concerned. Their measurements are comparable with those of our specimens (the degree of coiling of *L. gallitellii* is 0.42 and not 0.40, as the biometric measurements supplied by Pinna himself, 1965; pag. 5). The differences in the depth of the sulci, on the other hand, depend on the different dimensions of the two specimens.

The feature which differs substantially between the types of *L. gallitellii*, *L. lombardica*, *L. sima* and the specimens here attributed to *L. gallitellii*, is that of the suture line. As noted by Wendt (1966), the holotype of *L. gallitellii* has only one umbilical lobe. Unfortunately, we do not know the diameter at which the line figured first by Gallitelli (1963) and then by Pinna (1965) was measured, and so we can not know whether this feature is linked to the ontogenesis or, indeed, to the preparation of the specimen; neither can we exclude individual variations due to pathologies or which, more simply, come within the species variability range. For example, the suture lines on specimen Pe25, measured at 16mm diameter (Pl. 1, fig. 24), and on specimen 435MMdt, measured at 12mm (Pl. 1, fig. 26), demonstrate the existence of such variations in the course of different individuals ontogenetic development. The former specimen, whilst reproducing the visible suture line at a greater diameter, has a less fringed, less differentiated U_2 lobe in a position closer to the umbilical border compared with the other specimen. We therefore believe that *L. lombardica* and *L. sima* should be considered synonyms of *L. gallitellii*, in the first case due to page priority and in the second due to the year of publication, given that *L. gallitellii* was published in 1965 and *L. sima* in the following year.

The tendency towards doubling of the final ribs in the phragmocone of specimen 435MMdt and in the body-chamber of 435MMdt. and 436MM6.65 might be a sign of the maturity of the individuals, confirmed by the approximation of the suture lines in the final half-whorl, or, more simply, a feature which comes within the individual variability range. The same feature can be seen in *L. ionica*, which differs from *L. gallitellii* in always having double ribs in the phragmocone, confirming what has been said above regarding the strong similarities between *L. gallitellii* and *L. ionica* in spiral section, rib shape and suture line. The number of specimens is too limited to allow us to carry out more detailed statistical and biostratigraphical studies which might demonstrate that they are two extremes within the variability range of the same species.

Leukadiella attenuata Wendt is also included in the synonymy, its differences from *L. sima* consisting, according to Wendt (1966), in its having three umbilical lobes and lighter ornamentation. The presence of three umbilical lobes in specimens 435MMdt and 436MM6.65 show that the presence of U_3 is linked to ontogenesis, and we also consider that the relief of the ribs is within the species variability. Factors relating to the preservation of the specimens in different diagenetic environments can not be ruled out either.

The specimen figured by Jacobs *et al.* (1994) and Jacobs (1995) as *Leukadiella ionica* Renz & Renz is attributed to *L. sima* only tentatively, as it comprises a fragment of body-chamber ornamented only by simple ribs. It might therefore be attributed to *L. ionica paganiensis* Renz or *L. gallitellii*.

LEUKADIELLA aff. JEANNETI Renz, 1927
Pl. 1, fig. 20; pl. 2, fig. 16; pl. 3, fig. 15

Material – Specimen Le18, found by F. Venturi at Secchiano in the detritus of the *H. bifrons* Zone.

Description – This is a fragment of phragmocone which preserves two successive portions, $1/4$ whorl in length. The spiral section is sub-quadrate with moderately convex sides. In the venter area the keel is flanked by two slightly engraved sulci. Ornamentation comprises wide, prorsiradiate ribs, slightly concave towards the opening. These are in significant relief in the umbilical area and then, just beyond the umbilical margin, become more flattened and even wider; they finally end at the insertion point of the spines, which does not project beyond the ventro-lateral margin.

The suture line is similar to that of *L. helenae*, in that L is sub-triangular, as wide as ES and wider than LS_1 , and the umbilical portion is suspended with dentiform U_2 .

Observations – This specimen has been linked to *L. jeanneti* because of the extreme width of the ribs (see Renz, 1927; Wendt, 1966), although the suture line and the development of the ribs are significantly different from those observed in the holotype.

LEUKADIELLA n. sp.
Pl. 1, fig. 19; pl. 2, fig. 25; pl. 3, fig. 18

1972 *Leukadiella* sp. LEVI SETTI, p. 42; fig. 2; pl. III, fig. 4a-c.

Material – Specimen CG10, found by S. Isabettini at the Grilli Quarry in P.so del Furlo (PS).

Description – Involute shell due to rapid growth of the spiral, and spiral section slightly wider than it is high; convex sides and sub-rounded, bisulcate venter area with raised keel. Ornamentation comprises forward-leaning ribs starting from stretched reliefs which can reach half-way up the side and which terminate at the ventro-lateral spine insertions. In the body-chamber the proximal segment of the ribs is backward-leaning, but upon reaching the umbilical margin the ribs bend sharply forwards, fork and rise into a tubercle located on the middle of the side. Finally, they bend even further forwards and terminate at the spine insertions located near the siphon grooves.

In the suture line, E (contrary to what normally occurs in the genus) is shorter than L, which is narrow and stretched with a forked end; U₂ and U₃ are clearly distinct. ES is wide with two accessory lobes, the larger of which is the inner one.

Observations – The only form with which comparison can be made is figured by Levi Setti (1972) as *Leukadiella* sp., because of the development both of the ribs and of the suture line, except for the greater degree of evolution.

Genus RENZICERAS Arkell, 1957

Type species – *Hildoceras nausikaae* Renz, 1913, pp. 607-612, text-figs. 25-25a, pl. XIV, fig. 4, by original designation.

Stratigraphic distribution – Upper part of the *H. serpentinum* Zone, *O. dowillei* level.

Original diagnosis – The genus was erected by Arkell (1957; in Arkell *et al.* 1957) based on a single specimen figured by Renz (1913) found in Greece and attributed by the latter to the genus *Hildoceras* Hyatt. The diagnosis of the genus, according to Arkell, is as follows: “coronate inner whorls with divergent sides; ornamentation comprising strong, simple, well-spaced ribs which terminate in robust ventro-lateral tubercles. In the final whorl the devel-

opment of the ribs suddenly changes and becomes moderately falcate, the tubercles disappear and the spiral section becomes quadrate; the shell is evolute and planulate, whilst the venter area is mono-carinate. Hildoceratine suture line”.

New definition – The morphological variability of the specimens in our possession allows us to redefine Arkell's diagnosis (1957) as follows: evolute shell due to slow growth in height of the whorls and slight overlap. Wide venter area, ranging from monocarinate to bisulcate and tri-carinate. The development of the ornamentation shows two characteristic ontogenetic stages: the first (generally up to about 18mm diameter) has strong ribs, which may be straight or L-shaped and always terminate in ventro-lateral tubercles that can be interpreted as spine insertions. These project significantly both laterally and ventrally, giving a trapezoidal outline to the spiral section. Sometimes the ribs originate from small peri-umbilical reliefs, which in one specimen are triangular, with the apex pointing towards the centre of the shell and seem to touch on a supplementary rib to the rear as well. The umbilical wall is small and rounded. Over about 20mm diameter, the ornamentation may comprise straight or slightly flexuous ribs, less pronounced than the inner ones, or strong, slightly falcate, clavate ribs. In this case, the peri-umbilical segment is slightly forward-leaning, and the point of inflexion is located near the umbilical step, which, in these stages, becomes higher and almost straight. In both cases they project ventrally, fusing with the external keel.

The suture line is similar to that of *Pseudomercaticeras* Merla and *Hildoceras sublevisoni* Fucini in the presence of two single-branch external umbilical lobes (U₂ and U₃), with dentiform U₃ and E not as deep as L (L>E). The latter terminates in two or three points, and is generally wider than LS₁. External saddle ES is further forward than LS₁ and 1.5–2 times wider.

Observations – The most salient differences between *Renziceras* and *Leukadiella* are to be found in the different ratio of the relative lengths of lobes L and E, respectively L>E and L<E, and in the more evolute coiling, due to a lower value of the Wh/D ratio.

RENZICERAS NAUSIKAAE (Renz, 1913)

Pl. 1, figs. 5-8; pl. 2, figs. 1-6; pl. 3, figs. 1-5, 21

1913 *Hildoceras nausikaae* n. sp. RENZ, p. 607, fig. 25; pl. XIV, fig. 4.

? 1985 *Leukadiella* sp. BRAGA, JIMÉNEZ & RIVAS, p.554, fig. c.

Material – Four specimens: B.ER32, found by L. Picconi in the F. Bosso sequence; CP61 and Bu 39, found by F. Venturi in the Cima Panco (Monti Martani) and F. Burano sections, respectively; and

588MM5.14, found by F. Macchioni at Migiana di M. Malbe. The specimens come from the upper part of the *H. serpentinum* Zone (*O. douvillei* horizon), and CP61 and Bu39 were found in the detritus.

Description – Evolute shell with sub-quadrate spiral section and slightly convex sides; ventral sulci just discernible in the inner whorls and absent in the body-chamber; gentle, rounded umbilical wall in the first stage of ornamentation (up to about 15mm of diameter), then becoming steeper.

The first stage of growth almost entirely occupies the phragmocone (up to about 15mm of diameter). The ribs here are strong and rectiradiate until half-way up the side, at which point they bend sharply backwards and grow up to two times wider before turning forwards again to the ventro-lateral margin, forming parabolic tubercles. In specimen B.ER32, the shape of the ribs does not change from 15mm to 19mm diameter, but they widen and are flattened in the middle, with a tendency to split. The peri-umbilical relief is also there in specimen CP61, but without the tendency to split the ribs. In the outer whorls the ribs are simple, either rectiradiate or slightly flexuous, and project very little ventrally.

Suture line characteristic of the genus in specimens 588MM5.15 and Bu39 (Pl. 2, figs. 1-2); that of B.ER32 (Pl. 2, fig. 4) has a narrow E with two short terminal points. In specimen CP61 (Pl. 2, fig. 3), on the other hand, L is slender with two terminal points, slightly narrower than LS_1 and about as high as E. The external saddle (ES) is wide, more than twice as wide as LS_1 (LS_1 approx. $2/5$ ES), further forward than the latter and with two accessory lobes.

Observations – Regarding ornamentation, specimens 588MM5.14, Bu39 and CP61 are extremely similar to Renz's holotype (1913). Only B.ER32 differs from it because of its suture line with narrow lobe L and its tendency to split ribs; however, these features are here considered within the morphological variability of the same species.

The specimen of *Leukadiella* sp. figured by Braga *et al.* (1985), which one of us has viewed at first hand and of which a cast is figured here (Pl. 3, fig. 21), has also been attributed to *R. nausikaae*. Unfortunately, the suture line is not visible in the specimen in question, but the evolution of the spiral is significantly greater than that of the relief-ribbed *Leukadiella* (such as e.g. *L. helenae* and *L. cf. helenae*). This opinion is also shared by Braga and Jiménez (personal communication, 1998). Its attribution to *R. nausikaae* remains tentative, given that the small size of the specimen does not allow us to examine the successive stages of development.

RENZICERAS cf. NAUSIKAAE (Renz, 1913)
Pl. 1, fig. 9; pl. 2, figs. 8-9; pl. 3, fig. 11

1913 *Hildoceras nausikaae* n. sp. RENZ, p. 607, fig. 25; pl. XIV, fig. 4.

Material – Sa52, found by C. Nannarone in a block of detritus, probably from the *H. serpentinum* Zone, in the S. Anna Quarry (Furlo, PS).

Description – Evolute shell with only a slight overlap of the spiral ($1/8$ approx.); this has a sub-quadrate section with rounded umbilical step. Wide venter area, tri-carinate and bisulcate, with the keel just protruding. The ornamentation varies with the ontogenesis: as mentioned in the diagnosis of the genus, the stage with rursiradiate ribs (12 per whorl) reaches as far as approximately 18mm diameter, and that with rectiradiate ribs reaches and includes the body chamber. Immediately after the spiny stage the ribs are rectiradiate, and then gradually become slightly falcate and are projected onto the ventral margin.

Hildoceratitic suture line; L terminates in 3 or 4 points, is as long as E and about half as wide as LS_1 . Two umbilical lobes, denominated U_2 and U_3 . Saddle ES more than twice as wide as LS_1 , and the two are equally far forward.

Observations – Differs from *R. nausikaae* in having a greater number of ribs in the first inner whorl (about 16) and a carinate, bisulcate venter area. However, the hypothesis that this is a macroconch of *R. nausikaae* can not be excluded.

RENZICERAS sp.
Pl. 2, fig. 7; pl. 3, figs. 8-9

Material – Two specimens: SIE38, found by P. Brascugli in the S.I.E.L.P.A quarry at Cingoli; 432MM5.21, found by F. Macchioni in the *H. serpentinum* Zone (*O. douvillei* level) of the Migiana di M. Malbe section.

Description – Evolute shell with sub-rectangular, slightly compressed spiral section. Venter area with wide, shallow grooves, similar to that of *L. helenae*; keel just protruding. Ribs are in strong relief, clavate, slightly falcate and rursiradiate over the whole ontogenetic development. Suture line typical of the genus.

Observations – Differs from *R. nausikaae* in maintaining strong ribs beyond the 18mm diameter. From the feature of the venter area and from the ornamentation, this species could be included in the genus *Leukadiella* except for the presence of L lobe which is deeper than the external lobe, a typical feature of *Renziceras*.

Subfamily BOULEICERATINAE Arkell, 1950
Genus NEJDIA Arkell, 1952

Type species – *Nejdia bramkampii* Arkell, 1952, p. 267, by original designation.

NEJDIA BRAMKAMPI Arkell, 1952
Pl. 1, fig. 2; pl. 4, fig. 6

1952 *Nejdia bramkampi* n. sp. ARKELL, p. 267, fig. 6; pl. 17 figs. 5-7; pl. 18, fig. 3-6.

Material – Sa58, found by F. Venturi in the detritus of the *H. bifrons* Zone in the S. Anna Quarry in P.so del Furlo (PS).

Description – Fragment of shell with discoidal morphology and sub-trapezoidal spiral section, with smooth, slightly convex sides. The venter area is carinate but not grooved. Suture line with L, E and U₂ all wide and not very deep; U₃ is dentiform. U₂ is not as deep as E.

Observations – The specimen varies from the holotype in having shallower lobes and saddles and in U₂ not being as deep as E.

NEJDIA PSEUDOGRUNERI (Thévenin, 1908)
Pl. 4, fig. 7

1908 *Harpoceras pseudo-Gruneri* n. sp. THÉVENIN, p. 116, fig. 8 a; pl. 1, figs 5-5 a.

1973 a *Nejdia* aff. *pseudogruneri* Thévenin - GUEX, p. 1; fig. 1 a-d.

1973 b *Nejdia* aff. *pseudogruneri* Thévenin - GUEX, p. 507; pl. 10, fig. 1.

Material – Fu70, found by F. Venturi in the *H. bifrons* Zone detritus in the S. Anna Quarry in P.so del Furlo (PS).

Description – Fragment of phragmocone with smooth, slightly convex sides. The venter area is tabulate and carinate.

The suture line is a little fringed, probable due to a slight corrosion which affected the specimen. Lobes L and E are wide and not very deep; U₂ and U₃ are dentiform.

Observations – The species differs from others in the genus in its less discoidal morphology, a more evolute shell, more flattened ventral area and fewer umbilical lobes. As noted by Guex (1973 a), the lack of light ribbing and of a high-relief keel, present in Thévenin's type (1908) but absent both in this specimen and that found by Guex (1973 a and b), might be due to the difference in size and to the absence of the test.

PHYLOGENETIC COMMENTS

When we compare the degree of coiling and the characters of the ribs in the known forms of *Leukadiella* with those of *Bouleiceras*, some similarities can be observed between *L. amuratica* and *L. ionica-sima* and, respectively, *B. elegans* Arkell (cf. Arkell, 1952; fig. 10 a, b, c) and *B. cf. elegans* (see Geyer,

1965, fig. 2, pl. 5). These similarities are also to be seen in the spiral section of the same specimens. Nevertheless, generally speaking the *Leukadiella* have sections which are wider than they are high, even if only slightly, whilst those of *Bouleiceras* are sub-trapezoidal, higher than they are wide.

The hypotheses proposing derivation of *Leukadiella* from *Bouleiceras*, put forward by numerous authors, are however based on the presence in both genera of tubercles and a simplified suture line. In specimens of the former, both figured and described in publications (see Jacobs, 1995), it is clear that the ventro-lateral tubercles are the natural extension of long spines which developed parallel to the shell plane of symmetry, whilst in *Bouleiceras* the spines are short and perpendicular to the plane.

There are also differences in the suture lines with respect to the degree of fringing, the development of the umbilical portion and the relationship between the width of lobe L and that of saddle LS₁. In *Leukadiella* both the lobes and the saddles are always fringed, and the umbilical portion is generally reduced and suspended. Lobe L is always wider or at least as wide as saddle LS₁, in contrast with what we observe in most cases in *Bouleiceras*, which has a pseudo-ceratic suture line with well-spaced, easily identifiable lobes and saddles. With the exception of the presence of slight fringing in the saddles, the aforementioned features of the *Bouleiceras* suture line remain almost unaltered in *Nejdia*, in which there is a further development of the discoidal morphology. This supports Guex's hypothesis (1973 a, 1974) regarding the development of the latter genus from the former.

The gap between *Bouleiceras* and *Leukadiella* widens when one considers the clearly hildoceratine nature of the suture line of the Apenninic *Leukadiella*. Such types of lines suggest a relationship with the genus *Mercaticeras* Buckman (Wendt, 1966), similarly excluded because of their significantly different shell morphology. However, the development of *Leukadiella* by neoteny from *Renziceras* seems plausible: the latter has the inner whorls extremely similar to those of *Leukadiella*, and almost certainly also has ventro-lateral spines on the internal whorls. Furthermore, the suture lines of *R. nausikaae* and *L. morettinii* n.sp. differ only in the L/E ratio, i.e. L>E in the former and L<E in the latter; moreover, the two species are coeval, having both been found at the top of the *H. serpentinum* Zone. There are therefore no biostratigraphic impediment to the development of one genus from the other, in contrast to the case of *Bouleiceras* and *Leukadiella*; in fact, *Bouleiceras* stratigraphically ranges from the *D. tenuicostatum* Zone to the first third of the *H. serpentinum* Zone (Mouterde, 1970; Dubar *et al.*, 1970; Mouterde & Rouget, 1975; Goy *et al.*, 1988), while the data currently in our possession limit the first appearance of *Leukadiella* to the *O. dowillei* level, or at the very top of the *H. serpentinum* Zone.

Specimen	D	Uw	Wb	Wh	Wb/Wh	Wh/Wh1	Wb/Wb1	Whr/Wh1	b.c.	mat.
434MM6.37	25(1)	11(0.44)	10(0.40)	10(0.40)	1.00	0.44	0.60	<0.2	0.50	mm
	20(1)	9(0.43)	10(0.50)	8(0.40)	1.25	/	/	/	/	/
Pe35	23.8(1)	10(0.42)	10(0.42)	8(0.33)	1.25	/	/	/	/	/
	17.5(1)	7.1(0.40)	7.6(0.43)	6.1(0.35)	1.23	0.56	0.59	0.22	0.50	/
MC76	21(1)	9(0.43)	9.6(0.46)	6.8(0.32)	1.41	0.44	0.84	0.33	0.75	mi
13LCTdt.	24.5(1)	9.3(0.38)	/	/	/	/	/	0.25	0.50	mm
	18.7(1)	5.6(0.30)	10.5(0.56)	6.5(0.35)	1.61	/	/	/	/	/
CP120	17(1)	6.8(0.38)	10(0.60)	6(0.35)	1.67	0.68	0.57	0.59	0	mm
	13(1)	4.2(0.32)	8.8(0.60)	4.5(0.35)	1.95	/	/	/	/	/
MC26	22(1)	8(0.36)	12.5(0.57)	8(0.36)	1.56	0.51	0.56	0.23	0.50	mi
LE19	26.5(1)	10.2(0.38)	11.5(0.43)	10(0.38)	1.15	0.50	0.45	0.22	0.375	/
Po20	30(1)	11.6(0.36)	10(0.33)	12(0.4)	0.80	0.37	0.71	0.22	0.50	?
	20(1)	7(0.35)	9(0.45)	7.7(0.385)	1.17	/	/	/	/	/
Pe21	33.5(1)	14.2(0.42)	11.2(0.33)	11.2(0.33)	1.00	0.63	0.62	0.14	0.25	/
MC5	29(1)	13(0.45)	12(0.41)	11.5(0.39)	1.04	0.52	0.58	<0.1	0.50	/
068FCT3.70	35.8(1)	15.8(0.44)	13.8(0.38)	12.3(0.34)	1.12	?	0.66	?	0.375	/
	Pe25	27(1)	9(0.33)	9(0.33)	8.5(0.31)	1.06	0.58	0.55	0.10	0.50
436MM6.65	21.3(1)	12.5(0.46)	7(0.33)	6.5(0.30)	1.08	/	/	/	/	/
	46.5(1)	21.8(0.47)	15.2(0.37)	14.2(0.32)	1.10	0.55	0.60	0.20	0.50	Mm
435MMdt.	35.1(1)	15.5(0.44)	13(0.37)	11(0.31)	1.03	/	/	/	/	/
	43.5(1)	19.8(0.45)	12.9(0.29)	14(0.32)	0.92	0.50	0.45	0.23	0.50	Mi
	37(1)	15.5(0.42)	11.1(0.30)	12(0.32)	0.92	0.58	0.63	/	/	/
	27.2(1)	12(0.44)	9.2(0.33)	9.2(0.33)	1.00	/	/	/	/	/
	21(1)	9.1(0.43)	6.2(0.29)	6.5(0.31)	0.95	0.49	0.58	/	/	/
	11.5(1)	4.4(0.38)	4(0.35)	4.2(0.36)	0.95	0.50	0.62	/	/	/
Le18	8.3(1)	2.9(0.35)	3.1(0.37)	3(0.36)	0.97	0.5	0.64	/	/	/
	/	/	14.60	13.7	1.07	0.38	0.43	0.24	/	/
CG10	36(1)	11(0.31)	14(0.39)	11.8(0.33)	1.27	0.50	0.50	0.20	0.50	Mi?
	25.5(1)	8.5(0.33)	10.2(0.40)	10.8(0.42)	0.94	/	/	/	/	/
B.ER32	28.9(1)	15.3(0.53)	8.0(0.28)	7.9(0.27)	1.01	0.51	0.625	<0.1	0.50	/
	20.5(1)	9.3(0.45)	7(0.34)	7(0.34)	1.00	/	/	/	/	/
CP61	25(1)	12(0.48)	8(0.32)	7.5(0.30)	1.07	0.67	0.81	<0.16	?	/
	20(1)	9.5(0.475)	7.2(0.36)	6.5(0.325)	1.11	0.46	0.76	0.10	/	/
588MM5.14	27(1)	13.5(0.50)	8(0.30)	8(0.30)	1.00	0.625	0.75	0.10	0	/
	21.1(1)	14(0.65)	6.4(0.30)	/	/	/	/	/	/	/
Bu39	33(1)	16(0.48)	9(0.27)	8.5(0.26)	0.94	0.61	0.70	0.10	0.57	?
SA52	56.7(1)	28(0.49)	16(0.28)	16(0.28)	1.00	0.625	0.71	0.10	0.50	?
	44(1)	20(0.45)	11(0.25)	10(0.23)	1.10	/	/	/	/	/
432MM5.21	48.8(1)	24.8(0.51)	14(0.29)	13.2(0.27)	1.06	0.69	/	0.06	0.375	Mi
SIE38	34.2(1)	18(0.52)	12(0.35)	9(0.26)	1.33	0.67	0.67	0.33	0.25	Mi
Fu58	137c(1)	30(0.22)	36(0.26)	63(0.46)	0.57	/	/	0.34	0.08	Mi
Fu70	128c(1)	40c(0.31)	34(0.26)	63(0.40)	0.54	/	/	0.47	0	/

Tab. 1 - Measurements in mm of the specimens mentioned in the text: b.c.= length of the body chamber as fractions of a whorl; mat.= degree of maturity, M= macroconch, m= microconch; the letters i and m which follow indicate, respectively, whether the specimen is immature or mature (e.g.: mm= mature microconch). For an explanation of the other symbols, see Text-fig. 3.

The stratigraphic position of *L. morettinii* n.sp. (Text-fig. 4) allows us to state that it was the starting point of the genus, modifying Wendt's hypothesis

(1966) on the origin and evolution of the genus. This author considered *L. helenae* Renz to be the starting point of an evolutionary lineage, which derives from

AGE	ZONES	SUBZONES	
TOARCIAN	<i>H. bifrons</i>	<i>C. gemma</i>	<i>L. sima</i> —
		<i>H. semipolatum</i>	<i>L. ionica</i> —
		<i>H. lusitanicum</i>	<i>L. helenae</i> —
		<i>H. sublevisoni</i>	<i>L. aff. morettinii</i> —
	<i>H. levisoni</i>		<i>R. nausikae</i> —
			<i>Renziceras</i> n. sp. —
			<i>L. morettinii</i> —
			<i>Renziceras</i> —
			<i>Leukadiella</i> —

Text-fig. 4 - Stratigraphic distribution of the Leukadiellinae mentioned in the text. The zonal scheme is taken from Elmi *et al.* (1994; 1997). The subdivision of the *H. bifrons* Zone into subzones is taken from Parisi *et al.* (1998).

Bouleiceras and terminates in *L. sima* Kottek. Within the genus, evolution is considered to come about via the gradual reduction in the number of the umbilical lobes, together with the progressive tendency to form ever more evolute and flattened shells. In addition, in the various specimens of *Renziceras* figured here we can see nuclei that possess the ornamental features of both *Leukadiella* gr. *helenae* (without peri-umbilical tubercles) and *Leukadiella ionica-gallitellii* (with peri-umbilical tubercles; cf. B.ER32 and CP61). For this reason, it is also possible that *L. helenae* represents a phyletic branch independent of the one which led to the development of *L. ionica-gallitellii*. Nevertheless, according to the stratigraphic position of the specimens described here (Text-fig. 4), *L. ionica-gallitellii* are the last representative species of the genus, in agreement with Wendt's hypothesis (1966).

Unfortunately, the scarcity of further biostratigraphic data prohibits us from examining the subject in more detail and from producing a phyletic overview which would complement that of Wendt (*op. cit.*).

Again with the ornamentation and the suture lines in mind, we would likewise exclude the succession *Bouleiceras*→*Leukadiella* via the genus *Renziceras*: indeed, the above-mentioned elements lead us to associate the latter two forms with the Hildoceratines, such as *Hildaites* Buckman or *Orthildaites* Buckman, with large, sometimes rursiradiate ribs, or, in the case of the features of the later stages in growth of *Renziceras*, with *Hildaites*, with slightly flexuous ribs. Also, the presence of a mono-bipolar lobe I in the specimens of *L. sima* and *L. aff. jeanneti* figured here (Pl. 2, figs. 16 and 12) is an element which leads us in the same direction. The same may be seen in *L. sima* find by Kottek (1966, fig. 60, p. 120) and in the *Leukadiella* sp. of Levi-Setti (1972; fig. 2 a, p. 39).

The existence of specimens of *Renziceras* of a size greater than 50mm and still not mature allows us to exclude the hypothesis that it was a microconch of *Furloceras* Elmi & Rulleau (1995), put forward by the authors of this latter genus; indeed, at 50mm of diameter there are still significant morphological differences, such as diverse development of the ribs and the absence both of tubercles in *Furloceras* and of peristomatic constrictions in *Renziceras*.

CONCLUSIONS

The first representatives of the genus *Leukadiella* (*L. morettinii* n. sp.) appear in the upper part of the *H. serpentinum* Zone, together with *Renziceras* and *Orthildaites*, and have a typically hildoceratine suture line. The last representatives, on the other hand, belong to the *L. ionica-sima* group, partially confirming the evolutionary trend proposed by Wendt (1966), which suggested a phyletic line starting from *L. helenae* Renz and terminating in *L. sima* Kottek.

We confirm the observations by Pinna (1965) that the genera *Bouleiceras* and *Leukadiella* are very different in terms of ornamentation and suture line, meanwhile we reject the hypothesis that the former developed from the latter on biostratigraphic grounds as well. The major similarities of the genus *Leukadiella* are in fact with the genus *Renziceras*, which Arkell (1957) places within the Hildoceratidae together with *Mercaticeras* Buckman, *Hildaites* Buckman and *Hildoceras* Hyatt. We suggest that *Leukadiella* appears through a process of neoteny with early appearance of the innovation (Dommergues *et al.*, 1986), supported by the presence of ventro-lateral spines in the *Renziceras* nuclei. The specimens in our possession show no appreciable difference in the size of the adult stages of both genera, although further biometric studies are needed in order to delineate more precisely the framework of this heterochronic evolution.

Consequently, as we do not accept the supra-

generic collocation suggested by previous authors, we propose instituting the subfamily Leukadiellinae (Hildoceratidae) with the aim of placing *Leukadiella* and *Renziceras* in a more appropriate taxonomic category.

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