Variability patterns and classification of *Hildoceras* species based on the assemblages from the "Rosso Ammonitico" near Terni, Umbria (Central Apennines)

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ABSTRACT - Variability in *Hildoceras* species is outlined on the basis of the stratigraphical distribution as inferred from Rosso Ammonitico outcrops near Polino (Terni, Umbria). Ontogenetic variability is interpreted, together with anagenetic trends, as responsible for historically-based questions concerning systematics. The attempt at a classification which takes into account variability related to development appears to exclude reference to characters lacking any taxonomic significance. As a direct outcome, characters available for classification reveal a smaller number of species considered valid than in the recent past. In upward succession the following taxonomic scheme is suggested: *Hildoceras laticosta* Bellini, 1900, *Hildoceras lusitanicum* Meister, 1913, *Hildoceras bifrons* (Bruguière, 1789), *Hildoceras semipolitum* Buckman, 1902. Previously a similar result was attained by Howarth (1992) but different criteria are herein adopted to separate *Hildoceras laticosta* from *Hildoceras lusitanicum*.

KEY WORDS: Toarcian, variability, classification, *Hildoceras*, Rosso Ammonitico, Umbria.

INTRODUCTION

During the last century *Hildoceras bifrons* (Bruguière, 1789) has been widely figured by authors from both Mediterranean and Boreal regions. However, the so called typical forms appear to be quite rare in the Rosso Ammonitico marls (Donovan, 1958; Gallitelli-Wendt, 1970). As a result it has become costumary among authors to refer to *Hildoceras bifrons* specimens lacking a true lateral groove, indeed this idea is widespread (Bellini, 1900; Prinz, 1904; Fucini, 1905, 1922; Renz, 1911, 1913; Meister, 1913; Zuffardi, 1914; Principi, 1915; Mitzopoulos, 1930; Ramaccioni, 1939; Lippi-Boncambi, 1947; Zanzucchi, 1963; Pelosio, 1968; Pinna, 1969).

Analogously, the more primitive forms of *Hildoceras* were similar but not exactly corresponding to the English representative *Hildoceras levisoni* (Simpson, 1843), turned into Hildaites levisoni by Buckman in 1921. *Hildoceras sublevisoni* Fucini, 1922¹, was

¹ Howarth (1992, Part 2, pp. 176, 178, 180) replaces the date 1919, usually assigned to Fucini's species, with 1922. I was informed by an anonymous reviewer that Vol. 25 of *Palaeontographia Italica*, although dated 1919, was published only in 1922 and that a letter from Prof. Stefanini, accompaning the volume, stated the delay. In fact, such letter is attached to the Natural History Museum copy.

established to group these Mediterranean forms, but no holotype was designated. Merla (1933, p. 51) indicated a type among the specimens listed in the synonymy (Fucini, 1922, p. 182) but he then interpreted the species in too broad a way. *Hildoceras sublevisoni* has thus subsequently been interpreted by forms with various morphologies.

In the broadest sense, *Hildoceras sublevisoni* embraces both the varieties previously referred to *Hildoceras bifrons* and the more archaic forms showing no kind of lateral groove, not even a slight one (Donovan, 1958; Gallitelli-Wendt, 1970; Jiménez & Rivas, 1992). In the more restricted sense several species are considered apart from *Hildoceras sublevisoni*, mainly by the means of different ribbing patterns (Guex, 1972; 1973; Gabilly, 1976; Elmi, 1977). However, variability due to anagenetic trends, combined with variability depending on ontogenesis, makes the determination of taxonomical characters difficult.

In the present work an attempt is made to contribute to this question by ruling out the morphologic variability related to development, in order to base systematics on characters of reliable taxonomic value. To attain this end some Rosso Ammonitico outcrops of the Umbria region have been considered and bed by bed collecting was carried out where very favourable exposures existed. Variability patterns, as inferred from the stratigraphical distribution of morphological types, have provided the means of distinguishing no more than two taxonomic units, that are species, within the widest interpretation of *Hildoceras sublevisoni*. Moreover, nomenclatural problems arise since senior synonyms exist (Howarth, 1992) in respect of *Hildoceras sublevisoni*. Hence *Hildoceras laticosta* Bellini, 1900, and *Hildoceras lusitanicum* Meister, 1913, are herein applied to the two morphological units into which *Hildoceras sublevisoni* is splitted.

The comparatively rare grooved specimens are all referred to *Hildoceras bifrons* and *Hildoceras semipolitum* Buckman, 1902. Any attempt to distinguish other species than these results in ambiguity, as among grooved specimens too the numerous transitional morphs confer continuity to the variability field.

PALAEONTOLOGY AND SYSTEMATICS

Provenance and preservation of the Hildoceras fauna

The outcrops studied are in the Umbria region, on the western slope of M. La Pelosa (east to Terni; fig. 1). They are well exposed along the road approaching the town of Polino, where other Jurassic and Cretaceous Formations of the Umbria-Marche sequence (Calcare Massiccio of the Hettangian-early Sinemurian, Corniola of the late Sinemurian-Domerian, Bositra marly limestones of the Dogger, Calcari Diasprigni of the Oxfordian-Kimmeridgian, Maiolica of the Titonian-Hauterivian, etc.) also crop out. Among the sections collected there is the one worked on by Nicosia & Pallini (1977), but great deal of the palaeontological and stratigraphical data have been acquired from a better exposed outcrop just preceding it along the road. The total thickness is here of about 17 metres, from the basal contact with the Corniola Formation to the upper boundary with the Bositra beds.

Nearly 500 specimens referable to *Hildoceras* species have been examined, of which about half are broken fragments. The preservation is that typically exhibited by Rosso Ammonitico ammonites, namely internal moulds. The entire specimens are never really complete since they consist of phragmocones with only part or none of the body-chamber. Each specimen is labelled with the abbreviation PO (which is for Polino) followed by a double number; the first refers to the yielding layer and the second to the successive



Fig. 1 - Localization of M. La Pelosa, area of the exposures.

numbering of the samples. When a specimen is marked with the successive number only, it is from an unknown level.

Among the whole specimens, the majority have maintained part of the body-chamber, generally badly preserved and, in some cases, showing very little of the ribs and other ornament (for instance specimen PO 10M/242, pl. 3, fig. 4). This is to some degree due to the absence of septa, which makes the body-chamber more likely to be damaged during transport as well as after being buried. Moreover, it may be that the missing part of the body-chamber, indeed all of it, was lost from the internal mould, re-exhumed after lithification.

This suggests that ammonites were likely to undergo diagenesis, becoming an internal mould, in a very brief time, that is much before deep burial. In accord with this is another common phenomenon, that is partial disinterment of somewhat hardened moulds, as proved by the weathered upper surfaces, in some cases also settled by epibionts.

Introduction to the classification

The genus *Hildoceras* was established by Hyatt (1867) including, besides *Hildoceras* bifrons, *Hildoceras walcoti* (Sowerby, 1815) and *Hildoceras hildense* (Young & Bird, 1822). In 1889 Buckman designated *Hildoceras bifrons* as the type species, primarily characterized by the lateral groove that separates the somewhat smooth innermost flank from the ribbed outer part. According to Donovan (1958) the lateral groove, even if little impressed, should be considered as diagnostic of the genus. However, some morphotypes lack it totally.

Hildoceras sublevisoni Fucini, 1922, was established to group the grooveless morphs that several authors had previously referred to *Hildoceras levisoni*. As a holotype had not been originally designated, Merla (1933, p. 51) assumed the specimen figured by Dumortier (1874, pl. 9, fig. 3) as type-form among those included in the synonymy (Fucini, 1922, p. 182). It was indicated as the morphotype to which a greater part of the known specimens compared.

In reality the majority of the specimens is better represented by the one previously figured by Fucini as *Hildoceras levisoni* (1905, pl. 6, fig. 3), also the only in the synonymy to be directly studied by the author. That is because of the peculiar conformation of the dorsal flank, similar to many other forms, despite wider variability involving the shape, strength and density of the ribs. In this specimen the umbilical wall, on the smooth and convergent innermost whorl, is well developed toward the middle flank, where instead of being flat, like in Dumortier's form, it produces a raised edge referred to as periumbilical relief. In numerous specimens the rounded or slightly angled periumbilical relief overhangs the ribs as they tend to become evanescent, so that a somewhat grooved or "pseudogrooved" look is perceptible.

A periumbilical relief is evident in Merla's figures of *Hildoceras sublevisoni* (1933, pl. 7, figs 1, 10) but it is not so in Dumortier's form, which was probably not well interpreted by Merla when he indicated the most common and typical form. This was first argued by Donovan (1958, p. 50), who remarked on the fact that the two *Hildoceras sublevisoni* figured as typical by Merla (1933, pl. 7, figs 1, 10) differ from the specimen referred to as type. In fact, Donovan accepts only Merla's figure of *Hildoceras sublevisoni* var. *raricostata* Mitzopoulos (Merla, 1933, pl. 7, fig. 4) as a corresponding form. However, he considers those of figure 1 and 10, with more numerous ribs, as belonging to the same unique but variable species.

Subsequently other authors have remarked on the possibility that these two particular morphs could be distinct (Zanzucchi, 1963; Geczy, 1967; Howarth, 1992), or that even further specific subdivisions could be considered as valid (Guex, 1972; 1973; Gabilly, 1976; Elmi, 1977).

Stratigraphical sequence and variability of morphological types

At the main section of Polino, Dumortier-like morphotypes are the only to occur in the lowermost part of the *Bifrons* zone (from bed 10A1, at 3.5 m, to bed 10A3, at 4.0 m; fig. 2). In the overlying levels they are no longer found and specimens with a well developed periumbilical relief replace them. This latter form ranges up to bed 10N (at 5.80 m) throughout a series of gradually varying populations (fig. 2). The transition between the two morphotypes should occur within bed 10B but, unfortunately, this layer was unfossiliferous. In addition beds 10C and 10D have only yielded fragments, so that the first meaningful data about the evolving sequence start from bed 10E (at 4.5 m).

Concerning this sequence, variability patterns are better evidenced by populations of beds 10L, 10M and 10N, which have yielded the greater part of the studied specimens. The first results show that variability in shell parameters seems mainly related to size, thus to development. For instance, measurement of shell parameters has revealed a slow but perceptible decrease in whorl overlap parallel to growth. On the contrary, variability involving thickness and density of the ribs is mainly due to anagenetic trends. In the underlying beds 10F, 10G, 10H and 10I, poor preservation makes it difficult to obtain relations between size and shell parameters, while a better preserved and dimensionally varied fauna was still available in bed 10E.



Fig. 2 - Morphotypes representing populations and their vertical distribution in the low-middle part of the *Bifrons* zone.

Within the population from bed 10E the number of ribs per whorl is quite constant and it shifts between 31 and 34. Variability among specimens from this layer seems to depend on development, as proved by the contemporaneous occurence of smaller and larger individuals showing different features. The former maintain more embracing whorls and complete ribs, while the latter attain a wider umbilicus and incomplete ribs on the inner flank, due to the fading of the ribs' forward projection. This is replaced by inflected spots homologous to a spiral groove and, at this stage, forming up a discontinuous pseudogroove. Thus, the appearance of the pseudogroove is also related to development.

By analogy, among specimens from the higher beds 10L, 10M and 10N early whorl ribbing is characterized by complete ribs starting right down from the umbilical margin. At earlier developmental stages the ribs also bend backward much more suddenly in respect to larger whorl ribbing. Differences in respect to populations from bed 10E consist of rib density (ribs are about 40 to 45 per whorl nearly at any diameter) and in a more evident impression of the pseudogroove. In many cases comparison reveals that in specimens from beds 10M and 10N the pseudogroove is precocious in respect to those from lower levels. This may suggest that the appearance of pseudogroove (linked to ontogenesis) could have been advanced in younger forms with respect to older ones.

In beds 10F-10G poorly preserved moulds show a coarse and spaced-out ribbing, never noticeable in populations from bed 10L to 10N and more similar to specimens of bed 10E. Specimens recovered in the intermediate beds 10H and 10I represent a transitional population with respect to those from lower (10E to 10G2) and higher levels (10L to 10N). They are not well preserved and all are less than 45 mm in diameter. Therefore comparison of different developmental stages is not possible. Very poor preservation only allows calculation of rib numbers, which are around 35 to 39, thus according with an increasing tendency leading, by continuity, from an average of 31-32 (in populations from bed 10E to 10G2) to one of 42-43 (in populations from bed 10L to 10N).

In beds 10C and 10D just a few fragments were found, showing periumbilical relief and well spaced, coarse ribs. These features are very close to those of forms from beds 10E to 10G2.

Classification

According to the morphological variability, as inferred from the sequence of morphotypes, populations from bed 10C to 10N may be referred to one chronospecies within which variability is continuous. Differences due to ribbing patterns or involving whorl parameters are related to anagenetic trends and/or to ontogenesis. Therefore they do not allow further specific subdivisions. On the contrary, the stock of forms corresponding to Dumortier's specimen (occurring from bed 10A1 to 10A3) could be considered as a differing and separable species. In fact, though belonging to the same phyletic lineage, the lack of the periumbilical relief is a more definite and objectively recognizable evidence in respect of rib coarsening and density.

In the literature, specimens corresponding to both these morphological types had been figured as varieties of *Hildoceras bifrons* even before *Hildoceras sublevisoni* was established. In particular Bellini figured as *Hildoceras bifrons* var. *laticosta* (1900, p. 146, fig. 12) a specimen resembling Dumortier's type, while Renz's *Hildoceras bifrons* var. *graeca* (1911a, p. 283, fig. 3) falls within the variability field of the above chronospecies. It is therefore the oldest name bearing representative (Renz, 1913, p. 615) of all the morphs with periumbilical relief.

Howarth (1992), in a broad and detailed monograph on family Hildoceratidae, underlines the priority of the specific name *laticosta* for the older forms of *Hildoceras*. Hence, the specific name *Hildoceras sublevisoni* should follow its name bearer (Dumortier's type) as junior synonym of *Hildoceras laticosta* (Howarth, 1992, Part 2, p. 180). Whereas the latter name has never been used since 1900 and, on the contrary, the former has been widely used, it may be thought of as a *nomen oblitum*. Nevertheless the broad application of *Hildoceras sublevisoni* has been accompanied by too many discordant opinions and, perhaps, confusion linked to this name may cease once it is abandoned.

However, Howarth groups under the name *laticosta* specimens with spaced ribs, usually less then 40 per whorl, although showing a well developed periumbilical relief. Specimens with closer and more numerous ribs are referred to *Hildoceras lusitanicum* Meister, 1913, also prior to *Hildoceras sublevisoni*. Having considered the periumbilical relief a distinct and subsequent character in respect to the umbilical wall, it seems to me reasonable to restrict *Hildoceras laticosta* to specimens lacking the former character, in order to obtain a stronger resemblance with the holotype as indicated by Howarth (1992, Part 2, p. 179). Howarth also invalidates the chronological priority of *Hildoceras graecum* over *Hildoceras lusitanicum* because of the poor description and figure of the untraceable holotype (1992, Part 2, p. 182).

In my opinion, Renz's figure is sufficiently clear to determine the specimen's most peculiar features and, therefore, it could have been a proper representative. However, considering that its chronological priority is negligible (both specific names are dated 1913) and that taxonomic stability must be maintained, *Hildoceras lusitanicum* is preferred in place of *Hildoceras graecum*, as previously suggested by Howarth.

The "typical" Hildoceras bifrons occurs quite rarely in the Rosso Ammonitico facies.



Fig. 3 - Vertical distribution of *Hildoceras bifrons* (a) and *Hildoceras semipolitum* (b) in the middle and high part of the *Bifrons* zone.

More common, although not abundant, are the small-sized forms with narrow umbilicus, interpreted as microconch by the virtue of the acceptance of sexual dimorphism (Gabilly, 1976; Elmi, 1977; Howarth, 1992). At Polino, a corresponding morphotype was found between bed 11A and 13 (fig. 3). Although sometimes figured as *Hildoceras semipolitum*, for the similarly involute spiral, it differs since the whorl grows less in height.

Hildoceras semipolitum occurs at higher levels, over a 1. 30 m ranging interval (from bed 14 up to bed 22).

Hildoceras laticosta Bellini, 1900

Pl. 1, figs 1-6; Text fig. 4

1874 Ammonites levisoni Simpson; Dumortier, p. 48, pl. 9, figs 3, 4.

1900 Hildoceras bifrons (Bruguière) var. laticosta Bellini, p. 145; p. 146, fig. 12.

- ?1900 Hildoceras bifrons (Bruguière) var. serraticosta Bellini, p. 145; p. 146, fig. 13.
- 1930 Hildoceras sublevisoni var. raricostata Mitzopoulos, p. 49, pl. 4, fig. 9.
- 1933 Hildoceras sublevisoni Fucini var. raricostata Mitzopoulos; Merla, p. 51, pl. 7, fig. 4.
- 1933 Hildoceras caterinii Merla, p. 53, pl. 7, fig. 5.

1942 Hildoceras sublevisoni Fucini var. raricostata Mitzopoulos; Magnani, p. 109, fig. 2.

- 1947 Hildoceras sublevisoni Fucini var. raricostata Mitzopoulos; Lippi-Boncambi, p. 139, pl. 6, figs 15, 6.
- 1963 Hildoceras sublevisoni Fucini; Zanzucchi, p. 124, pl. 14, fig. 12; pl. 17, fig. 1.
- ?1963 Hildoceras sublevisoni Fucini var. ; Zanzucchi, p. 125, pl. 16, fig. 13.

1966 Hildoceras (Orthildaites) sublevisoni Fucini; Behmel & Geyer, p. 23, pl. 1, fig. 1; pl. 6, fig. 8.

- 1966 Arieticeras cf. falciplicatum (Fucini); Behelm & Geyer, p. 20, pl. 3, fig. 7; pl. 6, fig. 7.
- 1966 Mercaticeras geyerianum (Fucini); Behmel & Geyer, p. 24, pl. 3, figs 4, 5 (?); pl. 6, figs 2, 11.

1968 Hildoceras sublevisoni Pelosio; p. 147, pl. 18, figs 7, 9, 12.

- 1969 Hildoceras caterinii Merla; Pinna, p. 10, pl. 1, fig. 5.
- 1973 Hildoceras sublevisoni Fucini; Guex, p. 505, pl. 6, fig. 4.
- 1974 Hildoceras sublevisoni Fucini; Elmi, Atrops & Mangold, p. 61, pl. 2, figs 2, 4.
- ?1976 Orthildaites douvillei (Haug); Gabilly, p. 120, pl. 20, figs 1-5.
- ?1976 Hildoceras sublevisoni Fucini; Gabilly, p. 128, pl. 22, figs 1, 2.
- 1976 Hildoceras sublevisoni Fucini; Gabilly, p. 128, pl. 20, figs 6, 7.
- 1977 Hildoceras sublevisoni Fucini; Elmi, p. 82, pl. 1, fig. 10.
- 1979 Hildoceras sublevisoni Fucini; Mariotti, Nicosia, Pallini, Schiavinotto, pl. 1, fig. 13.
- 1979 Orthildaites douvillei (Haug); Mariotti, Nicosia, Pallini, Schiavinotto, pl. 1, fig. 12.
- ?1992 Hildoceras laticosta Bellini; Howarth, p. 179, pl. 34, figs 2, 4, 5, 6.

1992 Hildoceras sublevisoni Fucini; Jimenez & Rivas, p. 66, pl. 6, figs 4, 5; pl. 7, figs 1, 2, 5, 6, 7 (?);

pl. 8, figs 1-4; pl. 9, fig. 1; pl. 11, fig. 11.

- 1992 Orthildaites douvillei (Haug); Jimenez & Rivas, p. 62, pl. 6, fig. 3.
- 1994 Hildoceras gr. sublevisoni Fucini; Faraoni, Marini, Pallini, Venturi, p. 252, pl. 13, figs 16-18.

Type: the holotype, as indicated by Howarth (1992, vol. 2, p. 179), is the original of Bellini's drawing (1900, p. 146, fig. 12). I have searched for the original specimen and I found it preserved at the Palaeontology Museum of University of Naples. However on the label which accompanies it there is only specification of the provenance (the Rosso Ammonitico of M. Subasio, near Assisi, Umbria), without any reference to the figure published in Bellini's paper, nor to the name (*Hildoceras bifrons* var. *laticosta*) assigned to it.

The absence of this information is problematic, since the original specimen, though recognizable, is not faithfully reproduced by its drawing, which does not show any of the fractures and other characterizing features due to preservation. Nevertheless it seems to me reasonable to affirm the correspondence between the drawing and the unnamed specimen supposed to be its original. This assumption is also based on the fact that the other figures



Fig. 4 - Specimen supposed to be the original of Bellini's figure (Bellini, 1900, p. 146, fig. 12), representing *Hildoceras bifrons* var *laticosta*.

of Bellini's paper are also clean and regular. In fact, they exhibit a degree of preservation unlike ammonites from the red nodular marls and in contrast with that of the specimens of the collection I have observed (nearly all of them are fractured or damaged). Perhaps it was customary of Bellini to touch-up the figures of his ammonites.

After these considerations a figure of the possible original holotype is here given (fig. 4). It is a partially complete specimen reaching a diameter of 52 mm at the fourth whorl, of which the last half is the remaining part of the body-chamber. Ribs, badly preserved on the body-chamber, are about 31-32. They have a gentle concave shape and stop at the inner flank as they meet a smooth umbilical wall.

Material: 8 specimens.

Stratigraphical distribution: from bed 10A1 to 10A3, which are in the lowermost part of the *Bifrons* zone (fig. 2).

Distinctive character: umbilical wall; no periumbilical relief or evidence of pseudogroove.

Diagnosis: evolute whorl, compressed cross section with nearly flat parallel flanks, except for the sloping umbilical wall. The venter shows a central keel and two evident lateral sulci bordered on each side by the keel-like edge of the outermost flank, which is due to the confluence and fading of the ribs.

Ribs are thin, sigmoidal and backward bending at first, and they reach quite regularly to the umbilicus. Then, in older stages, they end against the smooth and flat surface of the umbilical wall, also becoming coarser, further spaced, and with a radial course and a straight or gently forward-concave shape. In the holotype they seem to keep a constant number although coarsening but, in other corresponding forms (for instance the specimen PO 10A2/172, pl. 1, fig. 1), the inner whorls attain more numerous ribs in respect to the latest (generally 30-33).

Remarks: the species' main features are fully outlined by Merla (1933) in the attempt to distinguish his *raricostata* variety from specimens having a periumbilical relief, which the author ascribes to *Hildoceras sublevisoni* (*Hildoceras lusitanicum* in this paper). Merla, in fact, separates the above mentioned variety from the typical *sublevisoni* "perchè manca la carena longitudinale che nel *sublevisoni* delimita una parete ombelicale inclinata" (1933, pp. 51-52).

The distinction between morphotypes with or without periumbilical relief may become difficult when dealing with immature specimens, in which the complete ribs cover the yet poorly developed periumbilical relief of *Hildoceras lusitanicum*. Also the pseudogroove, never perceptible in *Hildoceras laticosta*, is little or not at all impressed in juvenile *Hildoceras lusitanicum*.

Hildoceras lusitanicum Meister, 1913

Pl. 1, figs 7-10; Pl. 2, figs 1-10; Pl. 3, figs 1-8

1879 Ammonites levisoni Simpson; Reynes, pl. 7, fig. 2. 1886 Hildoceras levisoni Simpson; Seguenza, p. 1380. 1904b Hildoceras bifrons (Bruguière); Prinz, p. 126, pl. 6, figs 1-4, 7. 1905 Hildoceras levisoni Simpson; Fucini, p. 113, pl. 6, fig. 3. 1905 Hildoceras bifrons (Bruguière); Fucini, p. 113, pl. 5, figs 13-15. 1906 Hildoceras levisoni Simpson; Parisch & Viale, p. 155, pl. 11, figs 7-9. 1911a Hildoceras bifrons (Bruguière) var. ; Renz, p. 283, figs 2, 3. 1913 Hildoceras bifrons (Bruguière) var. graeca Renz; p. 615. 1913 Hildoceras bifrons (Bruguière) var. lusitanica Meister; p. 548, pl. 12, fig. 3. 1914 Hildoceras bifrons (Bruguière); Zuffardi, p. 613, pl. 11, fig. 12. 1922 Hildoceras sublevisoni Fucini; p. 182. 1922 Hildoceras bifrons (Bruguière); Fucini, p. 181, pl. 16, fig. 2. 1930 Hildoceras sublevisoni Fucini; Mitzopoulos, p. 48, pl. 4, fig. 8. 1930 Hildoceras sublevisoni Fucini var. sulcosa Mitzopoulos, p. 50, pl. 5, fig. 1. 1930 Hildoceras bifrons (Bruguière) var. acarnanica Mitzopoulos, p. 43, pl. 4, fig. 5. 1930 Hildoceras bifrons (Bruguière) var. lombardica Mitzopoulos, p. 44, pl. 4, fig. 6. 1930 Hildoceras bifrons (Bruguière) var. crassa Mitzopoulos, p. 45, pl. 4, fig. 7. 1933 Hildoceras sublevisoni Fucini; Merla, p. 51, pl. 7, figs 1, 9, 10. 1933 Hildoceras bifrons (Bruguière); Merla, p. 52, pl. 7, fig. 9. 1939 Hildoceras bifrons (Bruguière); Ramaccioni, p. 171, pl. 11, fig. 18. 1947 Hildoceras bifrons (Bruguière); Lippi-Boncambi, p. 137, pl. 6, fig. 12. 1958 Hildoceras sublevisoni Fucini; Donovan; p. 50. 1963 Hildoceras sublevisoni Fucini; Zanzucchi, p. 124, pl. 17, fig. 2. 1963 Hildoceras sublevisoni Fucini var.; Zanzucchi, p. 125, pl. 15, figs 3, 6, 7, 8; pl. 16, figs 1, 2, 4, 5 (?), 6 (?), 7-12; pl. 17, fig. 3. 1963 Hildoceras venzoi Zanzucchi; pl. 17, fig. 10. 1963 Hildoceras cfr. semicosta Buckman; Zanzucchi, p. 126, pl. 14, fig. 11. 1963 Hildoceras bifrons (Bruguière); Zanzucchi, p. 120, pl. 14, fig. 10; pl. 15, figs 1, 9 (?). 1963 Hildoceras bifrons (Bruguière) var. ; Zanzucchi, p. 122, 123, pl. 15, figs 4, 10; pl. 16, fig. 3; pl. 17, figs 8, 9, 11. 1966 Hildoceras graecum graecum Renz; Kottek, p. 66, pl. 3, fig. 8; pl. 4, fig. 1. ?1966 Hildoceras graecum sublevisoni Fucini; Kottek, p. 67, pl. 4, fig. 2. 1966 Hildoceras graecum lusitanicum Meister; Kottek, p. 69, pl. 4, figs 3, 4. 1966 Hildoceras semipolitum Buckman; Kottek, p. 61, pl. 3, fig. 4. ?1966 Hildoceras (Orthildaites) ambiguum Fucini; Behmel & Geyer, p. 23, pl. 1, fig. 3; pl. 6, fig. 12. 1967 Hildoceras sublevisoni Fucini; Elmi, p. 231, fig. 3. 1967 Hildoceras lusitanicum Meister; Elmi, p. 235, fig. 1.

1968 Hildoceras sublevisoni Fucini juv. ; Pelosio, p. 147, pl. 18, fig. 5.

1968 Hildoceras bifrons (Bruguière) f. graeca Renz; Pelosio, p. 151, pl. 18, figs 3, 4; pl. 23, fig. 10.

1969 Hildoceras bifrons (Bruguière); Pinna, p. 10, pl. 1, figs 1, 4, 11.

1970 Hildoceras sublevisoni Fucini; Gallitelli-Wendt, p. 24, pl. 3, figs 2, 3 (?), 4, 5.

1972 Hildoceras sublevisoni Fucini; Guex, p. 639, pl. 6, fig. 2.

1972 Hildoceras lusitanicum Meister; Guex, p. 639, pl. 7, fig. 4. 1973 Hildoceras sublevisoni Fucini; Guex, p. 505, pl. 10, fig. 3.

1973 Hildoceras graecum Renz; Guex, p. 505, pl. 10, fig. 4.

1975 Hudocerus gruecum Kenz, Ouex, p. 505, pl. 10, fig. 4.

1974 Hildoceras sublevisoni Fucini; Elmi, Atrops & Mangold, p. 61, pl. 2, fig. 5.

1974 Hildoceras aff. lusitanicum Meister; Elmi, Atrops & Mangold, p. 62, pl. 2, fig. 6. 1976 Hildoceras tethysi Geczy; Gabilly, p. 137, pl. 21, figs 1-4; pl. 23, figs 6, 7.

1976 *Hildoceras sublevisoni* Fucini; Gabilly, p. 137, pl. 21, fig. 14, pl. 25, f.

1976 Hildoceras sabievision Fucini, Gabilly, p. 126, pl. 21, fig. 5. ?1976 Hildoceras caterinii Merla; Gabilly, p. 135, pl. 22, figs 3-6.

1976 Hildoceras crassum Mitzopoulos; Gabilly, p. 143, pl. 23, figs 1-5; pl. 24, figs 1, 2; pl. 25, figs 1, 2.

1976 Hildoceras lusitanicum Meister; Gabilly, p. 147, pl. 24, figs 3-6; pl. 25, figs 3-6.

1977 Hildoceras graecum Renz; Nicosia & Pallini, p. 267, pl. 1, fig. 3.

1982 Hildoceras lusitanicum Meister; Venturi, p. 70, fig. 99.

1982 Hildoceras sublevisoni Fucini; Venturi, p. 70, fig. 101.

1982 Hildoceras acarnanicum Mitzopoulos; Venturi, p. 70, fig. 100.

1992 Hildoceras lusitanicum Meister; Howarth, p. 181; p. 183, fig. 42; pl. 34, fig. 7; pl. 35, figs 1-4; pl. 36, figs 1-3.

?1992 Hildoceras laticosta Bellini; Howarth, p. 179, pl. 34, fig. 8.

1992 Hildoceras bifrons (Bruguière); Howarth, pl. 37, fig 8.

1992 Hildoceras sublevisoni Fucini; Jimenez & Rivas, p. 66, pl. 7, figs 3, 4; pl. 8, figs 5-11; pl. 9,

figs 2-8; pl. 10, figs 1, 2; pl. 11, fig. 12 (?).

1994 Hildoceras lusitanicum Meister; Faraoni, Marini, Pallini, Venturi, p. 249, pl. 13, fig. 4.

1994 Hildoceras gr. sublevisoni Fucini; Faraoni, Marini, Pallini, Venturi, p. 252, pl. 13, figs 7, 11, 13, 20.

1994 Hildoceras sublevisoni var. sulcosa Mitzopoulos; Faraoni, Marini, Pallini, Venturi, pl. 13, figs 10, 21.

1994 Hildoceras gr. acarnanicum Mitzopoulos; Faraoni, Marini, Pallini, Venturi, p. 249, pl. 13, fig. 8.

1994 Hildoceras graecum Renz; Faraoni, Marini, Pallini, Venturi, p. 249, pl. 13, fig. 19.

Type: the holotype is the specimen figured by Meister (1913, pl. 12, fig. 3), which comes from Marmeleira, Portugal.

Material: 152 entire specimens and many fragments.

Stratigraphical distribution: from bed 10C to 10N, corresponding to the low-middle part of the *Bifrons* zone (fig. 2).

Distinctive character: periumbilical relief; no spiral groove, sometimes replaced by variable pseudogroove.

Diagnosis: evolute and rather quadrate whorl in earlier forms and earlier developmental stages, then becoming more perceptibly compressed and more evolute by slight uncoiling at larger diameters. The umbilical wall is well developed toward the mid flank in a rounded or angled periumbilical relief, bordered by a differently impressed pseudogroove. The pseudogroove is tendentially precocious in later forms.

Ribs, typically sigmoidal in shape, are complete at younger stages and cut off by the umbilical wall in older ones. They show a forward bending "elbow" near the periumbilical relief and a concave arc on the outer flank, swinging backward markedly in the juvenile, almost radial in the adults.

Their number per whorl shifts in continuity from a minimum of 31-32, in the older, to

40-45 in the later representatives (although few individuals with 48-50 ribs were recovered too). The venter is bisulcate-tricarinate from the central keel, the two sulci and the confluence of the ribs to form the two lateral and less pronounced keels.

These features are evidenced by the two large individuals PO 10E/286 (pl. 1, fig. 9, completely phragmoconic, from the lower assemblage) and PO 10N/283 (pl. 3, fig. 8, with body-chamber partially preserved, from the higher assemblage). Differences shade off at the equally large final whorl and they differ in rib numbers only. In fact both specimens show the periumbilical relief (more rounded in the recent form) bordered by the pseudogroove. But in the inner whorls of PO 10E/286 evidences of a pseudogroove vanish more suddenly than in PO 10N/283.

Remarks: the major distinctive traits in respect of *Hildoceras laticosta* have already been listed. Transitional morphologies may occur independently from anagenesis and thus they may not be represented by populations stratigraphically intermediate between the two species. Such morphologies may be related to variability as due to ontogenesis and development. Hildoceras lusitanicum, as considered in this paper, becomes a rather wideranging species but, on the other hand, this avoids excessive taxonomic splitting based on characters representing ontogenetic or continuous variability.

Hildoceras bifrons (Bruguière, 1789) Pl. 3, fig 9; Pl. 4, figs 1-5

1789 Ammonites bifrons Bruguière; p. 40. 1879 Ammonites bifrons Bruguière; Reynès, pl. 7, figs 8-23. 1904b Hildoceras bifrons (Bruguière) mut. quadrata Prinz; p. 126. 1906 Hildoceras bifrons (Bruguière); Parisch & Viale, p. 155, pl. 8, figs 5, 6. 1930 Hildoceras bifrons (Bruguière); Mitzopoulos, p. 39, pl. 3, fig. 6. 1930 Hildoceras bifrons var. quadrata Prinz; Mitzopoulos, p. 41, pl. 4, fig. 1. 1930 Hildoceras bifrons (Bruguière) var. angustisiphonata Prinz; Mitzopoulos, p. 41, pl. 4, fig. 2. 1930 Hildoceras bifrons (Bruguière) var. graeca Renz; Mitzopoulos, p. 42, pl. 8, fig. 3. 1933 Hildoceras semipolitum Buckman; Merla, p. 52, pl. 7, figs 3, 6, 7. 1938 Hildoceras bifrons (Bruguière); Roman, pl. 11, fig. 115. 1952 Hildoceras bifrons (Bruguière) var. angustisiphonata Prinz; Nicotra, p. 72, pl. 3, fig. 4. ?1952 Hildoceras semipolitum Buckman; Nicostra, p. 73, pl. 3, fig. 5. 1958 Hildoceras bifrons (Bruguière); Donovan, pp. 49-50. 1966 Hildoceras bifrons bifrons Bruguière; Kottek, p. 63, pl. 3, fig. 6. 1966 Hildoceras bifrons walcoti (J. Sowerby); Kottek, p. 65, pl. 3, fig. 7. 1966 Hildoceras semipolitum Buckman; Kottek, p. 61, pl. 3, fig. 5. 1966 Hildoceras bifrons (Bruguière); Behmel & Geyer, p. 23, pl. 2, fig. 4; pl. 6, fig. 5. 1966 Hildoceras semipoliyum Buckman; Behmel & Geyer, p. 23, pl. 2, fig. 3; pl. 6, fig. 9. 1967 Hildoceras bifrons (Bruguière); Elmi, p. 235, fig. 3. 1968 Hildoceras bifrons (Bruguière); Pelosio, p. 149, pl. 18, figs 1, 13; pl. 23, fig. 3. 1968 Hildoceras semipolitum Buckman; Pelosio, pl. 18, figs 8, 11. 1969 Hildoceras bifrons (Bruguière); Pinna, p. 10, pl. 1, fig. 3. 1970 Hildoceras bifrons bifrons (Bruguière); Gallitelli-Wendt, p. 28, pl. 3, fig. 6. 1970 Hildoceras bifrons angustisiphonatum Prinz; Gallitelli-Wendt, p. 31, pl. 4, figs 1, 2. 1970 Hildoceras semipolitum Buckman; Gallitelli-Wendt, p. 33, pl. 4, fig. 5. ?1972 Hildoceras graecum Renz; Guex, p. 639, pl. 6, fig. 6. 1972 Hildoceras bifrons (Bruguière); Guex, p. 639, pl. 6, fig. 7; pl. 7, fig. 8. 1972 Hildoceras semicosta Buckman; Guex, p. 639, pl. 6, fig. 8. 1974 Hildoceras apertum Gabilly; Elmi, Atrops & Mangold, pl. 2, fig. 10.

1975 Hildoceras gr. semipolitum Buckman; Venturi, pl. 30, figs 1, 3.

- 1977 Hildoceras bifrons (Bruguière); Nicosia & Pallini, p. 267, pl. 1, fig. 6.
- 1979 Hildoceras apertum Gabilly; Mariotti, Nicosia, Pallini, Schiavinotto, pl. 1, fig. 6.
- 1982 Hildoceras angustisiphonatum Prinz; Venturi, p. 70, fig. 98.

1992 Hildoceras bifrons (Bruguière); Howarth, p. 185; p. 34, fig. 10D, pl. 36, fig. 4; pl. 37, figs 1-7, 9, 10, pl. 38, figs 3, 7.

1992 Hildoceras bifrons (Bruguière); Jimenez & Rivas, p. 69, pl. 10, fig. 3.

Type: the holotype is the by now famous specimen from the Whitby shales, at Yorkshire, already figured by Lister in 1678 and afterwards considered by Bruguière when designating *Ammonites bifrons*.

Material: 19 specimens, all less than 45 mm in diameter.

Stratigraphical distribution: from bed 11B to 13, which are in the middle part of the *Bifrons* zone (fig. 3).

Distinctive characters: spiral groove, quadrate or compressed whorl slowly growing in height.

Diagnosis: quadrate to compressed whorls at various degree of embracement, shifting from the minimum of about one third, in macroconchs, to the maximum of about a half in the microconch individuals. The rounded and prominent umbilical wall, as a whole with the periumbilical relief, is gradually or abruptly confluent with the marked spiral groove cutting off the ribs at their elbow-like projection. In many cases striae and relict ribbing are preserved at the dorsal flank, which are likely to be related to the growth of lappets. Density and thickness of the ribs are variable, the ventral area is bisulcate-tricarinate.

Remarks: plenty has already been said upon *Hildoceras bifrons* by the numerous authors who have been engaged with Toarcian ammonites. A further contribution can be brought only by underlining the apparently diversified geographical distribution of the dimorphic pairs (Howarth, 1992).

Concerning the microconch form, it is also important to note its distinction from *Hildoceras semipolitum*, to which it has been often ascribed. Although the involution of the spiral is comparable, *Hildoceras semipolitum* differs primarily in the greater height of the whorls, and is also more widely-flanked and further compressed.

The stratigraphical distribution is quite different too, thus at Polino, *Hildoceras* semipolitum occupies the highermost layers of the *Bifrons* zone, never occurring together with *Hildoceras bifrons*.

Hildoceras semipolitum Buckman, 1902 Pl. 4, figs 6-9

1889a Hildoceras bifrons (Bruguière) var. Buckman, p. 112, pl. 22, figs 31, 32; pl. A, fig. 28. 1902 Hildoceras semipolitum Buckman, p. 4.

1930 Hildoceras bifrons (Bruguière) var. involutissima Mitzopoulos; p. 43, pl. 4, fig. 4.

¹⁹⁰⁴b Hildoceras bifrons (Bruguière) mut. angustisiphonata Prinz; p. 126.

¹⁹³⁹ Hildoceras semipolitum Buckman; Ramaccioni, p. 172, pl. 11, fig. 19.

1952 Hildoceras semipolitum Buckman; Venzo, p. 118, pl. B, fig. 13.

- 1952 Hildoceras semipolitum Buckman var. compressum Venzo; p. 120.
- 1958 Hildoceras semipolitum Donovan; p. 50.
- 1968 Hildoceras semipolitum Buckman; Pelosio, p. 153, pl. 18, figs 2, 6.
- 1969 Hildoceras semipolitum Buckman; Pinna, p. 10, pl. 1, fig. 2.
- 1972 Hildoceras angustisiphonatum Prinz; Venturi, p. 28, fig. 2e.
- 1972 Hildoceras semipolitum Buckman; Guex, p. 639, pl 6, figs 1, 4, 5; pl. 7, fig. 5.
- 1972 Hildoceras angustisiphonatum Prinz; Guex, p. 639, pl. 6, fig. 3; pl. 7, fig. 1.
- 1972 Hildoceras semicosta Buckman; Guex, p. 639, pl. 7, fig. 2.
- 1974 Hildoceras semipolitum Buckman; Elmi, Atrops & Mangold, p. 63, pl. 3, figs 3-8.
- 1974 Hildoceras bifrons (Bruguière); Elmi, Atrops & Mangold, p. 62, pl. 2, fig. 9.
- 1974 Hildoceras bifrons (Bruguière) var. angustisiphonata Prinz; Elmi, Atrops & Mangold, p. 63, pl. 3, fig. 7.
- 1977 Hildoceras snoussi Elmi; p. 80, pl. 4, fig. 3.
- 1977 Hildoceras semipolitum Buckman; Nicosia, & Pallini, pl. 1, fig. 4.
- 1982 Hildoceras semipolitum Buckman; Venturi, p. 70, fig. 97.
- 1992 Hildoceras semipolitum Buckman; Howarth, p. 188, pl. 38, figs 1, 2, 4-6, 8.
- 1992 Hildoceras semipolitum Buckman; Jimenez & Rivas, p. 71, pl. 10, figs 4-7; pl 11, figs 1-10.

Type: the holotype is the specimen first figured by Buckman as variety of *bifrons* (1889a, pl. 22, figs 30, 31) and in 1902 elevated as the species known today by Buckman himself.

Material: 12 specimens all less then 55 mm in diameter.

Stratigraphical distribution: from layer 14 to 22, corresponding to the highermost part of the *Bifrons* zone (fig. 3).

Distinctive characters: spiral groove, highly compressed whorls, also widely-flanked and involute.

Diagnosis: The ornamental features and their variability are almost the same as outlined for *Hildoceras bifrons*. Differences include the overlap and compression of the whorl, which are both brought to extreme degree. Thus a nearly flat spiral, up to one half covered, is attained.

Remarks: among the recovered morphotypes some kind of variability is noticeable in the density of the ribs. That is evident by comparing specimens PO 18/246 (pl. 4, fig. 7) and PO 19B/188 (pl. 4, fig. 9), respectively with finer ribs, and with coarser, more spaced ones. The former, by the way better resembling the holotype, comes from lower layers than the latter. However, considering that the number of collected specimens is very small, no relation between ribbing patterns and stratigraphical position could be suggested with certainty. Also perceptible is some variability in compression and overlap of the whorls.

Elmi (1977, p. 80) established *Hildoceras snoussi* on a single specimen from Algery, which shows a very narrow umbilicus (1977, pl. 4, fig. 3). This new species is herein considered as synonymous with *Hildoceras semipolitum*, in line with the somewhat wide variability field recognized for all other species. Otherwise also specimens with wider umbilicus and less involute whorls, which often do occur, should be distinguished from *Hildoceras semipolitum*. However, in any case Elmi's species is to be considered as synonymous, for it is fully comparable with the *Hildoceras bifrons* var. *involutissima* figured by Mitzopoulos (1930, p. 43, pl. 4, fig. 4).

MORPHOLOGICAL CHARACTERS		GABILLY 1976	JIMENEZ & RIVAS 1992	HOWARTH 1992	PRESENT WORK
SPIRAL GROOVE	Highly compressed whorls with wide flanks; embracement ratio about 1/2.	H. semipolitæn Buckman, 1902	H. semipolitum Buckman, 1902	H. snoussi Elmi, 1917	H. semipolitum Buokanaa, 1902
	These characters are generally pronounced in later specimens.			H. semipolitum Buckman, 1902	
	Quadrate to compressed whorin.	H. bifrons (Bruguière, 1789)			
	Embracement ratio about 1/2 in microconche, about 1/3 in macroconche.	H. apertum Gabiliy, 1976			
PERIUMBILICAL RELIEF	PROGRESSIVELY THINNER RIBS	H. lusitanicum Moister, 1913	H. sublevisoni Fucini, 1919	H. lusitanicum Moistor, 1913	H. Iusitanicum Moistor, 1913
		H. crassum Mitzopoulos, 1930			
		H. tethysi Géczy, 1967			
		H. caterinii Merle, 1933		H. laticosta Bollini, 1900	
UMBILICAL WALL		H. sublevisoni Fucini, 1919			H. laticosta Bollini, 1900

Fig. 5 - Comparative scheme summarizing some of the different classifications proposed for *Hildoceras* species.

CONCLUSIONS

Accurate bed by bed collecting among Umbrian Rosso Ammonitico outcrops enabled an evaluation of the taxonomic significance of characters concerned in classification. By contrast the variability patterns depending on ontogenesis have been emphasised, since they have hitherto not been outlined.

This has led to a different approach to systematics, in that better attention was addressed to the distribution of morphological types rather than to differences, though remarkable, between single specimens. Such a procedure prevented reference to any somewhat different trait during classification. In fact, the attempt was to redifine the distinction between species based on varied populations and not on varied individuals in which nearly all variants are somehow thought to be of taxonomic value.

These general lines of the research work, together with the prerogative of considering the more objectively recognizable characters, have had the result of reducing the number of taxonomically useful characters. In consequence, the number of reliable species has diminished too (fig. 5).

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All of the figured ammonites have been whitened with ammonium chloride and are preserved, as collection NS 87, at the Palaeontology Museum (Dipartimento di Scienze della Terra) of the University of Rome "La Sapienza".



 Figs 1-10 Hildoceras lusitanicum Meister, 1913. 1) PO 10F/205; 2) PO 10G2/210; 3) PO 10H/287; 4) PO 10H/189; 5) PO 320; 6) PO 10L/231; 7) PO 10L/232; 8) PO 10L/301; 9) PO 10L/37; 10) PO 321. All figures ca. x 0. 7.

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Figs 1-8 -	Hildoceras lusitanicum Meister, 1913. 1) PO 10M/48; 2) PO 10M/49;
	3) PO 10M/50; 4) PO 10M/242; 5) PO 10N/180; 6) PO 10N/226; 7)
	PO 10N/179; 8) PO 10N/283.
Fig. 9)	Hildoceras bifrons (Bruguière, 1789); PO 380. All figures ca. x 0. 7.



Plate 4

Figs 1-5 -	Hildoceras bifrons (Bruguière, 1789). 1) PO 12/230; 2) PO 12/239; 3)
	PO 13/186; 4) PO 52; 5) PO 228.
Figs 6-9 -	Hildoceras semipolitum Buckman, 1902. 6) PO 14/71; 7) PO 18/246;
	8) PO 17/247; 9) PO 19B/188. Figures 1-3, 5, 6, 8, ca. x 0. 9; figures
	4, 7, 9, ca. x 0. 7.



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