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Heterochrony and evolution in some Toarcian ammonites. Speculations and insights

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ABSTRACT - The record of *Hildoceras* species from the Rosso Ammonitico marls (Toarcian) near Terni (Central Apennines) is analysed in order to outline a possible relationship between ontogenetic and phylogenetic variability. Bed by bed sampling provides evidence of ontogenetic variability in shell morphology that parallels evolutionary change, suggesting a possible control by heterochrony. Specifically, heterochrony is proposed as a potential mechanism by which: 1) discontinuous inflections accompanying rib fading at the inner flank of *Hildoceras lusitanicum*, initially a character of later growth stages, are progressively anticipated during ontogeny, finally culminating in the spiral groove of *Hildoceras bifrons*; 2) delayed maturation and inhibition of the adult "uncoiling" stage of *Hildoceras bifrons*, concomitant to allometric growth of whorl height, result in the overall involute and relatively compressed shell structure observed in *Hildoceras semipolitum*. Interrelated to heterochrony is also the concept of "developmental polymorphism", considered as a plausible alternative and more general frame in which to place sexual dimorphism as displayed by *Hildoceras bifrons*.

Keywords: *Hildoceras*; ontogeny; sexual dimorphism; Rosso Ammonitico.

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1. INTRODUCTION

Discriminating ontogenetic variability in the fossil record is worth for inferring developmental processes that also affect morphological change within phylogenetic lineages, as for instance heterochrony. With reference to this category of morphological complexity, the structure of ammonite shells is remarkably liable in unveiling developmental variability and its possible influence on morphological changes retaining evolutionary significance (e.g. Gerber et al., 2008). Whereas in the last two-three decades this "morpho-developmental" approach has been increasingly applied to ammonites of the Northern Europe (Boreal) palaeogeographical province (e.g. Dommergues et al., 1986; Meister, 1988; Dommergues and Meister, 1991; Mignot et al., 1993; Neige et al., 1997; Yacobucci, 2004; Gerber et al., 2007), Mediterranean populations have largely escaped a revision under the view of this enlarged domain of individual morphological variability.

The Toarcian genus *Hildoceras* from the Rosso Ammonitico facies of the Central Apennines is herein analysed in the light of heterochrony as a possible cause for morphological transformations achieved by successive species. The Rosso Ammonitico fauna, early described by Meneghini (1867-1881; 1885) and Bonarelli (1893), is renowned for the richness of *Hildoceras* species (Donovan, 1958; Gallitelli-Wendt, 1969; Venturi, 1972, 1975). Although ontogenetic variability in *Hildoceras* species has been early recognized (Taramelli, 1880), it has passed almost completely ignored in more recent taxonomic issues. By underrating the relevance and patterns by which ontogenetic variability displays, also the effect of heterochrony, in determining evolutionary change, has long remained undisclosed. Premise to a reversal of this approach herein attempted is the evidence from the stratigraphic record that individuals of *Hildoceras* species show phenotypical changes depending on overall size and number of whorls of the shell (Ridente, 1996).

The study herein presented is based on the ammonite fauna from Rosso Ammonitico outcrops located near the town of Polino (Umbria, Central Apennines). The main section (Fig. 1), where greater part of the specimens was sampled, is ca. 17 metres thick from the basal contact with the Corniola Formation (Sinemurian-Hettangian) to the upper boundary with the Posidonia Marls Formation (Aalenian-Bajocian). Based on these data, an attempt is made at distinguishing ontogenetic variability within the highly polymorphic species of *Hildoceras*, in

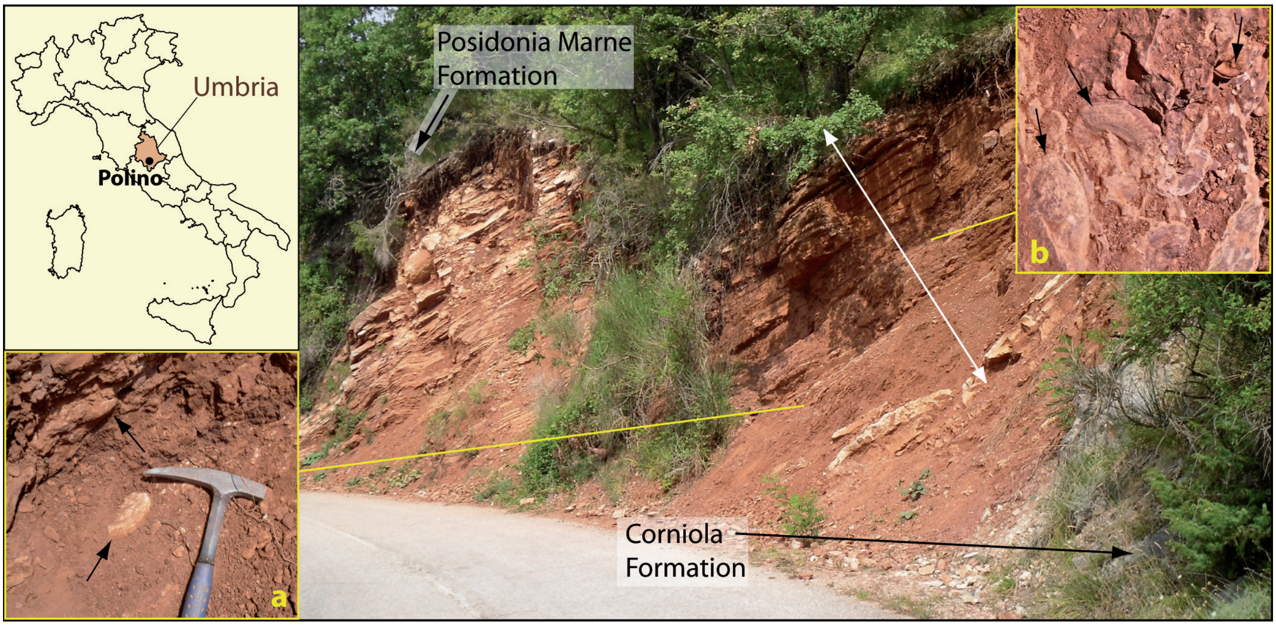

Fig. 1 - Location of the study area and view of the main Rosso Ammonitico section. The white double arrow indicates the Bifrons Zone interval from which specimens of *Hildoceras* have been recovered. Insets "a" and "b" show fossil concentration (black arrows) in beds 10E-F and 10N, respectively (see Fig. 6 for a detailed description).

order to define: 1) the possible effect of heterochrony in driving morphological changes leading from one species to another, namely from *Hildoceras laticosta* Bellini, 1900 and *Hildoceras lusitanicum* Meister, 1913 to *Hildoceras bifrons* (Bruguière, 1789), and from this to *Hildoceras semipolitum* Buckman, 1902; 2) a pattern of developmental polymorphism *sensu* Matyja (1986, 1994) that accounts for the palaeogeographical partitioning of micro- and macroconch sex dimorphs of *Hildoceras bifrons*.

2. BACKGROUND AND DATA

2.1. Classification of *Hildoceras* species. Brief overview

Genus *Hildoceras* was established by Hyatt (1867) with the grouping of three pre-existing species and their renaming as *Hildoceras bifrons*, *Hildoceras walcotti* (Sowerby, 1815) and *Hildoceras hildense* (Young and Bird, 1822). In 1889 Buckman designated *Hildoceras bifrons* as the type species, primarily characterized by the lateral groove that separates the smooth innermost flank from the ribbed outer part (Fig. 2). The lateral groove typically displays a variable degree of impression and shape; according to Donovan (1958), even when poorly engraved it should be considered as diagnostic of the genus (see also Buckman, 1921, p. 55). However, since early times, a considerable amount of morphotypes referred to *Hildoceras bifrons*, or to other varieties, happened to lack it completely (Fig. 3).

Hildoceras sublevisoni Fucini, 1922 was established to group the non-grooved morphs, most of which had been previously referred to *Hildoceras levisoni* (Simpson, 1843), later assigned to genus *Hildaites* by Buckman (1921) and eventually regarded as junior synonymous to *Hildaites murleyi* (Moxon, 1841) by Howarth (1992). Because Fucini omitted to designate a holotype for *Hildoceras sublevisoni*, 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). Donovan (1958, p. 50) remarked on the fact that the two *Hildoceras sublevisoni* figured as typical by Merla (1933, Pl. 7, Figs. 1, 10) differed from the specimen referred to as type (i.e. Dumortier's form; herein shown in Fig. 3a). However, he considered *Hildoceras sublevisoni* as a broad-ranging, polymorphic species, which may embrace both Merla's specimens (with more numerous ribs) and Dumortier's type. In contrast with this view, later authors envisaged the possibility that *Hildoceras sublevisoni* could split into two (Zanzucchi, 1963; Géczy, 1967; Howarth, 1992) or even more than two species (Guex, 1972, 1973; Gabilly, 1976; Elmi, 1977).

According to Ridente (1996), the preponderance of specimens from the Apennines is more closely represented by the morphotype figured by Fucini in 1905 (Pl. 6, Fig. 3), also the only in the synonymy of *Hildoceras sublevisoni* to be directly studied by Fucini. This specimen (Fig. 3b) shows a peculiar conformation of the dorsal flank that is shared by the majority (though not by all) of non-grooved forms, despite wider variability involving the shape, strength and density of the ribs: the smooth and sloping innermost part of the whorl, referred to as "umbilical wall", is slightly raised toward the middle flank instead of being flat like in Dumortier's specimen (Fig. 3a). The rim-like outer edge of the umbilical wall, termed "periumbilical relief" (Ridente, 1996), has been occasionally described in the literature ("carena longitudinale" of Merla, 1933, pp. 51-52; "cercine periombelicale" of Magnani, 1942, p. 18), though not invested of any specific taxonomic value

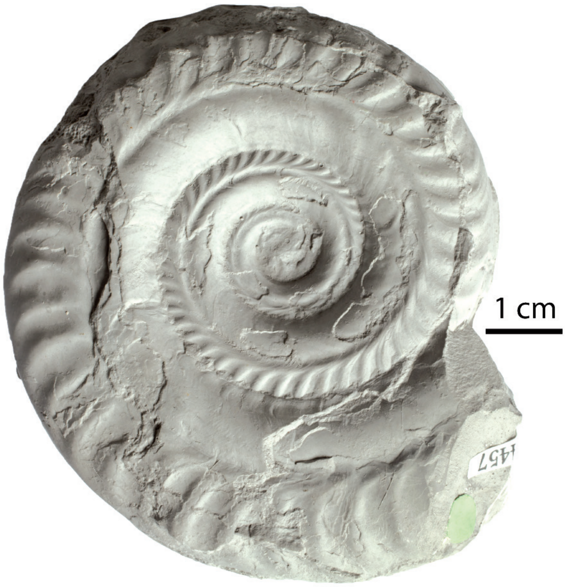

Fig. 2 - *Hildoceras bifrons* (Bruguire, 1789), Neotype (http://www.3d-fossils.ac.uk). Note ribbing pattern partially visible in the inner whorls.

among the several species and subspecies that stemmed from the comprehensive *Hildoceras sublevisoni*.

By considering the presence or absence of the periumbilical relief as a more objective character compared to variability in ribbing pattern, no more than two morphotypes can be distinguished within the broadly interpreted *Hildoceras sublevisoni*. Because, according to Howarth (1992), *Hildoceras sublevisoni* is a junior synonymous of *Hildoceras laticosta* Bellini, 1900, the two species into which non-grooved *Hildoceras* should be grouped are *Hildoceras laticosta,* lacking the periumbilical relief; and *Hildoceras lusitanicum*, with periumbilical relief occasionally flanked by marked inflections that confer a somewhat grooved or "pseudogrooved" morphology (Fig. 4). Nevertheless, a screening of literature data dealing with *Hildoceras* species reveals the persistence of *Hildoceras sublevisoni* in classification and biostratigraphic schemes (Neige and Rouget, 2002; Page, 2004; Galácz et al., 2010; Kovács, 2011; Sassaroli and Venturi, 2012).

Plainly grooved specimens, commonly referred to *Hildoceras bifrons* or *Hildoceras semipolitum*, are typically less abundant in the Rosso Ammonitico marls than their pseudogrooved ancestors (Ridente, 1996). Specimens of *Hildoceras bifrons* display diameter usually ranging between 25 and 45 mm, depending on the preservation of the body chamber. These relatively small morphotypes also show embracement up to one half the whorl height, thus matching the covering ratio typical of *Hildoceras semipolitum*, although in the latter the whorls grow taller and relatively compressed. Gallitelli-Wendt (1969) assigned these smaller and more involute specimens to *Hildoceras bifrons angustisiphonatum* Prinz, 1904, distinguishing the "typical" *bifrons* as *Hildoceras bifrons bifrons.* Gallitelli-Wendt (1969, p. 29) also concluded that the typical *bifrons* is actually replaced by the *angustisiphonatum* type in the Toarcian of Umbria.

All the above considered, the state of the art of the classification of *Hildoceras* species remains problematic (Bardin et al., 2016). Of the many species of *Hildoceras* reported in the literature, several have been questioned and regarded as synonymous, according to author's viewpoints. Nevertheless, nearly all these different species survived complete dismissal (though many never attained a general consensus), resulting in the present state of redundancy of names and classification schemes.

Given that taxonomic issues are not the focus of this work, *Hildoceras* species are hereinafter referred to the following four taxa among those described above: *Hildoceras laticosta*, characterised by a smooth umbilical wall interrupting rib termination along the inner/dorsal flank; *Hildoceras lusitanicum*, with variably developed umbilical relief and discontinuous pseudogroove flanking the umbilical wall; *Hildoceras bifrons*, with a neat, continuous spiral groove and an overall involute

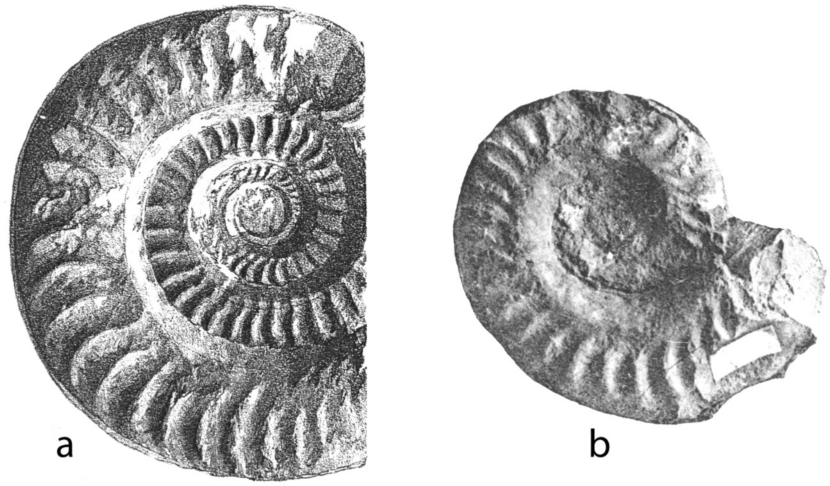

Fig. 3 - Example of early figured specimens of *Hildoceras* without any evidence of lateral groove (a, Dumortier, 1874) or with a very poorly defined one on the half final whorl (b, Fucini, 1905). Note the flat, sharp-edged umbilical wall in Dumortier's type in contrast with the rounded relief of the umbilical wall in Fucini's type (compare with Fig. 4, see text for discussion). Specimens are not at the same scale.

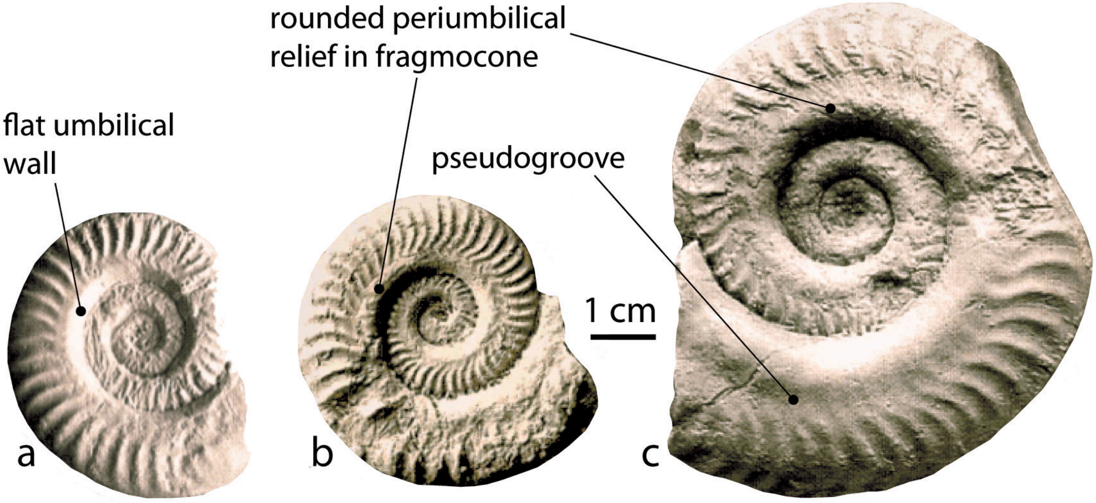

Fig. 4 - Examples of morphotypes previously grouped into *Hildoceras sublevisoni*: a) with umbilical wall but no periumbilical relief (*Hildoceras laticosta*, from bed 10A3; see Fig. 6); b-c) with variably developed periumbilical relief (*Hildoceras lusitanicum*, from detritus between beds 10E and 10N; see Fig. 6). Note the slight inflection (pseudogroove) along the fading of rib termination on the body chamber (c).

shell (similar to the *angustisiphonatum* type described by Gallitelli-Wendt, 1969); *Hildoceras semipolitum*, with a compressed-tall whorl section (corresponding to the typical form described by Buckman, 1904) in addition to spiral groove and involute coiling.

2.2. Heterochrony and developmental polymorphism

The concept of Heterochrony has been introduced by Haeckel (1866, 1875) and for this reason it has been long compared with his Biogenetic Law of "recapitulation" (e.g. "palingenesis" in Buckman, 1909), although its original significance served rather to account for exceptions to recapitulation (Gould, 1988, 2000). Heterochrony was later redefined by de Beer (1930) as a change through time in the appearance and/or rate of development of characters from ancestral to descent. However, it was only after the review by Gould (1977) that heterochrony attained revaluation as a driving mechanism in evolution. In particular, heterochrony has been rediscovered as a consequence of a variety of processes affecting development by retarding or hastening developmental rates (Alberch et al., 1979). Morphological effects caused by retarded or accelerated development are known as paedomorphosis and peramorphosis, respectively (Fig. 5), and manifest at the phylogenetical scale with respect to ancestor and descendant species (Alberch et al., 1979; McNamara, 1986).

According to the revised nomenclature of heterochrony (Alberch et al., 1979; McNamara, 1986; Gould, 2000), paedomorphosis is the result of incomplete growth and/or slower growth rates that cause a reduced development of some organs or of the individual as a whole. There are three phenotypical effects by which paedomorphosis can be expressed: progenesis, neoteny and post-displacement (Fig. 5). In peramorphosis, changes in developmental timing affect development in the opposite way, by an increase in growth rates that advances or even extends development. The three reverse processes leading to peramorphosis are: hypermorphosis, acceleration and pre-displacement (Fig. 5).

The morphological effects of heterochrony are paedomorphic or peramorphic species with respect to an ancestor species. However, also asynchronisms in the ontogenetic process of coeval individuals are in relation with developmental heterochrony, although not expressed by descendant and ancestor (Alberch et al., 1979; Travis, 1981; McNamara, 1982, 1986; Neige et al., 1997). In both cases developmental timing is altered, but during phylogeny in one case (hereinafter: phylogenetic heterochrony), and during lifespan (or few generations) in the other (hereinafter: ontogenetic heterochrony). Conceived at a lifetime scale, ontogenetic heterochrony may contribute to phenotypic variability within coeval individuals of populations and species (McNamara, 1986). The effect of increased morphological variability as a consequence of ontogenetic heterochrony has been described in ammonites as "developmental polymorphism" (Matyja, 1986, 1994).

When dealing with fossil records, the distinction between ontogenetic and phylogenetic heterochrony is plausible only by assuming the temporal interval represented by each stratigraphic layer as significantly condensed, and all the specimens from that layer as coeval representatives of a population. At this scale, and with the above approximation, the simple term "underdevelopment" can be used to indicate earlier maturation in respect of the total growth/development potential of the species. Similarly, an opposite phenomenon of overdevelopment, for instance adult stage characters anticipating full maturation, may contribute to phenotypic variability and polymorphism. Underdevelopment and overdevelopment occurring at a lifespan scale are the equivalent of the phylogenetic scale paedomorphosis and peramorphosis. Their

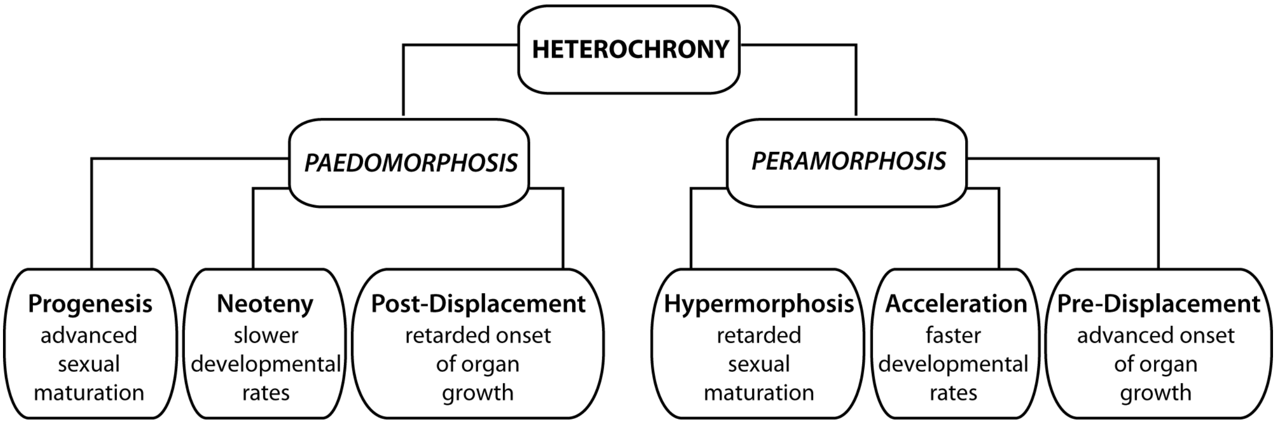

Fig. 5 - Heterochrony and the resulting retarding (Paedomorphosis) and accelerating (Peramorhosis) morphological effects. *Progenesis*: anticipation of sexual maturation to the juvenile stage and earlier cessation of development and size growth. As a consequence, the size of the adult descendant is smaller, although rates of (juvenile) development are the same as in the ancestor. *Neoteny*: reduced rates of development during the juvenile stage. If also sexual maturity is delayed, the descendant may result of larger size than the ancestor (although retaining juvenile characters). Neoteny may affect only some structures (dissociated) or the entire body. *Post-displacement*: delay in the onset of development of some organs (without affecting rates of development and size growth), which retain a smaller size in the descendant (in contrast with other fully grown structures and body size). *Hypermorphosis*: delay in sexual maturation by which the juvenile stage is protracted (although rates of development may be the same), thus the descendant retains juvenile characters in a larger adult stage (however, the extension of juvenile development may alter juvenile characters). It is opposite to progenesis. *Acceleration*: increased rate of morphological development by which adult characters appear at juvenile (sexually immature) stage. If also sexual maturity is accelerated (i.e. anticipated) the descendant attains smaller size. It is the opposite of neoteny, and may affect some organs only or the entire body. *Pre-displacement*: anticipation of onset of development of some organs (not affecting rates and time of cessation of development), which attain larger size relative to the ancestor (despite similar body size).

morphological result is developmental polymorphism (Matyja, 1986, 1994) expressed by underdeveloped and overdeveloped individuals (or populations) within a species, equivalent to paedomorphic and peramorphic species within a phyletic lineage.

2.3. Material and methods

Data herein used, although narrow in being derived from one main Rosso Ammonitico section (Fig. 6) and few other nearby outcrops, represent a bed-by-bed record of over 300 specimens, largely preserved as internal moulds of phragmocones (frequently fragmented), occasionally with a partially preserved body chamber. This record provides insights on the variability patterns among *Hildoceras* species that are worth for defining both ontogenetic and phylogenetic heterochrony.

In order to assess variability patterns, single-layer assemblages consisting of a minimum of 5-10 specimens where considered; this approach excluded the less fossil-rich intervals from morphological analysis. Despite the fossil richness of several layers, the available material, its preservation and the limited number of sampled outcrops only afford a qualitative approach to morphological analysis. With this limitation, an attempt is made at defining the range of morphological variability of assemblages from single beds, in order to constrain patterns of ontogenetic variability.

Variability patterns displayed by assemblages from one single bed were regarded as representing the variability field within a population of coeval individuals. Comparison of variability patterns from successive beds allowed evaluate the possible effect of heterochrony in controlling morphological change involved in the transformation from *Hildoceras laticosta* to *Hildoceras lusitanicum*, and from this to *Hildoceras bifrons* and *Hildoceras semipolitum*.

3. RESULTS

3.1. Peramorphosis and the *laticosta-lusitanicum-bifrons* transition

The spiral groove is a most remarkable morphological achievement in the evolution of *Hildoceras* species. The transition from non-grooved to grooved shell morphology required both structural (whorl shape) and ornamental (rib shape) modifications that involved the dorsal half part of the whorl flank. These changes are anticipated by the truncation of ribbing in the innermost whorl of non-grooved *Hildoceras* (Fig. 4), progressively replaced by the umbilical wall as it appears in *Hildoceras laticosta*.

In the sampled outcrop, *Hildoceras laticosta* (Fig. 4a) occurs in the lowermost part of the Bifrons Zone, from bed 10A1, at ca. 3.4 m, to bed 10A3, at ca. 3.9 m (Fig. 6). In the overlying levels (from 10C, at ca. 4.2 m, to 10 N, at 5.8 m), *Hildoceras laticosta* is replaced by *Hildoceras lusitanicum* with a well-formed periumbilical relief (Figs. 4 b-c, 7-9). The transition between the two morphotypes should occur within bed 10B but, unfortunately, this layer was barren. Beds 10C and 10D have yielded some fragments only, so that the first meaningful data documenting the diffusion of specimens with a pseudogroove start from

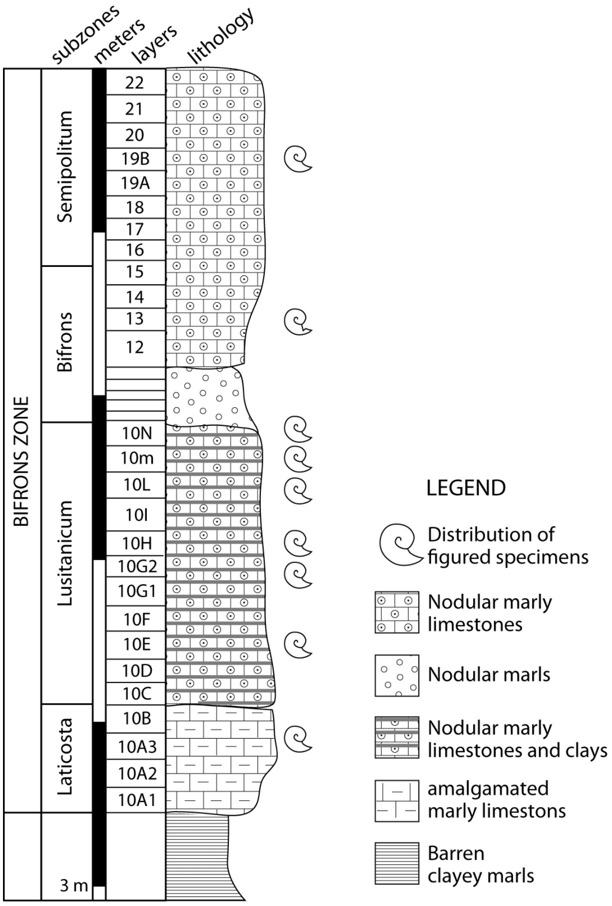

Fig. 6 - Stratigraphic log of the Bifrons Zone at the main Rosso Ammonitico section near Polino (see Fig. 1), where most of the studied specimens have been collected.

bed 10E (at 4.5 m; Fig. 7). Findings decrease again between 10G2 and 10I, becoming abundant in beds 10L, 10M and 10N, which have yielded the greater part of the studied material (Figs. 7-9).

In the earliest specimens of *Hildoceras lusitanicum* from beds 10C-10E (Figs. 6-7a), rib fading and truncation, as well as protruding of the umbilical relief, are not constant throughout subsequent whorls of the same individual, becoming more evident in the last ones (typically the 3rd-4th whorl, at D=40-50 mm). A similar pattern is shown by the pseudogroove flanking the periumbilical relief. Smaller specimens (D<35-30 mm) maintain more covering whorls compared to larger ones, and also show complete ribs invading the umbilical wall. The number of ribs per whorl is overall constant, ranging between 31 and 34.

In beds 10F to 10G2 (Fig. 6) few fragments and poorly preserved moulds show a periumbilical relief and well-spaced coarse ribs (Fig. 7b-c); also specimens recovered in beds 10H and 10I were scarce and all less than 45 mm in diameter (Fig. 7c). Therefore, comparison of different growth stages and determination of ontogenetic variability were not reliable. Rib number per whorl is around 35 to 39, thus slightly higher than in populations from bed 10E.

In the fossil-rich beds 10L, 10M and 10N (Figs. 6, 7-9), the relationship between ontogenetic development and morphological variability of shell ornaments and parameters is again evident. Early whorls show complete ribs extending to the umbilical wall; at this stage the ribs also tend at bending backward much more suddenly in respect to larger whorl ribbing. Measurement of shell parameters (when allowed by good preservation) has revealed a slow but perceptible decrease in whorl overlap

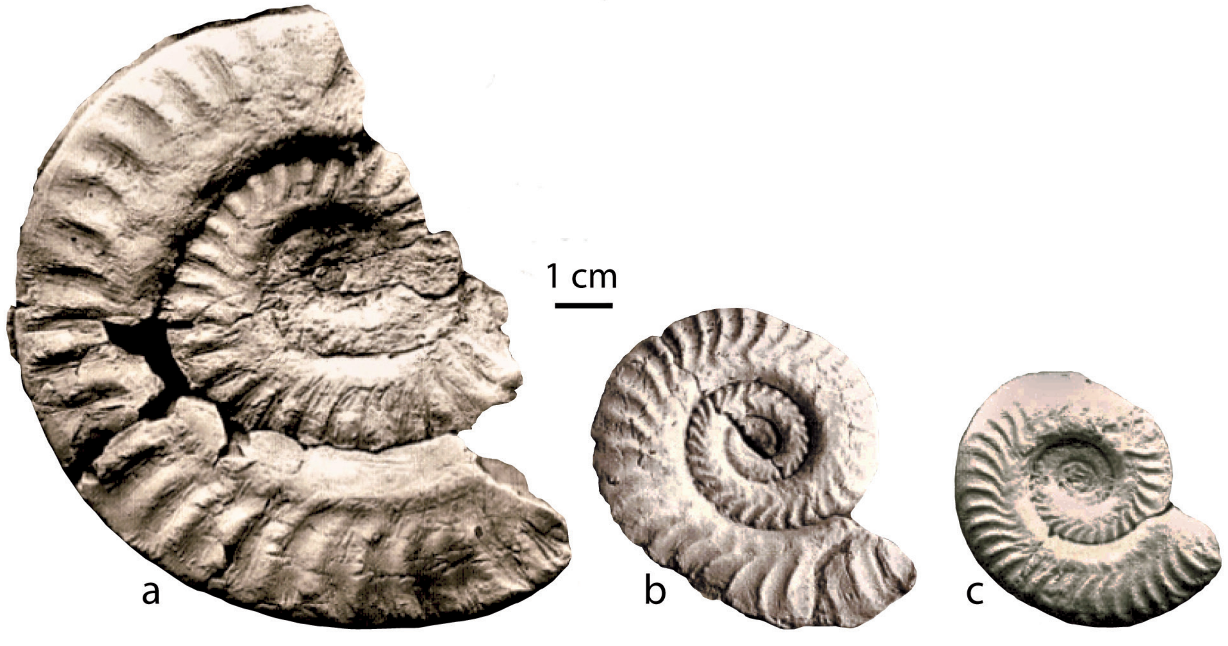

Fig. 7 - Specimens of *Hildoceras lusitanicum* from different layers of the lower Bifrons Zone (see Fig. 6): a = bed 10E; b = bed 10G2; c = bed 10H. Note the tendency of ribs of the early whorls to invade the umbilical wall, and the marked periumbilical relief in the adult body chamber (a).

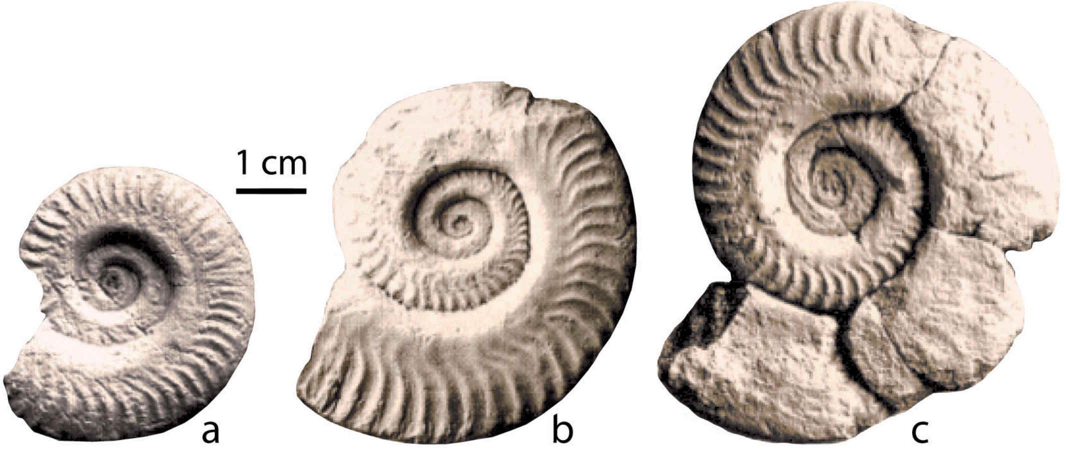

Fig. 8 - Specimens of *Hildoceras lusitanicum* from different layers of the lower-middle Bifrons Zone (see Fig. 6): a = bed 10L; b-c = bed 10M. In "b" part of the body chamber is preserved, showing fading of rib termination against the periumbilical relief (also note anomalous interspaced rib). In "c" the poorly preserved internal mould of the body chamber is still attached to a phragmocone with typical ribbing and a periumbilical relief extending half the whorl.

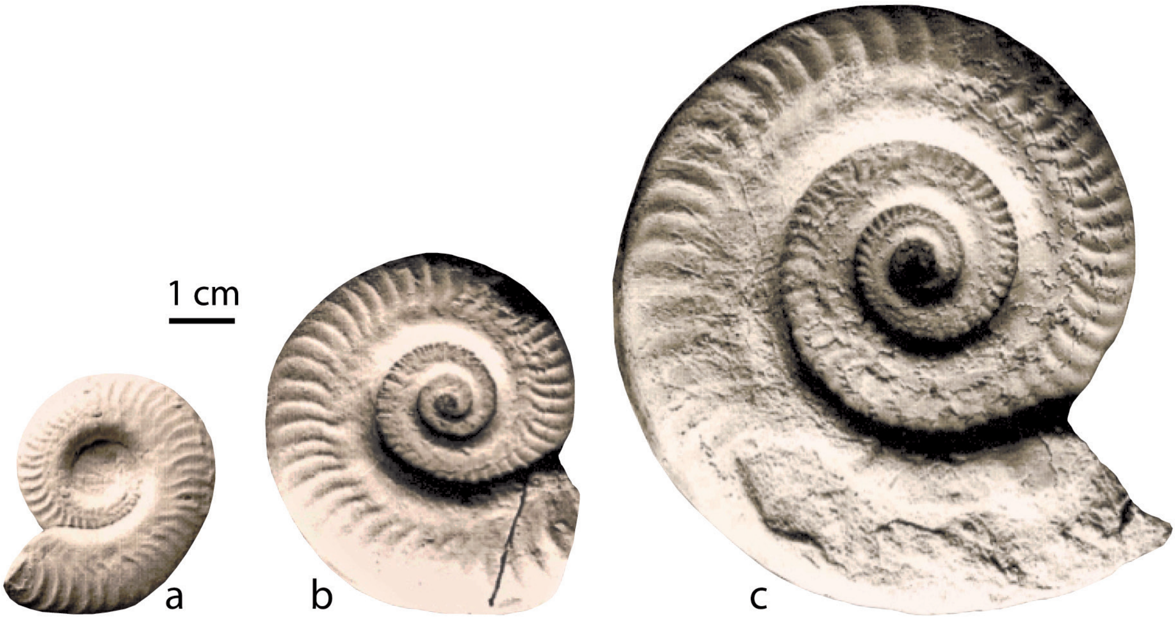

Fig. 9 - Specimens of *Hildoceras lusitanicum* from layer 10N (last occurrence; see Fig. 6). Note the well developed pseudogroove in "b" and "c" (adult stage with body chamber), instead evident only in the final part of the partially preserved body chamber of the immature specimen in "a".

parallel to growth. Differences in respect to populations from bed 10E consist in rib density (ribs are about 40 to 45 per whorl nearly at any diameter) and in a more engraved pseudogroove (e.g. Fig. 9). In particular, comparison with morphotypes from bed 10E reveals that the appearance of the pseudogroove is precocious relative to size and number of whorls in specimens from beds 10M and 10N. Finally, relatively small specimens with overall continuous and regular lateral groove (Fig. 10a), referable to *Hildoceras bifrons*, have been recovered from bed 11 to 14; these are succeeded by *Hildoceras semipolitum* (Fig. 10b) in beds 15 to 22 (Fig. 6).

Based on the above, it is suggested that the transition from *Hildoceras laticosta* to *Hildoceras lusitanicum*, and from this to *Hildoceras bifrons,* is marked by morphological changes that occur during ontogeny and are affected by heterochrony along with successive populations ranging from bed 10A to 10N. These changes consist in the:

1) broadening of the umbilical wall toward the middle flank, becoming pronounced in a rounded or angled edge, which is the periumbilical relief;

2) retreating and fading of ribs' termination, resulting in the lack of the forward projected trait and its replacement by a somewhat inflected spot, likely a precursor of the pseudogroove.

These "apomorphic" traits (periumbilical relief and pseudogroove) are most evident only in adult stage body chamber of *Hildoceras lusitanicum* from bed 10E, and are affected by heterochrony in the interval between bed

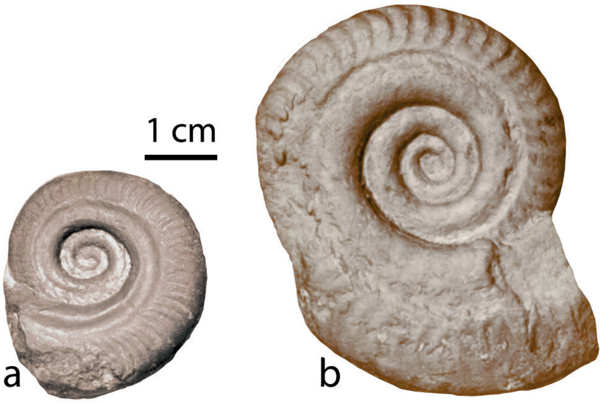

Fig. 10 - Specimens with neat lateral groove from the upper Bifrons Zone (see Fig. 6): a = bed 13; b = bed 19B. The former well corresponds to the description of *Hildoceras bifrons angustisiphonatum* made by Gallitelli-Wendt (1969); the latter matches the typical *Hildoceras semipolitum* in having taller and more compressed whorls (also note the more central position of the spiral grove).

10E and 10N. Developmental heterochrony by which the pseudogroove, initially a character of later stages, is progressively anticipated in growth, corresponds to peramorphosis (Aberch et al., 1979; McNamara, 1986). Namely, advancing the pseudogroove to earlier living stages provides evidence of pre-displacement (Fig. 5). The time at which the onset of the pseudogroove reaches (*via* heterochrony) the earliest growth stages, attaining continuity throughout greater part of the shell, marks the arising of *Hildoceras bifrons* as a peramorphic species with respect to *Hildoceras lusitanicum*.

3.2. Paedomorphosis and the *bifrons-semipolitum* transition

Historically, the degree to which whorl coiling becomes involute has provided the manner of distinguishing *Hildoceras bifrons* (whorl overlap <1/2) from *Hildoceras semipolitum* (whorl overlap ~1/2), despite the tendency at "uncoiling" in *Hildoceras bifrons* may occur at variable growth stages (Howarth, 1992). In the studied assemblages, the ontogenetic variability of *Hildoceras bifrons* and *Hildoceras semipolitum* is less constrained because of the fewer specimens recovered per layer. *Hildoceras bifrons* is represented by small specimens (D<35 mm; Fig. 10a), characterised by tighter coiling (1/2 whorl covering). *Hildoceras semipolitum* is distinguished from these because of a relatively taller (i.e. more compressed) whorl section, perceivable also at a slightly larger size (D=40-55 mm; Fig. 10b). Since these two species share the same degree of whorl overlap, an hypothetical transition from *bifrons* to *semipolitum* could be accomplished essentially by a relative increase in size and whorl height, resulting in an overall larger shell with a taller (relatively compressed) whorl.

It is herein suggested that the following processes are required in order to transform the small type *bifrons* into the relatively larger but still involute *semipolitum*: 1) a delay in the time of maturation, which would extend the time of growth and allow larger size; 2) the retention of the juvenile condition expressed by inhibition to the achievement of the uncoiling stage. This twofold heterochronic process corresponds to neoteny. However, if the involute coiling morphology is attained isometrically at diameters larger than the 30-40 mm, whorls would become inflated. This disproportional growth is avoided by a positive allometry in whorl height, resulting in the compressed whorl section of *Hildoceras semipolitum*.

We could expect an analogous morphological effect referring to a larger "macroconch-type" *Hildoceras bifrons* and suggesting a delay in the appearance of the uncoiling stage, that is post-displacement (Fig. 5), associated to allometric growth. In both the hypothetical transforming examples the intervening heterochrony is a type of paedomorphosis, and the result is the extent of the more covering microconch-type coiling to larger diameters in respect of those usual of underdeveloped or juvenile individuals.

3.3. Developmental polymorphism and sexual dimorphism

Sexual dimorphism in ammonites is a by now widely accepted fact. The first studies by which the phenomenon attained reliability refer mainly to Jurassic ammonites (Callomon, 1963, 1981; Westermann, 1964; Cope, 1967, 1968, 1978, 1994; Guex, 1968, 1969; Cecca, 1986; Dzyk, 1994), although examples from Palaeozoic ammonites have been also reported (Makowski, 1962, 1971; Davies, 1972).

Among *Hildoceras* species, dimorphism has been convincingly evidenced in *Hildoceras bifrons* (Howarth, 1992), with only limited evidence from other species (Gabilly, 1976; Elmi, 1977; Jimenez and Rivas, 1992) despite their broad and frequent occurrence. For instance, microconchs could not be found by Howarth (1992) within ca. 200 specimens of *Hildoceras lusitanicum* from different localities of Great Britain. This was also the case for *Hildoceras semipolitum*, and the author concluded that microconchs of species of *Hildoceras* other than *Hildoceras bifrons* are unknown in Britain (Howarth, 1992, p. 34). It is noteworthy that even in the case of *Hildoceras bifrons*, sexual dimorphism is documented by only 16 microconchs in front of 250 macroconchs (Howarth, 1992, p. 37).

In France, a biometrical analysis carried on 280 specimens of *Hildoceras bifrons*, (mostly consisting of phragmocones) was unworthy in distinguishing micro- and macroconch forms (David-Henriet, 1962). Evidence of sexual dimorphism in other *Hildoceras* species is limited to some large macroconchs of *Hildoceras semipolitum* (Gabilly, 1976; Elmi, 1977).

In Spain, sexual dimorphism in *Hildoceras semipolitum* is discussed by Jimenez and Rivas (1992), which describe five microconchs with short lappets from the Cordilleras Beticas. These display coarser ribs compared to the macroconch, also characterised by a taller flank and a markedly sinuous mouth border (Jimenez and Rivas, 1992, p. 71).

In Italy, examples of microconch *Hildoceras bifrons* with lappets are virtually unknown, and this can be only partly attributed to the rare preservation of specimens with complete body-chamber (Ridente, 1996). Macroconch types of both *Hildoceras bifrons* and *Hildoceras semipolitum* are equally rare (Donovan, 1958; Gallitelli-Wendt, 1969; Ridente, 1996). Among specimens collected by Gallitelli-Wendt (1969), 47 consist of the small *Hildoceras b. angustisiphonatum* and 10 are ascribed to *Hildoceras b. bifrons*; of these only four are larger than 45 mm (the largest being 64 mm). The *Hildoceras b. bifrons* figured by Gallitelli-Wendt (1969, Pl. 3, Fig. 6 a,b) is described as the most similar to the holotype, and it may represent an immature "macroconch" form (based on the out-spaced suture lines preceding the partially preserved body-chamber). Other examples of possible macroconchs are those reported by Mitzopolous (1930, Pl. 3, Fig. 6 a,b, from Alta Brianza, northern Italy), and Pelosio (1968, Pl. 18, Fig. 13, from Alpe Turati, northern Italy); a tendency towards an uncoiling stage, typical of macroconchs (or of non-underdeveloped individuals) can be observed in the specimen figured by Nicosia and Pallini (1977, Pl. 1, Fig. 6, from the Central Apennines), which is 61 mm in diameter.

Based on the above, a significant asymmetry exists in the pattern of occurrence and distribution of sexual dimorphs over the Mediterranean and North Europe palaeogeographical domains. With reference to *Hildoceras bifrons*, it is herein proposed, as a more general hypothesis, that the small-type *bifrons* of the Rosso Ammonitico facies differed from the larger "macroconch" forms of Northern Europe in reaching earlier sexual maturity, independently of sex. Therefore, the small-involute *bifrons* of the Apennines is not conceived as a sexual dimorph, but rather as a developmental polymorph (e.g. Matyja, 1986, 1994). Specifically, the Mediterranean type represents populations in which individuals are largely affected by ontogenetic heterochrony in the form of underdevelopment, caused by ceasing of growth before reaching the "uncoiling" stage by which enlargement and wider umbilicus are achieved in macroconchs.

Underdevelopment among coeval individuals/populations caused by ontogenetic heterochrony is equivalent to the phylogenetic heterochrony resulting from progenesis: i.e. preclusion of full size growth and structural underdevelopment paralleled by a smaller size (Alberch et al., 1979). At the scale of underdevelopment, it is possible to relate developmental polymorphism to ecological factors influencing the ontogenetic process (Kulicki, 1974; Matyja, 1986), by this determining interdemic differences in the resulting morphological effects.

4. DISCUSSION AND CONCLUDING REMARKS

As for other Early Jurassic ammonites, *Hildoceras* species show a broad palaeogeographical distribution over the Mediterranean and North European provinces (Donovan, 1958; Gallitelli-Wendt, 1969, Guex, 1972, 1973; Elmi et al., 1974; Gabilly, 1976; Jimenez and Rivas, 1992; Howarth, 1992; Metodiev et al., 2013). In some known cases of wide ranging ammonite groups, interdemic differences have revealed a correlation between individual size and palaeogeographical distribution, with average smaller size of specimens from populations of the Mediterranean domain compared to those of Northern Europe (Gabilly, 1976; Elmi, 1977). A relationship between palaeoecological factors and patterns of size distribution has been also defined within different areas of the same province (Elmi and Benshili, 1987).

It is reasonable to assume that, at least in some cases, the observed size-distribution patterns may reflect a more general pattern of developmental (i.e. ontogenetic) heterochrony and polymorphism, possibly related to the different environmental factors under which ammonite populations lived in different regions. Trends in ontogenetic heterochrony, persisting in time throughout subsequent populations (phylogenetic heterochrony), would result in significant morphological changes by which new morphotypes and species could arise.

With reference to *Hildoceras* species, heterochrony is thought to cause the progressive anticipation in earlier stages (progenesis) of the pseudogroove, at first manifesting only in the late (adult) ontogenetic stages of *Hildoceras lusitanicum*. As a consequence, the typically grooved *Hildoceras bifrons* arises as a peramorphic species from the latest *Hildoceras lusitanicum*, with a marked pseudogroove since early growth stages. It is also suggested that heterochrony in the form of paedomorphosis, combined with allometric whorl growth, can be responsible for the morphological transition from *Hildoceras bifrons* to *Hildoceras semipolitum*. For instance, neoteny affecting the small type Mediterranean *bifrons* (interpreted as underdeveloped compared to the more frequent Boreal "macroconch" morph) may account for the relatively increased size and whorl compression observed in *Hildoceras semipolitum*. All the above speciation events occur essentially as anagenetic trends (Fig. 11), although, at a broader palaeogeographical scale, speciation may result allopatric and the new morphotypes arising in one region may spread in another where populations of the ancestor species are still present.

As an implication of ontogenetic heterochrony, the interpretation of sexual dimorphism in *Hildoceras bifrons* is conceived within a more general frame of ecologically-linked developmental polymorphism, by which micro- and macroconchs can be more generally interpreted as eco-morphotypes differentiating in the Mediterranean and North Europe provinces, respectively. This hypothesis is in accordance with the asymmetric palaeogeographical distribution of micro- and macroconchs of *Hildoceras bifrons*, likely reflecting a pattern of ecologically-controlled heterochronic populations throughout the Mediterranean and Northern Europe palaeogeographical

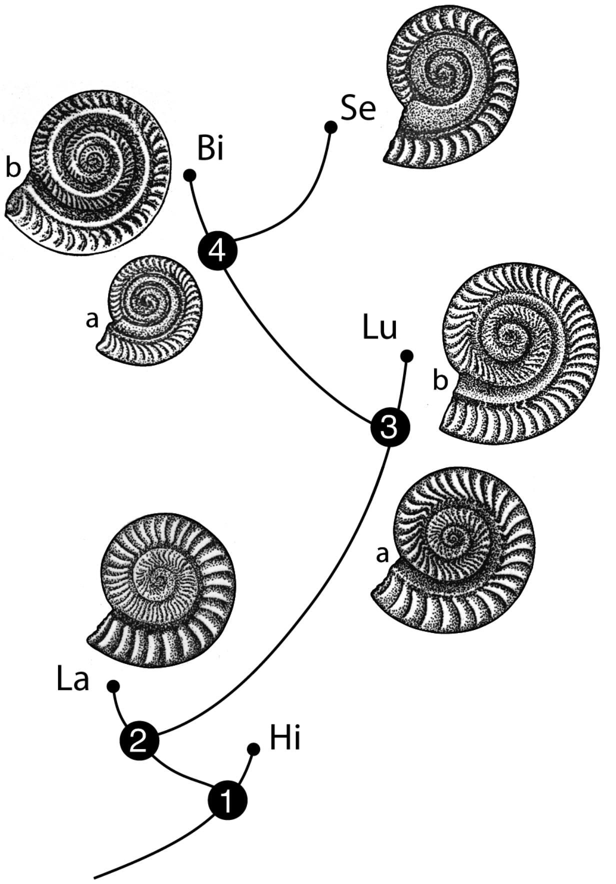

Fig. 11 - Phylogenetic tree of *Hildoceras* species based on the occurrence of "new" morphologies under the control of heterochronic processes: 1) smooth and flat umbilical wall, which marks the arising of *Hildoceras laticosta* (La) from *Hildaites* sp. (Hi); 2) periumbilical relief in *Hildoceras lusitanicum* (Lu), flanked by a variably impressed (lesser in "a") pseudogroove, progressively extending to early growth stages (in "b"); 3) lateral groove in *Hildoceras bifrons*, represented by small-size involute (a) and larger-size evolute morphotypes (b); 4) positive allometric growth of whorl height in *Hildoceras semipolitum*, while maintaining involute coiling at larger size than *Hildoceras bifrons* (in "a").

provinces. In this view, micro- and macroconchs of *Hildoceras bifrons* are interpreted, respectively, as underdeveloped and overdeveloped individuals, independently of their sex.

The presence of lappets as sexual characters in microconch *bifrons* is not in contrast with developmental heterochrony; because these are coincident with the growth line of the mouth border, they are subject to heterochronic processes and allometry, thus being variably developed at different whorl size. Therefore, a prominent mouth border in smaller underdeveloped individuals progressively becomes rounded in larger growing ones. For instance, the "sinuous" mouth border of the large *Hildoceras lusitanicum* (D=250 mm) figured by Howarth (1992, p. 183, Fig. 42) is proportionally protruding as much as any lappet of a microconch *Hildoceras*. Indeed the mouth border of this macroconch is ornamented by lappets.

It is noteworthy that developmental polymorphism is not a denial of sexual dimorphism; on the contrary, it can be regarded as a possible cause or mechanism by which sexual dimorphism is achieved (Neige et al., 1997). For instance, sexual dimorphs may consist of heterochronic individuals that achieved sexual maturity in different time. Therefore, the mechanism by which sexual dimorphs or developmental polymorphs arise is virtually the same, except for that, in one case, heterochrony affects the ontogeny of different sexes within a species (i.e. sexual dimorphism); in the other it affects different populations within the same species (i.e. developmental polymorphism). In both cases, developmental heterochrony may be the consequence of an adaptive strategy in response to ecological factors. Such phenomena have been widely described in modern cephalopoda (Wells and Wells, 1977; Mangold and Froesch, 1977; Cochran et al., 1981) and other molluscs (Rhoads and Pannella, 1970). More in general, examples are known of progenetic species that tend to be R-strategists within adverse environments (Gould, 1977), or of peramorphic size increase as a form of K-type strategy (McKinney, 1984).

The above results are to some degree speculative and would necessitate of more in-depth investigation extended to a greater number of case studies, in order to compensate the many biases descending from outcrop sampling and fossil record preservation. Despite this limitation, insights are provided on the importance of determining ontogenetic variability in ammonites before applying taxonomic schemes and defining evolutionary models.

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