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Carlo S.

Sea-level changes in the Kimmeridgian (Late Jurassic) and their effects on the phenotype evolution and dimorphism of the ammonite genus *Sowerbyceras* (Phylloceratina) and other ammonoid faunas from the distal pelagic swell area of the "Trento Plateau" (Southern Alps, Northern Italy)

CARLO SARTI

Dipartimento Scienze della Terra e Geologico-Ambientali, Capellini Museum, Università di Bologna, Via Zamboni 67, 40127 Bologna, Italy., E-mail: sarti@geomin.unibo.it

Abstract. Ammonite faunas from the Kimmeridgian part of the Rosso Ammonitico Veronese Formation of the "Trento Plateau" (Southern Alps, Northern Italy) show that the change of faunal assemblages is strongly affected by fluctuations in sea level. The "Trento Plateau" was a distal epioceanic swell in the Tethyan Ocean and the present study shows that the effects of sea-level changes were comparable to those of epicontinental environments with the difference that, extinction and phyletic changes occur in transgressive phases instead of in regressive phases. Also that the maxima and minima of intraspecific variability are the opposite to those of the epicontinental environment. *Sowerbyceras* (Phylloceratina) are particularly abundant on the Trento Plateau. During times of high sea-level (transgressive phases = slight bottom currents) *Sowerbyceras* faunas decreased in numbers, and were smaller, with a lower thickness ratio Wb/D (whorl breadth/Diameter) and a more evolute conch. During times of low sea-level (regressive phases = higher bottom currents) there is an increase in frequency of *Sowerbyceras*, which were larger, with a greater t.r. Wb/D, and a more involute conch. Morphological parameters D, Uw, wH, also vary with sea level. Sea-level lows (regressive phases) correspond to high intraspecific variability of D and lower intraspecific variability of Wb. Sea-level highs (transgressive phases) correlate with lower intraspecific variability of D and higher intraspecific variability of Wb. New species do not originate from a population that presents a wide range of intraspecific variability, but the speciation only occurs when this variability decreases and the population is also numerically reduced. In the Trento Plateau a transgressive phase led to a numerically small population of *Sowerbyceras* that in turn resulted in low intraspecific variability and as a consequence speciation occurred. This is of crucial importance for the survival of the species. In fact where, despite a low number of specimens, a high intraspecific variability is observed (at the top of the Beckeri-Pressulum Zone) *Sowerbyceras* became extinct in a short time. This observation assists the understanding of the process of extinction.

Key words - Sea-level changes, Evolution, Ammonites, *Sowerbyceras*, Kimmeridgian, Northern Italy.

Introduction

Benthic, pelagic and planktonic faunas are subjected to different degrees of ecological stress caused by changes in relative sea-level. The most sensitive faunas are mainly benthic and epibenthic. The Late Jurassic vagile ammonite *Sowerbyceras* (Phylloceratina) is included amongst the latter faunas. This paper deals with the very close relationship between the change of ammonite faunas in the Upper Jurassic of the "Trento Plateau" and sea-level changes. These changes strongly affect the evolution of faunal assemblages in distal, epioceanic areas (i.e. oceanic waters resting on continental crust. Epioceanic environments can be adjacent or not to neritic environment), and in particular the biological response of *Sowerbyceras* faunas to sea-level changes is exceptionally rapid and precise.

The ammonite faunas were collected *in situ* with a sampling interval of 1 cm from the Kimmeridgian part of Rosso Ammonitico Veronese Formation (RAV). The Kimmeridgian RAV limestones reveal depositional regimes with very low supply of sediment, and occur mainly in the region between Lake Garda and Monte Grappa (Southern Alps, Northern Italy) (Fig. 1). This facies was developed on a distal pelagic-swell system

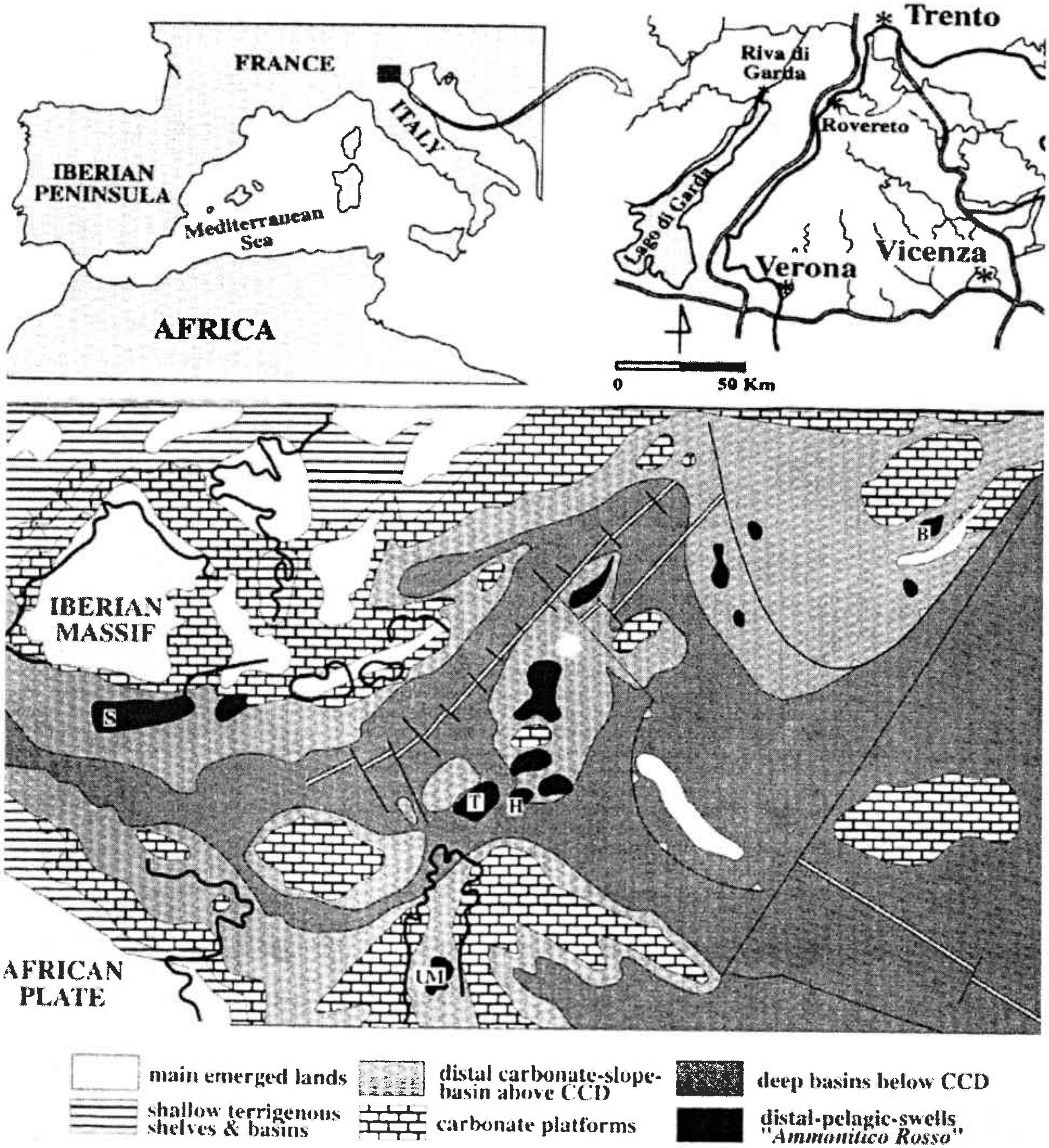

Fig. 1 - Location of the study area (above) and palaeogeographic sketch of the western Tethys in the Kimmeridgian (below) (modified from Caracuel et al., 1997), showing main areas of outcropping ammonitico rosso facies in epioceanic environment; B (Bulgary), H (Bakony Mts., Hungary), S (Subbetic, Southern Spain), T (Trento Plateau, Italy). UM (Umbria-Marche Apennines, Italy).

("Trento Plateau" or "Piattaforma atesina"). This epioceanic plateau was located in the northern part of the Apulian Block, which represented a part of the North Africa continental margin (Caracuel, Oloriz and Sarti, 1997, 1998) (Fig. 1).

Among West Tethyan epioceanic fringes, the Trento Plateau was surrounded by basins extending for some hundreds of kilometers, receiving pelagic marls and mudstones with occasional siliceous horizons. This pelagic sea-mount con-

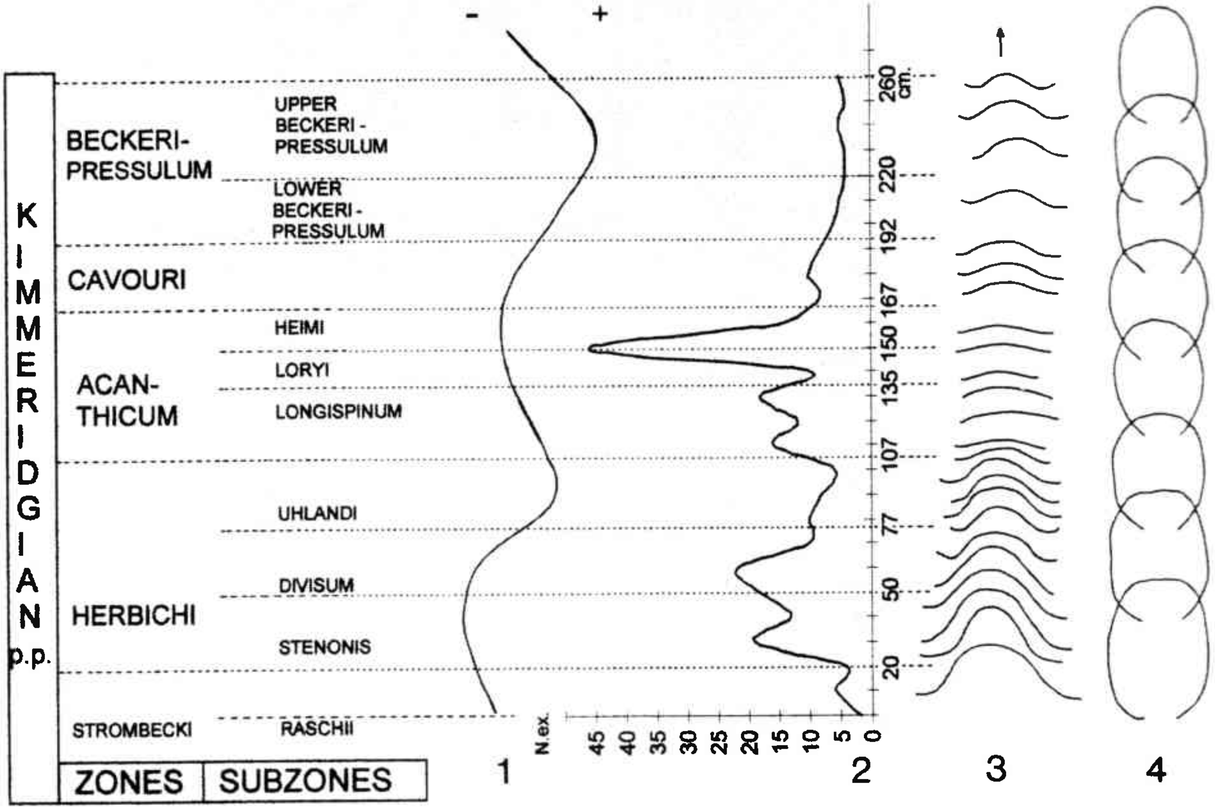

Fig. 2 - Bio-chronostratigraphy of the Kimmeridgian in the "Trento Plateau" showing : (2) fluctuations in the abundance of Sowerbyceras through time (N.ex. = number of examples ; cm. = thickness of the Kimmeridgian succession in centimeters); (3) morphological evolution of the constrictions and (4) whorl sections shape through time, and correlation with the (1) sea-level curve (3^{rd} order cycles) as proposed by Haq et al. (1988) (- = low sea level ; + = high sea level).

stituted a palaeogeographic unit free from terrigenous inflows and allochthonous carbonates which accumulated in surrounding troughs: the Lombard Basin to the West and the Belluno Trough eastwards.

As noted by many authors (e.g. Wiedmann, 1973; Hallam, 1975; Jablonski, 1980; Lehmann, 1981, etc...), some major evolutionary events throughout the Phanerozoic appear to be related to sea-level changes. As a generalization, inferred rises of sea-level appear to be correlated with diversity increase of neritic organisms and falls in sea level with diversity decrease, in extreme cases culminating in mass extinction (Hallam, 1987). Because paleoenvironmental and sequence stratigraphic models have rarely been worked out in epioceanic carbonate deposits, the causal relationships between sea-level changes and evolutionary events are not known in oceanic environments in swells offshore from the shelves to which the distal pelagic swell Trento Plateau belongs. In such a setting, due to the very irregular physiography of the plateau, fluctuations in relative sea-level would determine ecospace splitting, thereby affecting ecological conditions of energy, productivity, oxygenation, the pattern of marine currents and related effects. The depth of sea floor, which controls the other characters and particularly the degree of instability, has thus determined the geographical distribution of groups and also their evolutionary modalities not only on a large scale (see Cariou and Hantzpergue, 1988), but also on a small scale.

Remarks on the Sowerbyceras fauna

In this study it has been possible to follow the morphologic evolution and dimorphism through time of the genus *Sowerbyceras*. The fossils are available in large numbers (960 specimens). They are also closely controlled stratigraphically and can be related to the appropriate sea-level curve (Fig. 2).

In addition to following the progressive changes in ornamentation and shape of whorl cross-section through time, it is also possible to follow the variations of D (diameter), Uw (umbilical width), wH (whorl height) and Wb (whorl breadth) parameters and their intraspecific variability. Regarding D and Wb, an attempt is made to explain the enormous range of variability in terms of these parameters, as noted by many authors for ammonite faunas of various geological periods and localities (see Sarti, 1999). This is unexpected because these populations show a high homogeneity for other shell characters.

Moreover a peculiar dimorphism (sexual?) was noted and followed through time in *Sowerbyceras*, in which the micro- and macroconchs differ from each other in the venter width of the body chamber but not in the shell size (see Sarti, 1990b, 1993, 1999).

Morphologic evolution of Sowerbyceras was gradual, although any changes took place at very short stratigraphic intervals. In fact the Kimmeridgian *Sowerbyceras* lineage shows long periods without strong changes in morphological parameters, which are interrupted by three sudden events involving both dimorphs.

The morphological changes are related to increased ecological stress. Previous authors have considered that the more important stressing factors for ammonites are the major regressions of sea level and significant climatic fluctuations (e.g. Valentine, 1968; Hallam, 1987; Guex, 1992). Other authors have considered that faunal changes were related to, and affected by transgressions of sea level (e.g. Mouterde et al, 1990).

According to the authors, Phylloceratids and Lytoceratids were less affected by environmental changes, most especially eustatic oscillations, than other ammonoids during the Jurassic and Cretaceous. However, in the Trento Plateau they too underwent punctuated changes following eustatic oscillations.

In this study of *Sowerbyceras* it must be noted that we are always dealing with phyletic speciations (pseudospeciations). In this genus, it is clear that a new species does not originate from a population that presents a wide range of intraspecific variability. Pseudospeciation occurs only when this intraspecific variability decreases greatly and, at the same time, the population is also numerically reduced.

This mode of speciation partly recall the “bottleneck effect” model (Stanley, 1978). In my opinion this mechanism occurs in declining populations of ammonites, much dependent on a bottom environment, as a result of chance events. In the case-study the bottleneck was caused by marine transgressive pulses. As regards the true bottleneck effect (sensu Stanley, 1978), in the case of the Trento Plateau the phenomenon occurs much more slowly and less drastically: more than once the group successfully passed the crises of his history.

In the Trento Plateau a transgressive phase was marked by a low density of *Sowerbyceras* that led to low intraspecific variability. Mutations were spread within a shorter period of time and speciation took place. This was very important for the survival of the species. Despite a low number of specimens, a high intraspecific variability is present (at the top of the Beckeri-Pressulum Zone) the genus became extinct in a short time. This observation is especially interesting in terms of understanding extinction. Further examples of this type are recorded in other Jurassic and Cretaceous groups of ammonites: e.g. in the Callovian genus *Kosmoceras* and in the Hecticoceratinae, a transgressive condition, with progressive sea-level rise (and therefore increasing ecospace) occurred, bringing about a decrease in intraspecific variability and consequent morphological change (Marchand, Thierry, Tintant, 1985).

It is concluded therefore that the phenotype evolution of *Sowerbyceras* does not proceed as a series of explosive accidents, but rather by sequences of pseudospeciations related to and coincident with marine transgressive pulses.

The studied sections

The Rosso Ammonitico Veronese Formation (RAV) is a Venetian Alp carbonate formation of Middle and Late Jurassic age, that had been studied for the first time by Leonardo da Vinci (1505). In the last century, studies were made by Catullo (1853), Oppel (1862-63), Zittel (1870) and Neumayr (1873). Biostratigraphic research in the area was recently made by Clari, Martire and Pavia (1990, 1991); Pavia, Benetti and Minetti (1987), Sarti (1985, 1986a, 1986b, 1988, 1993) and by Caracuel, Oloriz and Sarti (1997, 1998). Sarti described the biostratigraphic ranges for ammonites and proposed a new ammonite zonation.

Correlations between different biostratigraphic units, and their position within the system of references provided by the ammonite scales, have been published by the French Group for Jurassic Studies (1997). Hantzpergue et al. (1997) covers the biostratigraphy of the Kimmeridgian (see also Caracuel et al, 1998).

The RAV Formation is divisible into 3 lithostratigraphic units in succession: the lower unit (Bajocian - Bathonian in age) consisting of massive nodular limestones, the middle unit (from late Callovian to Oxfordian and/or earliest Kimmeridgian) mainly consisting of siliceous limestones and marls, and the upper unit (Kimmeridgian - Tithonian in age) , which is composed of ammonite-rich nodular marly/calcareous limestones.

The RAV succession in the Trento Plateau has been differentiated into type “A” and “B” successions (Sarti, 1985, 1988). Between the lower and the upper units, the type “A” succession shows a significant and mineralized hardground in which neomorphic carcasses of ammonites and belemnite rostra (a quasi-belemnite battlefield *sensu* Doyle and MacDonald, 1993) are concentrated. The Cima di Campo di Luserna section shows a typical succession (Sarti, 1993). On the other hand, in the type “B” succession, cherty limestones (the Intermediate Unit of the RAV) are intercalated between the massive nodular limestones and the overlying nodular marly/calcareous limestones. Thicknesses in this siliceous deposit varies along the Trento Plateau, locally reaching 10m. At the top of this intermediate unit there is a bentonite-rich horizon (Bernoulli and Peters, 1970, 1974).

The ammonite faunas were collected bed-by-bed in sections along a direction extending from Eastern to Western margin of the Trento Plateau. The strata containing *Sowerbyceras* were deposited on the submarine Trento Plateau during Kimmeridgian time. *Sowerbyceras* were not present in 3 of the 13 sections studied in the area of about 2500 Km^2 of Trento Plateau; these three sections are located on the eastern (M. Grappa), western (M. Giovo) and southern (M. Timarolo) margins of the Trento Plateau. The eastern and western are the palaeogeographical margins of the plateau, the southern is the present limit, but is near the original palaeogeographical margin. Systematic sampling carried out over the last 20 years have yelded a very rich collection of *Sowerbyceras* obtained *in situ*. The very low supply of sediment (the thickness of the Kimmeridgian succession varies from 2,5 to 4 meters) has resulted in precise stratigraphic positioning, with a cm sampling-interval. A 1 cm wide sampling is rarely reported from Ammonitico Rosso facies, and gives the most precise information on the assumption that homotaxial successions are proven for ammonites, as it is the case-study.

The morphological changes occurring during the evolution of *Sowerbyceras* species, accompanied by an evolution in lithofacies show that, apart from recognizable hiatuses of different magnitudes, sedimentation is very low, but in many successions significantly more continuous than was estimated in the past.

Bioturbation is present only in few levels in the type “A” successions. According to published data from AR facies (see Sarti, 1993), it is extremely improbable that bioturbation could distort microstratigraphic order to the extent of reaching biostratigraphic significance. No doubts are about the incidence of burrowing in mixing, but it would be prior to inner-mould production early during diagenesis (e.g. Sadler, 1993). Thus, if lithification was relatively rapid, as usually it was in AR facies, it could be against any significant taphonomic displacement resulting in microstratigraphic disorder of skeletals together with the inner moulds previously formed. Distorsion of the relative location of inner moulds resulting in the biostratigraphic disorder of ammonite inner moulds would be even less probable (detailed taphonomic observations are available in Caracuel, 1996, and Caracuel et al., 1997).

The Trento Plateau area corresponds to high, comparatively unstable epioceanic bottom, with low and frequently condensed sedimentation. This environment was rich in ammonites (permitting precise dating) and the tectonic instability was minor. Lacking taphonomic noise, the differential record among the ammonite group studied and other ammonite groups could point to palaeobiological differences in response to environmental fluctuations. One of the factor assumed to force lithofacies evolution is the fluctuation in the relative sea level. Studying epioceanic ammonitico rosso from southern Spain, Oloriz et al. (1993, 1996) analysed ecostratigraphic and depositional signals in relation to expected trends according to the eustatic curve by Marques et al. (1991; adapted from Haq et al., 1988). In the Venetian Alps, lithofacies evolution in Upper Jurassic AR has been investigated by

Martire (1988, 1992) through the comparative analysis of the facies studied with the expected trend in deposition according to the eustatic curve in Haq et al. (1988). A recent interpretation of paleoenvironmental conditions of the Trento Plateau has been made by Caracuel, Oloriz and Sarti (1997). These authors produced a detailed correlation for the Kimmeridgian, tied into the eustatic cycle chart and sea level curve of Haq, Hardenbol and Vail (1987, 1988).

In the Trento Plateau it is possible to recognize relationship between facies distribution and expected depositional trend according to third-order eustatic fluctuations. The studies of Caracuel (1996), Caracuel et al. (1997), Sarti (this paper) by analysing megainvertebrate-assemblage evolution, isotopic and geochimical data, as well as taphonomic observations, supported the validity of the application of the eustatic curve to this case-study.

It could be take into account that according to more recent and volatile proposals (e.g. Gracianski et al., 1998), that made by Haq et al. could be an assumable reference. 3°-cycles and sequences have strong autocyclic control and, thus, they are difficult to correlate. In addition, the time span at the 3°-cycle is too large as widely recognized in the literature (for discussion on 3°-cycles see Hallam, 2001).

According to current proposals on global eustasy, the Trento Plateau deposits correlate with sea-level highs during uhlandi and beckeri Chrons of the Kimmeridgian.

Deposition of nodular-marly (lower energy currents), nodular-calcareous and pseudo-nodular-calcareous-massive (higher energy currents) Ammonitico Rosso facies were controlled by a combination of productivity and hydrodynamics, related to fluctuations in relative sea-level. The nodular marly facies (wackestones and occasionally packstones) are well represented in the Herbichi Zone (Uhlandi Subzone), in the Beckeri-Pressulum Zone (Kimmeridgian), and in some intervals in the Hybonotum and Albertinum Zones (Lower Tithonian). The nodular calcareous facies (mainly packstones, and some wackestones) are the typical facies, with or without stromatolitic overgrowths. The pseudonodular calcareous massive facies (mainly packstones, and some wackestones) are only present at the base of the Hybonotum Zone (Lowermost Tithonian).

It is interesting to note that sedimentation was strongly affected by sea-level changes, e.g. in the case of M.Pasubio (Sarti, 1986b, 1993): in the Col Santino section (type “A” succession) the coincidence of maxima condensations, or real hiatuses, with the maximum regressive pulses of sea level is significant. The Col Santo section (type”B” succession), that lies some hundred meters from the Col Santino section, was deposited in a small and deeper “basin” and is not a deposit with hiatuses (Sarti, 1993). The fact that these two sections are reasonably close and notwithstanding this fact, completely different, is consistent with the very irregular sea floors in epioceanic swells.

In the Col Santo section, the very scanty fauna found from the topmost Uhlandi Subzone upward, probably is indicative of oxygen starvation. Some of these small basins, sometimes with radiolaritic levels and cherty layers (e.g. Col Santo on M.Pasubio) were poorly oxygenated. The silica-rich sediments are consistent with very light (and therefore easily transportable) radiolarians being swept off from “intraplateau” raised areas, to become deposited in deeper areas (Cecca et al., 1990).

Faunal variations through time

The composition in the faunal spectrum of Trento Plateau for the Kimmeridgian is the following: *Sowerbyceras* (22.3%), other Phylloceratina (7.8%), Lytoceratina (7.2%), “Perisphinctoids” (= Ataxioceratidae + Idoceratinae) (25.5%), Aspidoceratidae (23.5%), Haploceratаceae (10.7%). In addition to these ammonite groups, 3 % of the total faunal spectrum is represented by benthic faunas (bivalves, echinoids, brachiopods) and some belemnites. Figs.2 and 3 show the diachronic fluctuations in the abundance of selected ammonite groups. Faunal frequency curves show that there is a very close relationship between the abundance of *Sowerbyceras* and variations in sea level. The synecological relations among faunas are very complex. Moreover, a complementary and persistent inverse correlation exist between *Sowerbyceras* and the Lytoceratina group. Strong decreases in *Sowerbyceras* and Lytoceratina only occurred during the maxima of transgressive phases. The two curves “other Phylloceratina” and *Sowerbyceras* show a trend to increasing numbers of Phylloceratina and decreasing numbers of *Sowerbyceras* during the transgressive phase of the Uhlandi Subzone. The large numerical increase of *Sowerbyceras loryi* in the upper Longispinum and Loryi Subzones is accompanied by a clear decrease of Phylloceratina and sparse and very discontinuous record of Lytoceratina, such that they largely disappear from the record until the middle-upper part of the Heimi Subzone.

Another complementary, inverse relationship exists between the Apidoceratidae and "Perisphinctoid" groups. Opposite to that could be expected, the curve of *Sowerbyceras* and the "Perisphinctoid" one, are closely similar and this fact corroborates, together with the exactly inverse correlation between *Sowerbyceras* curve and the Aspidoceratidae curve, a preference of *Sowerbyceras* for relatively shallow habitats. The proportion of Haploceratacea is related to increases and decreases in the other groups. Following the declining abundance of *Sowerbyceras* at the top of the Loryi Subzone, the three above-mentioned groups ("Perisphinctoids", Aspidoceratidae and Haploceratacea) increases again. As a whole, these three groups show increases, even if with ups and down, until the top of the Kimmeridgian, taking advantage of steady decline of *Sowerbyceras* (from the Cavouri Zone) and also decrease of Lytoceratina and others Phylloceratina. From the uppermost Beckeri-Pressulum Zone the Lytoceratina, "other Phylloceratina" and *Sowerbyceras* curves clearly diverge, due to the near extinction of *Sowerbyceras*.

Depth and "Leiostraca"

The impact of the sea-level changes on the composition of this ammonite assemblage is considered to be induced by ecospace fluctuations and their related abiotic parameters. For the neckto-benthic ammonites in the epioceanic swells the most important of these parameters seems to be the depth-dependent factors such as resistance to implosion and hydrostatic pressure. Other associated parameters include: temperature, oxygen, water hydrodynamics, trophic chain and predators (Marchand, Thierry, Tintant, 1985). This because ammonites were probably much more dependent on a bottom environment than is generally believed (Wiedmann, 1973). Many ammonoids and nautiloids lived, as the extant *Nautilus*, a neckto-benthic mode of life with limited horizontal motility, but some vertical migration. There was a high dependence on the bottom environment, feeding included. For this reason, many ammonite groups, were affected by eustatic oscillations of sea level.

Leiostraca (including the Phylloceratina and Lytoceratina) are usually considered to be deep-water forms (e.g. Kennedy and Cobban, 1976; Westermann, 1990; Cecca, 1992). When the percentage of these ammonite groups increases in the assemblage, facies characteristics indicate deeper environments. Many authors (e.g. Fernandez Lopez and Melendez, 1996; Cecca, Fozy and Wierzbowsky, 1990, 1993; Stevens, 1997) have correlated increases in abundance of Leiostraca with changes accompanying eustatic rises in sea level. On the contrary, in general a decrease in the Phylloceratidae-Lytoceratidae group and increasing benthos correlate with a reduction of ecospace and a greater current activity. This reduced ecospace corresponds with a falling of the sea-level in the epicontinental realm. Faunal spectra with higher percentages of the Phylloceratidae-Lytoceratidae groups and lower benthos correspond to comparatively enlarged ecospaces which would be related to transgressive and early highstand system tracts (Oloriz et al., 1996).

However it is prudent to not generalize. The generally smooth-shelled Leiostraca are generally accepted as being able to inhabit offshore or oceanic environments, although their local abundance in what are clearly shallow-water deposits indicate that they were not entirely confined to deeper-water situations (Kennedy and Cobban, 1976; Westermann, 1990; Cecca, 1992; Stevens, 1997) . This is the case of the "explosive" increase of *Lytoceras polycyclum* in the lowstand system tract (LST) at the base of the Divisum Subzone and *Sowerbyceras* in the Loryi acme Subzone of Trento Plateau. In fact these observations for a distal pelagic swell system, as in the case of the Trento Plateau, seem to be the opposite: in these environments the faunal variations related to fluctuations in sea-level have been reviewed by a number of authors in a "classical" way (e.g. transgression = increased number of Leiostraca) and putting together too long stratigraphic intervals which distort the data. It is very important, on the contrary, to work on structural types of ammonites or better, on ammonite genera, because within more wide groups there are morphologies that show very different interactions both autoecological (mostly due to the sea-level fluctuations) and synecological. As a matter of fact, in the sections studied herewith for many groups the contrary is true than was estimated in the past: e.g.

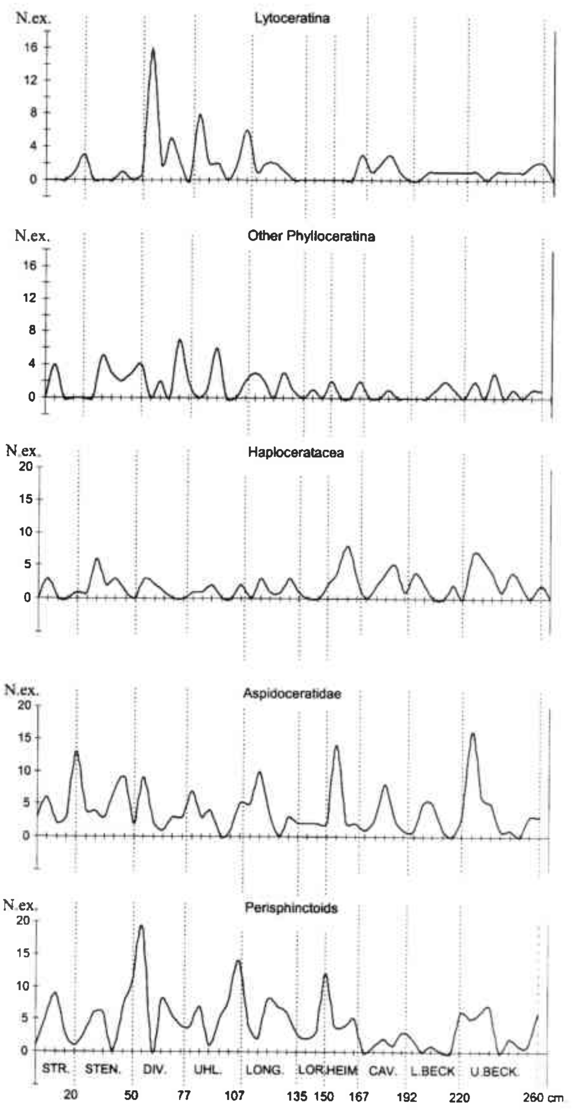

Fig. 3 - Fluctuations in the abundance of selected ammonite groups through time.
Abscissa: thickness of the Kimmeridgian succession (in centimeters) and biozones. Abbreviations: STR = Strombecki, STEN = Stenonis, DIV = Divisum, UHL = Uhlandi, LONG = Longispinum, LOR = Loryi, HEIM = Heimi, CAV = Cavouri, L.BECK = Lower Beckeri, U.BECK = upper Beckeri.
Ordinate: N.ex. = number of specimens.

decreases in abundance of *Lytoceras polycyclum* (a constricted form) and *Sowerbyceras* were related to sea-level highs; conversely, the number of *Sowerbyceras* increased during relative sea-level lows. On the other hand we correlate increases in abundance of other Phylloceratina with changes accompanying eustatic rises in sea-level.

We thus conclude that within the common range of depths for the Phylloceratidae - Lytoceratidae group and certain Ammonitina, ecological features other than depth were at work.

As cautioned by Kennedy and Cobban (1976) regarding Leiostracans, many of the features of, and evidence for, so-called "deep-water" occurrences are more a reflection of distance from land and terrigenous/freshwater influx than bathymetry. The "offshore" vs. "deep" faunas documented by Kennedy and Cobban (1976) coincide with studies by Oloriz (1985, 1990). The relative proximity/distance of an ecospace from the mainland, a condition not directly related with depth and ecospace volume may be more important in determining ecological factors and the effects on living populations than depth (Oloriz et al., 1996), especially on very irregular sea floors, as in the case of the Trento Plateau. But note that the Trento Plateau was situated more distal from the epicontinental shelves during the transgressive pulses and vice versa.

What is important here is the overlap in depth range in which the Phylloceratidae and Lytoceratidae species could coexist with certain Ammonitina. The range of depths in which Phylloceratidae, Lytoceratidae and Ammonitina are supposed to coexist was sufficiently wide, at least in the epioceanic fringe of the continental paleomargins in western Tethys (Oloriz et al, 1996). On the other hand, some constricted and/or flared Phylloceratidae (e.f. *Sowerbyceras* and *Ptychophylloceras*) are common in epicontinental assemblages (Oloriz et al., 1996).

This fits well with frequency curves of *Sowerbyceras* and Perisphinctoids on the Trento Plateau (Figs. 2 and 3).

Phylloceratids smooth or with pseudo-constrictions, have indicators for deep water (Hewitt and Westermann, 1986). Fernandez-Lopez and Melendez (1994) proposed that populations with high proportion of constricted Phylloceratina are typical of proximal outer platform and distal pelagic swell.

Populations with high proportion of Phylloceratina without constrictions are distal, outer environments faunas, beyond the epioceanic plateau.

The details of Leiostracan ammonite ecology are therefore a little controversial, but a consensus exists: 1) the mainly open-ocean character of Phylloceratids and Lytoceratids, which generally have smooth shells, variable coiling; 2) the eurytopy of the phylloceratid and shell-constricted *Sowerbyceras* within subtropical latitudes ; and 3) the relatively shallow environments for vagrant epibenthic or neckthic perisphinctids (Ataxioceratidae and Idoceratinae in the instance at hand), in both epicontinental and epioceanic waters (Oloriz et al., 1995).

Regarding other ammonite faunas, the record of Aspidoceratidae is not, as noted till now, facies independent, even if a certain pelagic mode of life could be envisaged. Fluctuations in the frequency of the group would be strongly related to changes in sea-level and ecological parameters (Fig. 3). Haploceratids have a less clear ecology, anyhow closely linked to the abundance of the other groups. As usual in epioceanic swells, there is low proportion of benthos (3%). Specialized Phylloceratids and Lytoceratids evolved consistently with the expected ecospace evolution, although, as mentioned above, the ubiquitous *Sowerbyceras* numerically increased largely under LST, instead of highstand systems tract (HST) conditions. This unexpected record of *Sowerbyceras* could exemplify a deviant record induced by the sea-level changes. Moreover, migration from others environments cannot be ruled out (Oloriz et al., 1995), especially in the Loryi acme Subzone.

Habitat is different among : 1) smooth and pseudo-constricted Phylloceratina, 2) Lytoceratina and 3) *Sowerbyceras*: the groups 1 and 2 lived beyond the plateau, and perhaps for this reason on the plateau they are less abundant. On the Trento Plateau, scarce specimens of Lytoceratina, confined to isolated horizons in the Strombecki - Divisum biochrons are interpreted as evidence of ademic (i.e. inferred out of the living area) or parademic organisms (that is, in a living area occasionally reached by passive bio-dispersal (see Fernandez Lopez and Melendez, 1994, 1996), except in horizons where there is a strong epibole of constricted *Lytoceras polycyclum*, (a demic population in my opinion). The exceptional fragility of the constricted *Lytoceras polycyclum* should be noted, because the very evolute shell and the very delicate umbilical portion of the shell is relatively thinner than in other ammonites.

Regarding the palaeobathymetric values, see Westermann (1996), Oloriz et al. (1997, 2000).

The Genus Sowerbyceras and its morphological change through time

The Genus *Sowerbyceras* Parona and Bonarelli, 1895 belongs to Phylloceratina Arkell, 1950.

The stratigraphic distribution of the genus is Callovian - Kimmeridgian - lowermost Tithonian. Regarding the Kimmeridgian species, the biostratigraphical range of *S. silenum* is limited to the Silenum, Strombecki and Herbichi Zone; the biostratigraphical range of *S. loryi* is: Acanthicum Zone, Cavouri Zone and lower Beckeri-Pressulum Zone. In the Trento Plateau a strong epibole of this species is recorded in the middle part of Acanthicum Zone (Loryi acme Subzone). Sarti (1993) described a *pseudosilenum* morphotype of *S. loryi*. In the present study the biostratigraphical range of *S. pseudosilenum* has been defined (from middle Beckeri-Pressulum Zone to lowermost Hybonotum Zone within the Tithonian). Since *loryi* and *pseudosilenum* represent different biostratigraphic ranges, and the first species could be ancestral to *pseudosilenum*, we can assume *loryi* and *pseudosilenum* to be two distinct species.

Types and material. The specimen of *Sowerbyceras loryi* figured by Pillet and Fromentel (1875, Pl.5, Figs. 3-4), originally stored at the Museum and Dept. de Science de la Terre de Lyon (France), is now lost (A. Prieur pers. com.). The type of *Sowerbyceras silenum*, figured by Dumortier and Fontannes (1876, p.33, pl.5, Figs. 2, 2a) is stored at the Museum and Dept. de Science de la Terre de Lyon. The type of *S. pseudosilenum*, figured by Sarti (1993, p. 55, pl.1, Fig. 2, and plate 3h in this paper) and all the specimens of *Sowerbyceras* described in this study are housed in the Museum of Geology and Palaeontology "G. Capellini", University of Bologna, Italy , collection "Rosso Ammonitico Veronese".

Key features for species identification in Kimmeridgian *Sowerbyceras*. A detailed description of *Sowerbyceras* is presented in Sarti (1993, 2002). The diameter of the specimens ranges from 40 to 95 mm. The ornamentation consists of constrictions which are constantly present on the body chamber and very rarely on the phragmocone (4 specimens on a total of 960 *Sowerbyceras*).

The constrictions change through time in number and position: the variability in the position of constrictions on the body chamber is obtained by calculating the angle between constriction and the line intersecting the last suture, taking the umbilicus center as starting point of the angle. The following are observed:

BIOZONES	numbers of constrictions	RANGE OF THE ANGLES				
		constr.1	constr.2	constr.3	constr.4	constr.5
Lower Hybonotum Zone	4	15-40°	90-110°	150-180°	220-230°	
Upper Beckeri-Pressulum Zone	5	5-20°	40-80°	110-120°	180-190°	210-220°
Lower Beckeri-Pressulum Zone	4	15-40°	100-120°	150-180°	200-230°	
Cavouri Zone	4	20-50°	100-120°	155-180°	220-230°	
Acanthicum Zone,Heimi Subz.	4	40-80°	110-140°	180-190°	220-230°	
Acanthicum Zone, Loryi Subz.	4	20-60°	90-140°	150-180°	210-220°	
Acanthicum Z., Longisp. Subz.	4	20-60°	95-125°	140-180°	210-230°	
Herbichi Zone, Uhlandi Subz.	4	20-70°	100-110°	140-180°	210-230°	
Herbichi Zone, Divisum Subz.	5	5-40°	50-80°	110-140°	180-190°	210-220°
Herbichi Zone, Stenonis Subz.	5	5-40°	50-100°	115-140°	180-190°	210-220°
Strombecki Zone	4	35-50°	100-110°	140-180°	210-220°	

When the constriction is near the suture line (forming an angle varying from 5° to 20°) it is usually very weak. Constrictions are gently falcoid on the flank. In general, all the constrictions on the one specimen have more or less the same concavity and forward projection. Only the adoral, last constriction (the fourth or fifth in the body chamber, according to the species), is slightly more projected forward than the others.

Many morphological features in *Sowerbyceras* indicates that there was probably a deceleration in the rate of growth as maturity approaches. The adult body chamber commonly shows a change in shape and a reduction in angular length. In addition constrictions tend to become more closely spaced toward the aperture (180°-210°, 220°). All of this evidence suggests a deceleration in the rate of growth and, ultimately, the cessation of growth. However, the time interval over which the rate of growth decelerated may have varied depending on the species.

Diagnostic elements among the Kimmeridgian *Sowerbyceras* (b.c. = body chamber):

SILENUM	*LORYI*	*PSEUDOSILENUM*
5 constrictions on b.c. (become 4 in the Uhlandi Subzone)	4 constrictions on b.c.	5 constrictions on b.c. (become 4 at the base of Hybonotum Zone
pronounced ventral ribs	without (or with very weakened) ventral ribs	flares or ventral ribs more or less marked
arcuate ventrolateral-ventral ribs and constrictions (convex forward)	ventro-lateral and ventral constrictions almost straight	ventral and ventro-lateral constrictions more arcuate of the last *S. loryi*
whorl section tending to be sub-rectangular	whorl section roundish-oval	whorl section tending to be sub-rectangular, compressed
constrictions on the ventro-lateral edge tending to weakening	constrictions mantain their depth on the ventro-lateral edge	ventro-lateral constrictions tending to weakening
the two borders of the constriction joining, starting to the outer third of the flank, forms a pronounced ventro-lateral ridge (weakened in the Uhlandi Subzone)	the two borders of the constriction converging, but without join together, they never forms ridges	without ventro-lateral ridge, but the two borders of the constriction can join on the venter forming a flare or a ventral rib

The species *silenum* and *pseudosilenum* can be distinguished by observing that:

1) *pseudosilenum* is smaller; 2) has more compressed whorls; 3) the ventral flare, not always presents, is more thick and rounded than in *silenum*; 4) the flare develops more high than in *silenum*, just at the beginning of the ventral edge.

The Kimmeridgian evolution of the Genus Sowerbyceras

Sowerbyceras silenum occurs from the base of Silenum Zone to the top of Uhlandi Subzone. In the Uhlandi Subzone we observe the transition from *S. silenum* to *S. loryi*, beginning with some characters from the lower Uhlandi Subzone, even if in the middle part of the Uhlandi Subzone, the *Sowerbyceras* are real *S. silenum*.

Near the topmost Uhlandi Subzone, some specimens are identified as *S. silenum* with some characters of *S. loryi*, i.e. : four constrictions (character of *loryi*), convex forward constriction on the venter (character of *silenum*), a fine ventral riblet transitional from *silenum* to *loryi*. At the same stratigraphic level others specimens are more similar to *loryi* than *silenum*: the evolutionary tranformation *silenum loryi* takes place only in 7 cm of stratigraphic distance: in the latermost 5 cm of the Uhlandi Subzone specimens are more similar to *S. silenum*, in the lowest 2 cm of the Longispinum Subzone they become like *S. loryi*. "Ancestral" *loryi* occur in the lowermost Longispinum Subzone, that is, with a little arcuate constrictions on the venter. The other phenotypic change *loryi pseudosilenum* takes place more gradually. From the base to the middle lower Beckeri-Pressulum Zone there are specimens of true *loryi* side by side with *loryi* transitional toward *pseudosilenum*. From the lower boundary of the upper Beckeri - Pressulum zone all the members of the *Sowerbyceras* assemblage are *pseudosilenum*: they possess 5 constrictions and the two borders of constriction frequently joining to produce a flare or a ventral riblet, or with the posterior border of the ventral constriction more prominent of anterior border.

Morphological evolution of the constrictions. Many Late-Jurassic to Cretaceous Ammonitina display periodic subradial grooves on shell surface and internal mold, called constrictions. Constrictions, analogous to the varices of gastropods, have generally been interpreted as reflecting discontinuities in growth (this interpretation is supported by a number of observations, see Bucher et al, 1996) and are indisputably related to former peristomes (Checa and Westermann, 1989). They are sometimes accompanied by a varix, that is, a thickening of the shell wall, caused primarily by an increase in the thickness of the nacreous layer. Varices may also occur without an associated constriction. Such varices have been called internal ridges or pseudo-constrictions (Westermann, 1990) and appear as grooves on the steinkern.

Constrictions of *Sowerbyceras*, unlike other Phylloceratina (*Calliphylloceras*, *Ptychophylloceras*) and also in the Lytoceratina, are acutely sigmoid true constrictions on test and internal mold, as in the case of the *Holcophylloceras*.

From the Strombecki Zone to the middle part of Divisum Subzone the specimens show very arcuate constrictions on the venter. Constrictions may traverse the flanks from the umbilicus to the venter. Others start from the mid-flank. The ventro-lateral ridges that are formed when two constrictions join on the outer third of flank are well developed in some specimens and less developed in others. On the specimens with very pronounced ventro-lateral ridges the constrictions, starting from the venter reach mid-flank at the most developed. On the contrary, the specimens without pronounced ventro-lateral ridges have constrictions that without interruption joins the umbilicus, which could be related to hydrodynamic and balancing efficiency.

From the top of Divisum Subzone the ventro-lateral ridge becomes progressively weaker, but regardless the specimens are *S. silenum*, with arcuate ventro-lateral and ventral constriction.

In the middle part of the Uhlandi Subzone are *S. silenum* with arcuate ventral constrictions, but they do not show the ventro-lateral ridges. Within the intraspecific variability of *S. silenum*, the two borders of the constriction, joining in the outer third of the flank, frequently causes the disappearance of constriction on the venter with the presence of a ventral riblet, or very rarely, starting from the ventro-lateral edge, the two borders of the constriction separate again, forming two distinct ribs instead of one single rib. However, in general, *S. silenum* possess a single ventral rib grown by the elevation of the posterior border of constriction.

At the base of Longispinum Subzone the specimens of all *Sowerbyceras* are *loryi*, with ventral constrictions markedly more straight. The constrictions are almost straight on the venter and

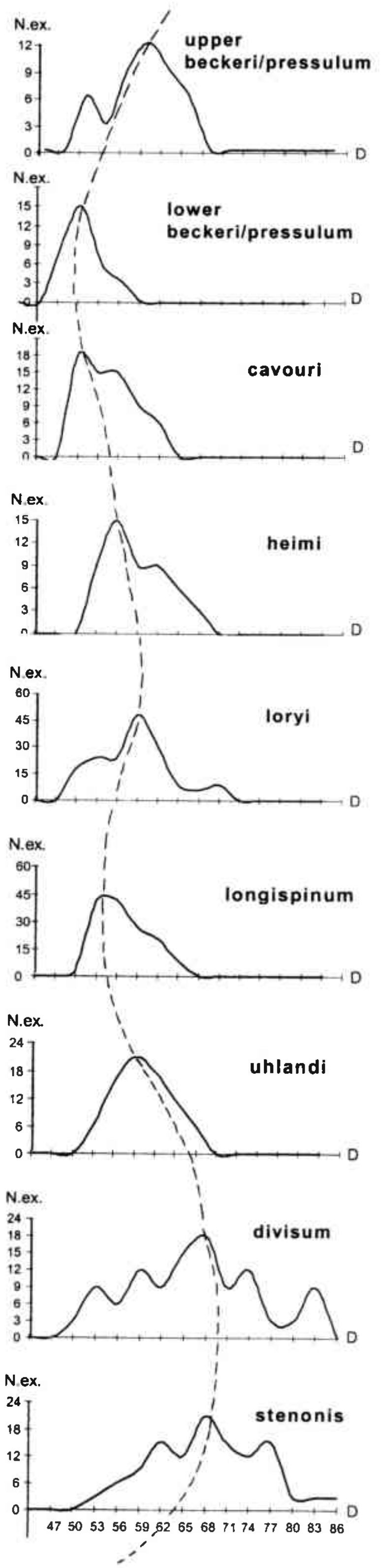

Fig. 4 - Diameter curves of kimmeridgian Sowerbyceras with the indication of the modes throughout time (note the similarity of the modal curve with the sea-level curve). D = diameter (in millimeters).

less falcoid starting from the outer third of flank.

In the lower part of the Beckeri-Pressulum Zone there is a slight tendency towards a more developed ventral sinus of constrictions in comparison to the previous biozones, but without ventro-lateral ridges and ventral ribs. In the middle Beckeri-Pressulum zone the change to *S. pseudosilenum* occurs.

In the evolution of *Sowerbyceras* during the Kimmeridgian, the change from five to four constrictions is the character that became modified more markedly. In fact, at the base of the Uhlandi Subzone even if in the presence of all the characters of *S. silenum*, the specimens modified showing four constrictions similarly to the following *S. loryi*. The sudden change takes place over a stratigraphic distance of 5 cm and is the same for all the specimens. Also we observe the change from four (*S. loryi*) to five (*S. pseudosilenum*) constrictions suddenly in the upper Beckeri-Pressulum Zone.

Another character that changes more slightly is the gradual reduction of the ventral rib produced by the elevation of the border (usually the posterior) of the constriction on the venter of *S. silenum*. This change corresponds to the more or less complete disappearance of the ventral rib in *S. loryi*.

The ridge produced by the junction of the two borders of constriction on the outer third of flank is another character that becomes modified relatively quickly and that disappears at the base of Uhlandi Subzone.

The progressive "straighteness" of the arcuate constriction on the venter (Fig. 2) is a character that suddenly accelerates near the top of the Uhlandi Subzone, only in 2 cm (about 10000 years in the Trento Plateau) which corresponds to the evolutionary change from *S. silenum* to *S. loryi*. More gradual is the change from *S. loryi* to *S. pseudosilenum*. At the beginning of the Beckeri-Pressulum zone, the constriction is gently more arcuate on the venter and the whorl section slightly less inflated than in the typical *loryi*. Some specimens show a light ventral flare before every constriction. In the lower Beckeri-Pressulum zone these specimens occur side by side with true *S. loryi*. Near the topmost lower Beckeri-Pressulum Zone specimens of *S. loryi* are still present with characters of *S. pseudosilenum* (whorl section, slight incurvation of the ventral constriction, posterior border of the ventral constriction more prominent). From the base of the upper Beckeri-

Pressulum Zone all the specimens of *Sowerbyceras* are *pseudosilenum*. At the topmost Beckeri-Pressulum Zone (i.e. at the Kimmeridgian / Tithonian boundary) the flanks of the specimens are decidedly flattened, and the whorl section compressed, as in the case of the only *Sowerbyceras* record reported from the Tithonian (a specimen from the lower Hybonotum zone, 35 cm above the K/T boundary, plate 3i).

The *Sowerbyceras* abundance variations. The number of specimens fluctuates throughout time clearly (see fig.2) showing a minimum within the middle to last third of the Uhlandi Subzone. A minimum also occurs in the middle Beckeri-Pressulum Zone, where the number of specimens is very low and preludes the extinction, but where in any case, even if moderately, it gradually augments again. Eventually, *Sowerbyceras* become extinct in the lower Tithonian. The maximum number of specimens can be found in the first third of the Divisum Subzone and in the Loryi acme Subzone. It is noteworthy that before every phyletic speciations, the number of specimens is very low. After the change from a species to the other, the specimens abundance increases again.

The diameter variations. The diameter of specimens also changes through time (Fig. 4). In particular, from the Strombecki Zone the forms show a gradual increase in size that reaches the maximum within the first third to the middle of the Divisum Subzone, then progressively decreases in the middle Uhlandi Subzone. From here the diameter gradually increases to the Loryi Subzone and subsequently it decreases again to the middle Beckeri-Pressulum Zone. From here it gradually increases again. We observe the maximum diameters of the genus *Sowerbyceras* within the last third of the Strombecki Zone to the first third of the Stenonis Subzone.

The Wb/D, wH/D and Uw/D variations. The thickness ratio Wb/D curve shows throughout time an analogous trend to the diameter curve (see Fig. 5). The wH/D and Uw/D variations through time show a specular, opposite trend, in fact the increase in wH/D ratio correspond to Uw/D decreases and vice versa: that is, an increase in whorl high leads to the ammonite involution. The wH/D curve through time, on the contrary is similar to the Wb/D and D curves.

It is apparent that these variations in parameters have definite morpho-functional reasons. The ammonite morphology is in fact directly connected with its way of life and, consequently,

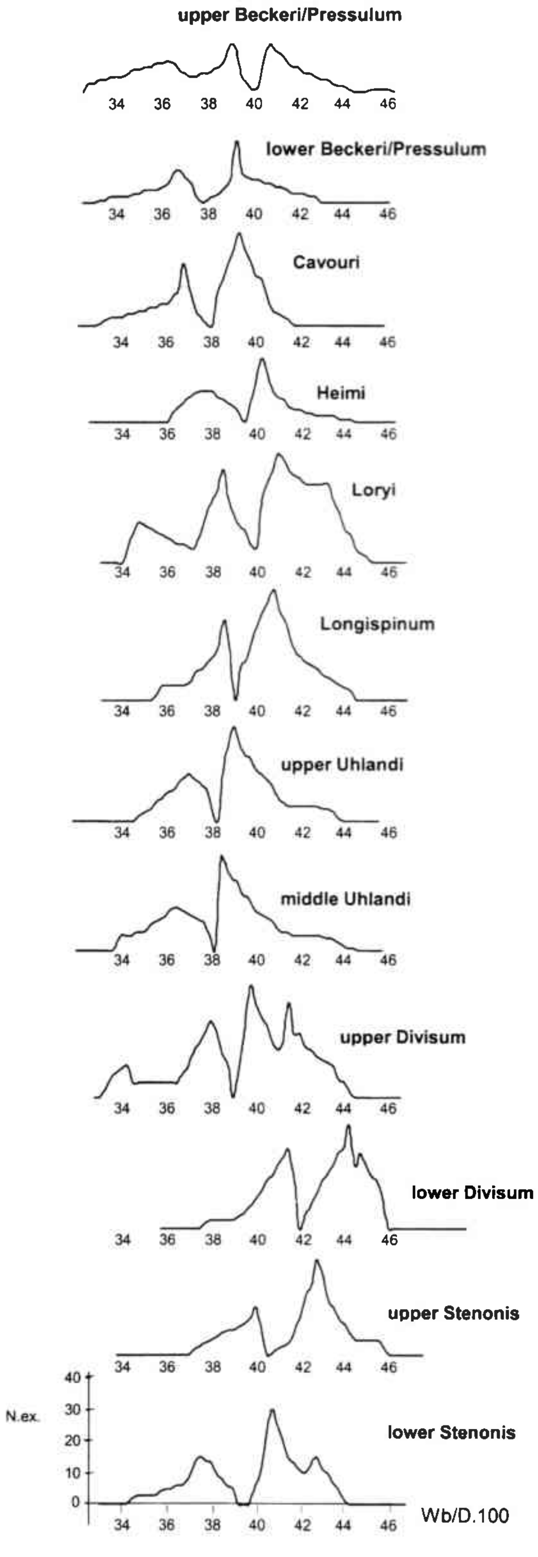

Fig. 5 - Wb/D ratio curves of Kimmeridgian Sowerbyceras throughout time (note the bimodality). N.ex. = number of specimens.

with its active swimming ability relative to its environment. The ammonite behaviour in the water is governed by the stability of the shell, its manoeuvrability (ability to change direction) and its hydrodynamic efficiency.

Here the crucial point is not covariation of shell features, but its correlation with environmental trends (i.e. sea-level fluctuations).

The immature shell of Sowerbyceras

Specimens of adult shells are far more common in the fossil record than those of immature shells. The frequency of immature specimens (with body chamber preserved) is only 2% of the *Sowerbyceras* (19 ex. in a total of 960). The literature documents many fossil occurrences where juveniles are absent, and where only specimens near maturity are present in collections (Kennedy and Cobban, 1976). Because other groups of ammonites show juveniles, probably an accettable hypotesis can be a strong segregation of adult and juveniles: the juveniles spent their early life near surface, moving onto the sea-floors only when adult. In fact the mature ammonites possessed greater resistance to hydrostatic pressure than the juveniles (Lehmann, 1981; Fernandez-Lopez and Melendez, 1996).

Westermann (1990) suggested that constricted ammonites of the type of *Sowerbyceras* lived on the slope as neckto-benthic and moved up the "distal platform" to lay eggs (active migration between life-cycles and feeding behaviour and diurnal migration). This may be true, but in the Trento Plateau area *Sowerbyceras* lived on the plateau and not on the slope (*Sowerbyceras* are absent from the margins of the Trento Plateau). However, the irregular sea-floors caused a similar effect: i.e. the eggs were laid on the raised areas of the very irregular Trento Plateau and then the juveniles when hatched, lived segregated for part of their life within the upper water column and not as neckto-benthics.

This pattern matches what is known of migratory behaviour in Recent cephalopods, and is supported by the striking morphological differences between juveniles and adults found in many ammonites, which is a reflection of life habits that changed through ontogeny (Kennedy and Cobban, 1976; Lehmann, 1981).

Allometric growth in Sowerbyceras

In the species of Kimmeridgian *Sowerbyceras*, the relative size of the Wb, wH and Uw is inversely correlated with adult shell size among individuals within the same species. The function of this inverse correlation is probably related to the way of life. This inverse correlation between adult shell size and the relative size of the Wb, wH and Uw reflect the consequence of a negative allometric relationship of these parameters in ontogeny. In fact in most specimens, even if not all, the Wb/D, wH/D and Uw/D ratios presents greater values within the smaller diameters and the values are decreasing little by little towards larger diameters. This allometric relation is very strong for the Wb/D and Uw/D ratios, and less clear for the wH/D ratio. Thus, maturation at a smaller shell size may have produced individuals with relatively larger Wb/D, wH/D and Uw/D ratios. Also in living cephalopods such as squids, the head is relatively much larger in juveniles than in adults (O' Dor, 1983; Nixon, 1983).

Modes of evolution

S. loryi is characterized by a small adult size. Also by the presence of morphological features at maturity typical of those of the juveniles of the more primitive species *S. silenum*, both in the whorl section shape and in the fact that the juveniles of *S. silenum* in the Stenonis Subzone show four constrictions (like the adults of *S. loryi* and the last morphs of *S. silenum* in the Uhlandi Subzone) instead of the five of adults and the constrictions are straighter on the venter than in other contemporary adult individuals.

It is evident from the analysis in this paper that the evolutionary change from *S. silenum* to *S. loryi* took place by the paedomorphosis, because some juvenile features of ancestral stocks are retained in the descendants. The transfer of characters during ontogenesis is sometimes recapitulative and sometimes hypomorphic. Hypomorphosis (sensu Reilly et al., 1997) is associated with accelerated shape acquisition and also with smaller size.

According to Checa and Oloriz (1988) the paedomorphic forms have a greater potential for adaptation, which would mean that they showed a higher tolerance compared to the more "elaborate" species. This is the case with *Sowerbyceras silenum* and *S. loryi*. Paedomorphosis is produced by a number of processes, notably hypomorphosis. The tranformation from *S. silenum* to *S. loryi* is still a heterochrony, but *loryi* is at the same time paedomorphic and smaller than its ancestor *silenum*. This heterochrony is of a hypomorphosis type (= paedomorphosis by truncation) produced by an acceleration of maturation relative to shape. This process generally results in a smaller adult size and shorter generation time. The rates of growth and morphological transformation are the same in both the forms hypomorphic and not hypomorphic. The hypomorphic form, however, reaches its maturity earlier; hence it is characterized by shorter longevity, smaller final size, and an earlier morphological stage at maturity. Moreover, the hypomorphic species resemble the juveniles of more primitive species (Landman et al, 1991).

If it is accepted that the evolutionary change from *silenum* to *loryi* took place by hypomorphosis: *S. loryi* appears hypomorphic because it reaches maturity at a relatively small size and displays a number of features characteristic of the more primitive species *silenum* at a juvenile stage of development. For example, the straight ventrolateral constriction is restricted to the early whorls of *S. silenum*, and is retained to maturity in *S. loryi* but, hypomorphic species are not simply juveniles at an arrested state of development. In contrast, they commonly develop a number of unique features at maturity as well as those associated with the mature stages of more primitive species (Landman et al, 1991).

Contrary to what happened in *S. silenum* and *S. loryi*, in *S. pseudosilenum* the projection forward of the constriction on the venter and the ventral flare occur later during ontogenesis, just in correspondence or after the 2nd constriction of the mature body chamber.

This transformation is not simply a heterochrony as in the case of the paedomorphosis: *S. pseudosilenum* frequently is more like the ancestral of its ancestral than a juveniles of its immediate ancestral. The change for instance, from straight to arcuate constrictions on the venter might seem an example of "proterogenesis" : phenomena involving the imbrication of a "juvenile innovation" with a paedomorphic process (e.g. deceleration sensu Reilly et al., 1997).

Conversely, the appearance for instance of the two borders of constriction joining very high on the venter of the adult body chamber of *S. pseudosilenum* in the upper Beckeri-Pressulum Zone and the presence of ventral flares instead of ribs could be construed as an example of "palingenesis" : imbrication of an "adult (= late) innovation", with a peramorphic process (e.g. acceleration sensu Reilly et al. , 1997). Thus, *Sowerbyceras* displays at least three kinds of features at maturity : 1) derived features reminiscent of those of the juveniles of ancestral stocks, presumably due to hypomorphosis, 2) mature features in common with *silenum*, and 3) unique features, whose presence is not clearly related to hypomorphic processes (see Landman et al, 1991).

The phyletic speciation from *S. silenum* to *S. loryi* occurs because *loryi* is hypomorphic, in fact hypomorphosis, that occurs by ecological stress, produced a size reduction due to environmental constraints such as regressive pulse of sea level or thermal or feeding stress. Lack of food is one of the main factors affecting shell growth (lower rates of growth, Boletzky, 1974; Mignot, 1993), but the persistence of a small-sized shell with a "juvenile" look does not prevent either sexual maturation or the reproduction. In addition to the lack of food, these effects are determined by colder water with low availability of calcium carbonate. The growth rates of the young ammonites varied with the temperature of their environment: in the case of the present study, speciation took place during transgressive phases. We observe : transgressive phases = colder water = small size of *Sowerbyceras*; this fact perhaps leads to a shorter life-span and a quicker succession of generations. Probably this is the reason of the very short time for the phyletic speciation from *silenum* to *loryi*. However it is prudent to not generalize: cold water is not necessary synonymous of small size and short-life span. It is nowadays demonstrated that in *Sepia officinalis* the span-life (cohort) and, consequently, the body-size, are higher in cold waters (e.g. English Channel) that in hot waters (e.g. Mediterranean) (Dommergues, pers. comm.).

The fact that characters unfold in *S. loryi* with a change of ventral constriction from very convex forward to almost straight may be interpreted as a decrease in the radial growth vector, that is, a fall in growth rate throughout ontogeny.

The Trento Plateau as a centre of evolution for Sowerbyceras

Callomon (1985) lists the following factors to recognize if an area is the true centre of evolution of a group: a) abundance, b) dominance, c) preservation, d) maturity, e) sexual polarisation, f) specific diversity, g) geographical stasis.

The *Sowerbyceras* assemblage conform to the seven factors of Callomon and therefore the Trento Plateau represented a true centre of evolution ("a" centre, not "the" centre). Probably is true the hypothesis of multi-origin centers for the morphological trends identified. Further, very detailed research in the AR facies around of western Tethys on this question is necessary, to resolve a hard debate on centres of origin which has dramatically opposed cladistic and dispersalist biogeographers.

In any case, the ammonites *Sowerbyceras* are demic, their remains are found in their living area and may be inferred in their breeding area (eudemic).

Dimorphism and thickness ratio Wb/D (Whorl breadth/Diameter) in Phylloceratina

The clearest indication of dimorphism in ammonites is considered to be the shell diameter between forms wich have identical inner whorls but which reached maturity at different sizes. Callomon (1955) coined the apt terms macroconch (M) and microconch (m) for the large and small forms, respectively. The character of the more or less inflated and broadened whorls of the body chamber clearly represented in the thickness ratio Wb/D, is another very important manifestation of dimorphism in my opinion. This character has been used to separate LARGIVENTER conch (= "L") from LEVIVENTER conch (= "l") at the species level and with a clear bimodal width distribution (Sarti, 1990b, 1993, 1999). The idea of dimorphism in phylloceratids based on the venter width, has been originally proposed by Joly (1976). The Joly's idea was hypothetic, because was based on specimens generally devoid of body-chambers. Recently, Joly (2000) described a "size" dimorphism in Phylloceratids, but it appears that the cited author is not aware that this datum is only of use when a great number of collected bed-by-bed specimens is available; it is highly desirable that additional material closely controlled stratigraphically be recovered. Within the suborder Phylloceratina, differences in whorl-width are the main phenotypical expression of sexual dimorphism. Useful terms for this type of dimorphism are: "Largiventer - L" (L as Large venter, from Latin *venter* = venter, and *largus* = large, broad, wide: broad conch morphotype) and "leviventer - l" (l as light venter, from Latin *levis* = light, slight, thin: more compressed conch morphotype).

This type of dimorphism is visible in *Nautilus*: living (Stenzel, 1952; Haven, 1977; Saunders and Spinosa, 1978) and fossil (Silberling, 1959; Makowski, 1962). In fact, in *Nautilus*, the shell diameter of the sexes is almost identical, but the relative width of the venter on the body chamber is greater in males than in females. This latter fact is related to the presence in the males of the spadix, a specialized copulating organ (Stenzel, 1952; Haven, 1977; Saunders and Spinosa, 1978).

In order to explain the differential size and the morpho-ornamental divergences between macro- and microconchs in ammonites, Guex (1981) proposed the occurrence of neoteny and hypomorphosis in the microconchs relative to the corresponding macroconchs. At an intraspecific level these heterochronic processes produce paedomorphic patterns of the retention of macroconch juvenile characters in the adult microconch. But this is not true for *Sowerbyceras* (and probably the Phylloceratina as a whole), perhaps for a reason linked to phenotype restriction in ammonoids with short body chambers. It so happens that the Macroconch - microconch dimorphism is not well established in many groups with short body chambers, at least in the Upper Jurassic (Aspidoceratidae, Oppelidae such as Taramelliceratinae, Phylloceratina, etc...). The most marked change in the growth of width of the whorl occurs at the onset of maturity. Dimorphs within the same species start to diverge at the beginning of the mature body chamber. The width of the whorl begins to increase more slowly or not at all in leviventer conch whereas it continues to increase at the same rate in largiventer conch.

In specimens of *Sowerbyceras* from the same stratigraphic level it is apparent that, apart from the heterochronic variation of the whorl section, two different morphologies are present, reflecting the two dimorphs: on the one hand a more wide and broad venter and more inflated whorl section and on the other hand a more arched venter and more compressed whorl section. Study of ventral constrictions is also significant. Here, the ammonoid sample can be subdivided into two groups that are a dimorphic couple Largiventer - leviventer, on the basis of slight differences in ornamentation (Sarti, 1993) and chiefly on the basis of whorl sections: the first group with thick venter and inflated whorls (Largiventer), the second group with thin venter and more compressed whorls (leviventer) (Fig. 5).

The most telling evidence in favour of the sexual interpretation of this dimorphism is its unchanging character over long stretches of lineage, through repeated evolutionary changes in morphology, in parallel. It is found that the dimorphic whorl breadth ratio, Wb/D (adult l) : Wb/D (adult L) is the most persistent character of all.

Largiventer conch outnumbered leviventer conch almost always; in the Beckeri-Pressulum Zone on the contrary we observe l= 62.5% and not by chance just afterwards, in the lowermost Tithonian, the extinction of the genus *Sowerbyceras* occurred:

BIOZONES	% Largiventer	% Leviventer
Beckeri-Pressulum Zone	37.5	62.5
Cavouri Zone	58.5	41.5
Acanthicum Zone,Heimi Subz.	57.2	42.8
Acanthicum Zone, Loryi Subz.	56.7	43.3
Acanthicum Z., Longisp. Subz.	63.9	36.1
Herbichi Zone, Uhlandi Subz.	63	37
Herbichi Zone, Divisum Subz.	62.9	37.1
Herbichi Zone, Stenonis Subz.	61.2	38.8
Strombecki Zone	60	40

The intraspecific variability and the phyletic speciation

Environmental factors affected the shape of the ammonoid shell. Such variation in shape as a result of environmental conditions is common in gastropods. In ammonoids, this may have produced a wide range of intraspecific variation (Kennedy and Cobban, 1976; Callomon, 1985; Landman and Waage, 1993; Bucher et al., 1996). We distinguish usually two types of variability : 1) a morphological continuum (variability as usual), 2) a discontinuous variability called polymorphism (Matyia, 1986, Guex, 1992; Stevens, 1997; Matyia and Wierzbowski, 2000). In the *Sowerbyceras* studied in this paper, the first type is apparent (apart from Wb parameter).

The existence of a relationship between ecological stress and increased variability has been the subject of a number of publications. For example, Williamson (1981) showed that the variability of lacustrine Mollusca in the Upper Cenozoic of Turkana increased during the regressions periods (see also Laurin, 1986, for the Brachiopods).

Regarding the ammonites, has been a long tradition of relating fluctuations in ammonoid diversity to sea level changes (e.g. Hallam, 1990; House, 1993; Rawson, 1993; Westermann, 1993; Yacobucci, 1999). Despite the abundance of literature, there is no clear consensus as to whether ammonoid diversity typically increases during transgressive or regressive pulses.

The debate can be clarified by the understanding that faunal diversity may be generated in two different ways. Regressions cause the breaking up of habitat, which will enhance the probability of isolates forming and surviving (Hallam, 1990; Becker, 1993; Rawson, 1993; Yacobucci, 1999). If this is true, we might expect to see an increase in diversity due to conventional speciation during a regressive pulse. On the other hand, transgressive pulses often involve the flooding of continents, which produces more unstable environments, with fluctuating oxygen and salinity levels (Checa and Oloriz, 1988). In my opinion the increase-decrease of a given species and the amount of intraspecific variability may be correlated with the ecological tolerance, which is doubtless connected with the "steno-" or "eurotopic" character of the species, and also with the epioceanic or shelf habitat. So during transgressions that flood continental areas, diversity would be generated by the selective unmasking and mixing of already-present variation by heterochronic processes (Yacobucci, 1999). Hence, we might expect ammonoid diversity to increase during both some transgressive and some regressive pulses, but for different reasons. The level at which diversity increases, however, may differ. According to Yacobucci (1999), transgressive pulse may produce many new lower level taxa, similar in overall form (e.g. the *Sowerbyceras* of the Trento Plateau), while regressive pulses may produce new higher level taxa and Bauplane. Regressive pulse of sea level fragments marine habitats, promoting vicariance and a large amount of intraspecific variability. This isolation could not produce speciation on the Trento Plateau because the isolation was very temporary and not complete. On the contrary, transgression creates epicontinental seaways with unstable environments, promoting the rapid radiation of developmentally plastic groups but low intraspecific variability on the epioceanic swell. In the *Sowerbyceras* of the present study, in fact, there is observed an increased intraspecific variability during the sea-level low (only Wb intraspecific variability decreased). Also in other characteristics the *Sowerbyceras* assemblage is different from the common rule in that the small-sized forms are more resistant to extinction and are usually more abundant in number of individuals. The probability of finding them at the beginning of new phyletic lines is therefore very high. This is true for *Sowerbyceras* (at the Kimmeridgian /Tithonian boundary the large-sized forms did not survive), but, when we observe the phyletic change from a species to the other, where the size of specimens are smaller, also the number of specimens, comparatively to the group history, decreases.

Constrictions. The constrictions of *Sowerbyceras* show a low intraspecific variability (with gradual variations through time) linked to the more or less arcuate ventral sinus and a lightly higher variability linked to the variable angle between the last suture line and the constrictions of the body chamber.

Diameter. The intraspecific variability increases from Strombecki Zone to Stenonis Subzone, with an acme within the first third to the middle part of the Divisum Subzone, then decreases and reaches a minimum within the last third of the Uhlandi to the base of the Longispinum Subzones. Successively increases again as far as the Loryi Subzone, decreases within the Heimi Subzone, increases in the Cavouri Zone and decrease within the lower to the base of upper Beckeri-Pressulum Zone (see fig.4), then increases again.

Wb parameter. Confronted with the variability of wH/D and Uw/D, regarding Wb/D the intraspecific variability is very high. Previous works exhibit that, in general, the Wb parameter in the ammonites shows an extraordinary range of intraspecific variability (e.g. Callomon, 1985; Cooper and Kennedy, 1987; Dagys and Weitschat, 1993; Sarti, 1999 and reference therein). This datum is only of use when a great number of specimens is available.

Very interesting is the comparate intraspecific variability of D and Wb/D through time : the two curves (variability of D and Wb/D) vary in an almost perfect manner: we observe in fact that when the intraspecific variability of the diameter increases, the Wb/D intraspecific variability decreases and *vice versa* (see figs. 4 and 5).

Uw and wH parameters. The range of intraspecific variability in umbilical ratio Uw/D and wH/D (whorl height/Diameter ratio) are very similar and their trend is also very similar to the variability of D parameter, but showing a lower range than D.

An interpretation. The more distinct morphological changes within the phyletic speciations of *Sowerbyceras* in the Kimmeridgian occur in the last third of Uhlandi Subzone and in the middle part of Beckeri-Pressulum Zone, where the RAV Nodular Marly Facies develops. What drives the evolutionary change? Why does the Nodular Marly lithofacies develop in tandem with this change?

It appears that is not the high intraspecific variability that primes the evolutionary change from a species to the other, being very low just where we observe the turnover of species, but this change is influenced by the opposite, that is, a low intraspecific variability accompanied by a small population. For example, the change from *S. silenum* to *S. loryi* the lowest number of individuals in the history of the genus during the Kimmeridgian, a part from the middle part of Beckeri-Pressulum Zone, see Fig. 2. A lower intraspecific variability of morphology, more easily leads to the change. This is true also for the phyletic change from *loryi* to *pseudosilenum* observed in the middle part of the Beckeri-Pressulum Zone, where the abundance of *Sowerbyceras* is the same as that of the Uhlandi Subzone, and also the intraspecific variability is very low.

Regarding the intraspecific variability of D, it is observed that maximum water depth corresponds to the very low intraspecific variability of D. Minimum water depth corresponds to the very high intraspecific variability of D (Fig. 4). In this second case the great differentiation of environmental niches in the very irregular sea floor of distal pelagic swell areas will induce high intraspecific variability. The *Sowerbyceras* occurrences on the Trento Plateau increased comprehensively the intraspecific variability (that decreased inside the several niches), but there was not sufficient time to change to new species when wider connection conditions (i.e. enlarging of ecospaces) returned.

Regarding the curve of intraspecific variability of Wb (here quantified by the thickness ratio Wb/D) we observe the contrary of what take place for D, that is minimum water depth corresponds to lowest Wb/D of intraspecific variability (not venter width that on the contrary is very broad!). The more shallower the sea, the lower is the intraspecific variability of the venter width, probably because shallower water mean less possibility to move up and down in the water column and then this is reflected in a lower variability of the venter width. On the contrary the maximum water depth corresponds to highest degree of intraspecific variability of venter width and of thickness ratio Wb/D.

In the studied section is observed: a high intraspecific variability of the parameters, (with the exception of Wb) during slowing sea-level, but this fact is clear because during regressive phases we observe a larger number of habitats in a irregular sea floor. And this is also true on submarine plateaux as in the case of the the Trento Plateau and it is also further confirmation that *Sowerbyceras* for various reasons prefered a necktobenthic behaviour (e.g. because they fed close to the bottom).

Sea-level changes and *Sowerbyceras* changes through time

It is apparent from the data presented in the following section of this paper that Trento Plateau marine faunas have been exposed to the effect of cycles of regression and transgression during the Late Jurassic. The biological effects of transgressive and regressive pulse have been reviewed by a number of authors (e.g. Jablonsky, 1980; Hallam, 1975, 1977, 1978, 1987; Stevens, 1990; Bucher et al.,1996).

Comparing the *Sowerbyceras* abundance curve and the sea-level curve we observe a very close resemblance between the two (Fig. 2). The increases in the number of *Sowerbyceras* can be related to shallowing water depth and vice versa, following the sea-level changes. In all the investigated sections, a considerable decrease in frequency or even an absence, of *Sowerbyceras* and other ammonites genera (Fig. 3) is observed in the upper Divisum, middle-upper Uhlandi Subzone and middle Beckeri-Pressulum Zone that precedes three morphological changes and the following numerical increase in *Sowerbyceras* fauna. This widespread phenomenon is related to deepening of the Trento Plateau, which produced a change in calcium carbonate deposition. In the Trento Plateau, biological changes that are likely to accompany rising sea levels include low diversity, and increases in speciation rates. Falling sea levels on the other hand are accompanied by high diversity, biostratigraphic gaps and increases in endemism (Stevens, 1997). Also in the epicontinental seas, transgressive pulses of sea level could induce a temporary change in water chemistry detrimental to some organisms which, in turn could disturb the trophic chains and consequently effect a rapid decrease in macrofaunal density (Marcinowsky, 1980).

In epicontinental environments, the disappearances of ammonite taxa are often explained by assuming that, as a consequence of a sea-level fall, many biotopes have disappeared (Hoedemaeker, 1995; Oloriz et al.,1996). This reduction of biotopes would have enhanced selection pressure and ultimate extinction. Maxima of diversity are ascribed to high eustatic sea-level stands. During such highstands, large parts of the shelf were inundated and many new biotopes created, which became occupied by new species (Hoedemaeker, 1995). But in distal plateaux as in the Trento Plateau, the contrary is observed, since with the high sea levels there is a reduction in biotopes, and *vice versa*. The two Kimmeridgian transgressions (near the boundary Uhlandi Subzone / Longispinum Subzone and at the middle Beckeri-Pressulum Zone) coincide with minima in the number of *Sowerbyceras*. The second transgressive pulse was so marked that it led to the extinction of *Sowerbyceras*. Also the *Sowerbyceras* abundance curve compared with the sea-level curve is compatible with the "offshore" shallow-water neckto-benthic habitat of these planulate ammonites.

The diameter (-D-) curve is also very similar to the sea-level curve (Fig. 4). The specimen diameter increases with sea-level fall and *vice versa* (deeper waters = smaller adult size; shallower waters = larger adult size) . Many environmental factors affect the rate of growth of cephalopods, including temperature, food availability, light intensity, pressure, dissolved oxygen, day length, and the abundance and type of predators (Marchand et al., 1985 ; Bucher et al., 1996). Temperature is one of the main factors affecting the rate of growth. Decrease in temperature is reflected by a deceleration in the rate of growth, a reduction in septal spacing, and an increase in the time of chamber formation (Hewitt and Stait, 1988). Wiedmann and Boletzky (1982) and Boletzky (1983) demonstrated that lack of food during the life cycle of *Sepia officinalis* results in lower rates of growth and closer septal spacing. On the Trento Plateau during the transgressive phases the greater water depths produced colder sea-water and the *Sowerbyceras* become small-sized. This fact is not unequivocal: other ammonoids that lived in deep water and grew more slowly than those that lived in shallow water (Bucher et al.,1996), in some cases presents larger size, because of lower methabolism (F.Oloriz, pers. comm.).

The same phenomenon of size reduction, in this case in heterochronic terms, is observed in synchronic terms among Liassic *Hildoceras* (Almeras and Elmi, 1982; Mignot, 1993), where there is a size difference linked to the hypomorphic stage of specimens in the Umbria-Marche Apennines (Italy). More accentuated hypomorphosis is observed in the ammonites of deeper areas, the diameter of Toarcian ammonites in the Umbria-Marche region being related to paleogeographic situation of outcrop (Almeras and Elmi, 1982; Cecca et al., 1990; Mignot, 1993). It is partially the "Platform effect" of Oloriz (1985). The "Platform effect" is transportable when there is a regressive pulse such as on Trento Plateau, because regressive pulse produces, partially, a similar effect to the Platform one in the proximal associations. This "effect" produces: 1) a tendency to increase size , in ecological and in evolutionary time ; 2) a tendency to develop ornamental exhuberance (in the case of *Sowerbyceras* more pronounced constrictions and ventro-lateral ridges) ; 3) an expression of characteristic phenotypes, differentiated from those of the distal association (on Trento Plateau is differentiated regressive from transgressive pulse) ; 4) selective opportunities to colonize (Oloriz, 1985). The large-sized ammonites lived on pelagic swells and in relatively shallow-water seas. The small-sized ammonites lived in deeper sea. Also the same species showed diversified diameters, according to shallower or deeper seas.

Also, the curve Wb/D through time follows the variation of D, because the whorl width of the specimens increases during shallowing sea-level and *vice versa*: the ratio Wb/D fits well with the eustatic curve (deeper sea = Wb/D decrease; shallower sea= Wb/D increase). Independent support for the relationship among large size, lateral compression, and higher sustained swimming velocities may be available from paleoenvironmental evidence: in the Kimmeridgian sections studied, the lithofacies analyzed by Caracuel et al. (1997) shows clearly that a nodular-marly deposit is consistent with deeper seas and lower bottom current velocities (and lower number of *Sowerbyceras*, this paper); whereas a nodular calcareous deposit is consistent with shallower sea and higher bottom current velocities (and higher number of *Sowerbyceras*, this paper).

In shallowing, nodular-calcareous facies, *Sowerbyceras* tend to be larger and less slender than those found in the deeper, nodular-marly facies. Therefore the morphological variations are a function of the sea-level changes and closely related (e.g. more slender form = deep sea; less slender form = shallower sea).

The relationship between low and high energy conditions and the variable whorl width of the *Sowerbyceras* (e.g. greater depth = lower Wb/D), is here interpreted as being related to the influence of slight bottom currents on the submarine plateau. This is because the more slender and smaller *Sowerbyceras* are found in nodular-marly facies which are deposited in deep waters. Therefore the deduction of "slender living chamber = deep-sea form" seems reasonable. On the other hand, those forms with broad and large living chambers offered a good deal of resistance to the waterbottom currents on the submarine plateau. These *Sowerbyceras* moved slowly, as they fed predominantly near the bottom, and were obliged to maintain their position relative to the bottom. They are frequently found in sediments of relatively shallower waters.

This situation is consistent with that described by Batt (1989) from the Cretaceous Seaway of North America, with the difference that Batt observed that laterally compressed forms were dominant in near-shore coarse-grained settings, whereas in the epioceanic plateau it is the contrary. Repeated cycles of evolution from smaller to larger more compressed forms are also reported from lineages in the Jurassic of the German Basin during periods of shallow water (Bayer and McGhee, 1984). This fact, involving the way of life of *Sowerbyceras*, is exactly the same also for the diameters of the specimens and numerical counts for the same reason: *Sowerbyceras* (and other ammonoids) descended to the bottom to forage or were otherwise closely associated with the benthic environment. Ammonoids that lived near, and depended on, benthic resources would have had to maintain their positions relative to the bottom. Ammonoids were neutrally buoyant; consequently, remaining stationary in a current required active swimming. Jacobs (1992) demonstrated that remaining stationary would have been extremely difficult for small adult and juvenile ammonoids. At 2.5 cm in diameter, none of the ammonoid shapes could have sustained speeds of more than 15 cm/s. Even maintaining swimming speeds of 10 cm/s would have been very taxing.

The maximum sustainable swimming velocity (MSV) increases dramatically with size. Jacobs (1992) calculated that, at 1 cm in length, slender forms had a MSV of 7 to 8 cm/s; less slender forms had a MSV of 10 cm/s. At 100 cm in length, slender forms had a MSV of 55-58 cm/s; less slender forms 41 to 46 cm/s. The *Sowerbyceras* analyzed have diameters ranging from 4 to 9 cm (in theUhlandi Subzone from 4 to 6 cm): at 4 cm in diameter, slender forms had a MSV of 28 cm/s, less slender forms = 40 cm/s; at 6cm in diameter, slender forms had a MSV of 42 cm/s, less slender forms = 60 cm/s.

Jacobs (1992) remarked that the slender forms of ammonites had descending coefficients of drag Cd (power consumption associated with constant swimming). Ornamented forms and inflated forms had higher Cd. Then the power consumption associated with constant swimming is significantly related to thickness ratio (t.r.). The results cited by Jacobs (1992) indicate that for planispiral ammonoids there is a strong relationship between the Cd and the t.r. Slender forms have declining Cd with increasing Re (swimming ammonoid velocity coefficient); less slender forms do not.

Reduction in whorl width (lower t.r.Wb/D) contributes directly to the hydrodynamic efficiency of the shell. Slender forms with a t.r. of 0.3 - 0.4 (i.e. the Wb/D range of *Sowerbyceras* during transgressive pulses) will have the lowest power required in very slight or absent bottom current conditions. Then the smaller sized *Sowerbyceras* of the transgressive phases are more slender and with smaller Wb than the L.S.T. one, because they have greater swimming advantages. Regarding the swimming velocity then, in nil or slight bottom current conditions, smaller, more slender forms with involute whorls, require substantially less power than larger, broad forms, but these last forms may become advantageous in stronger bottom current conditions. Jacobs (1992) suggested that larger, less slender forms would have been able to sustain higher bottom current speeds for longer periods of time. Consequently, larger more inflated and broader forms should have been preferred in high-energy environments where an ability to remaining stationary in a bottom current was critical. Smaller ammonoids could not have overcome even moderate current velocities and may have been restricted to low-energy conditions (Jacobs 1992).

The precise optimum depends greatly on the particular range of swimming and feeding behaviours that are selectively important to the specific ammonoid. In *Sowerbyceras* the large-sized and less slender shell is favoured during times of low sea-level because it more easily remainins stationary in the bottom currents.

Also in the Wb/D curves indices of dimorphic character, within the "males" and "females" with more (male ?) or less (female ?) breadth of venter, it is observed that increased whorl width corresponds to regressive phases of the sea and reduction in whorl width corresponds to transgressive phases. Furthermore, the same pattern occurs with Largiventer dimorphs with greater venter width, and Largiventer dimorphs with more slight venter width; and the same thing also within the laeviventer conch dimorphs.

Moreover, in the *Sowerbyceras* of the present study the variation of wH/D throughout time is similar to the variation of D, while increased Uw/D corresponds to decreased wH/D and vice versa. The Wb/D and D curves are similar and follow the trend of the sea-level curve, as well as also for the wH/D curve, clearly because wH changes proportionately to the diameter variation of specimens. On the contrary, as mentioned above, the exact inverse correlation is observed between the wH/D curve and Uw/D curve. This occurrence, that substantially is a more or less shell coiling (more involute during regressive phases and less involute during transgressive phases) also characterizes other ammonoid groups. This is due to two reasons: (1) greater resistence: the more involute conch giving the shell more strength during the turbulent times associated with low sea-level (Guex, 1992); (2) buoyancy decreases with increase in shell involution: the more slender and evolute a shell is, the greater the lift (Kennedy and Cobban, 1976).

The above factors relate to the observation that the more important *Sowerbyceras* variation in the Kimmeridgian is observed in the last third of the Uhlandi Subzone and in the middle part of the Beckeri-Pressulum Zone. This is also why there is correspondence between this fact and the development of Rosso Ammonitico Nodular Marly

Facies. Effectively during maximum transgressive system tract (-TST-) episodes (Uhlandi Subzone and Beckeri-Pressulum Zone) we observe in the first case the evolutionary change from *S. silenum* to *S. loryi*, in the second case from *S. loryi* to *S. pseudosilenum*. The maximum flooding period corresponds to minimum abundance of *Sowerbyceras*, correlated with the last third of the Uhlandi Subzone and the middle part of the Beckeri-Pressulum Zone (and phyletic speciation took place in both cases). This trend is superimposed onto a general trend toward a decrease in frequency of *Sowerbyceras* through time, starting from the Loryi Subzone. The faunal variations however concern all the Ammonoid groups, e.g. at the Herbichi /Acanthicum Zone boundary many species became extinct or gave rise to other species. This fact is clearly due to marine transgressive pulse in the Uhlandi Subzone.

Therefore, the changes in environmental (and general ecological) conditions, promoted change and diversification of the *Sowerbyceras* on the Trento Plateau. A transgressive phase of sea level reduced the number of specimens that in turn led to low intraspecific variability. Under these circumstances mutations spread more rapidly and speciation took place. This is a very important fact for the survival of the species, in fact where, despite a few number of specimens, a wide intraspecific variability is observed (top of Beckeri-Pressulum Zone in the Trento Plateau sections), the genus *Sowerbyceras* became extinct in a short time.

With regard to the number of constrictions on the body chamber of *Sowerbyceras*, it is a character indirectly influenced by sea-level changes, being linked to shell diameter variations in the group. In fact in the Stenonis and Divisum Subzone and in the upper Beckeri-Pressulum Zone it is observed that there are specimens with the larger shell diameters and five constrictions. In the other biozones we observe smaller shell diameters and four constrictions. It should be remarked that, in the populations we do not observe individuals side by side with four and others with five constrictions, but these are rigidly segregated in the different stratigraphic levels. In the population, from smaller to larger specimens, all the members possess the same number of constrictions (then it is a character of the species). Simply, in the subzones where we observe the greatest number of constrictions, the range of intraspecific variability of diameter reaches the greatest diameters of the shells, also with few specimens, and these are the subzones where the diameter intraspecific variability is higher. An exception is represented by the very sparse record of immature shells (2% of the total number of *Sowerbyceras*) that have been recorded in the Herbichi Zone (Stenonis and Divisum Subzone) and that are ornamented by four constrictions because the phyletic change is hypomorphic.

R-selection, K-selection and sea-level changes vs. a conclusion

In this study it is shown that sea-level changes strongly affect the evolution of faunal assemblages in the distal, epioceanic swell of the "Trento Plateau" in exactly the same way as occurs in epicontinental environments. However there is the difference that extinction and phyletic changes occur in transgressive phases instead of in regressive phases and also that maxima and minima of intraspecific variability are the opposite to those known from epicontinental environment.

Sowerbyceras are particularly abundant on the Trento Plateau. The evolution of the morphological parameters of this genus is clearly due to sea events. During a high sea-level (transgressive phases = slight bottom currents) occurs a decrease in frequency of *Sowerbyceras* faunas, a smaller size, a lower t.r. Wb/D, and a more evolute shell. During low sea-level (regressive phases = higher bottom currents) there is an increase in frequency of *Sowerbyceras* faunas, a larger size, a greater t.r. Wb/D, and a more involute shell.

High intraspecific variability of D and lower intraspecific variability of Wb correlate with times of low sea-level (regressive phases). Lower intraspecific variability of D and higher intraspecific variability of Wb correlate with times of high sea-level (trasgressive phases).

With regard to Kimmeridgian *Sowerbyceras*, the initial species *S. silenum*, present at the time of a regressive period, is characterized by many morphological features which bestows on the ammonite very high stability, some manoeuvrability and poor hydrodynamic efficiency. Many other Ammonite inhabitants of the "distal swell" have poor active swimming ability which restricts them to an epibenthic way of life. *Sowerbyceras* gave rise to diversified morphologies during maximum flooding period.

Analysis reveals that the phyletic change from

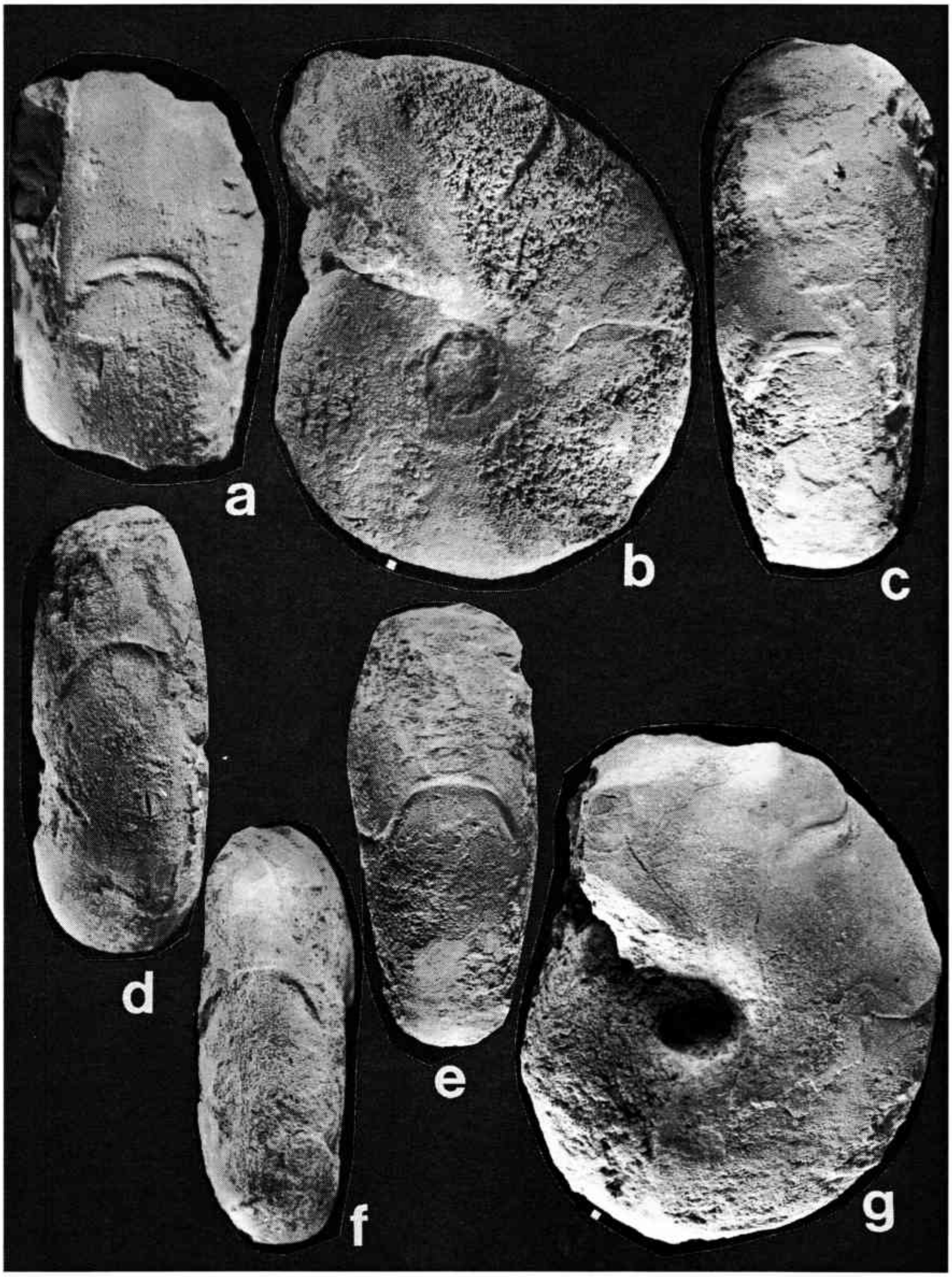

Plate 1. Sowerbyceras of the Trento Plateau, Rosso Ammonitico Veronese Formation. Sowerbyceras silenum. A : JMR2/11, ventral view, Lower Stenonis Subzone, horizon 25 cm. B, C : ME669, lateral and ventral view, Upper Stenonis Subzone, horizon 45 cm. D : MR9, ventral view, Upper Stenonis Subzone, horizon 40 cm. E : ME670, ventral view, Upper Stenonis Subzone, horizon 40 cm. F : V744-54bis, ventral view, Middle Divisum Subzone, horizon 60 cm. G : V742-53, lateral view, Middle Divisum Subzone, horizon 60 cm. x 1. The white point indicates the beginning of the body chamber.

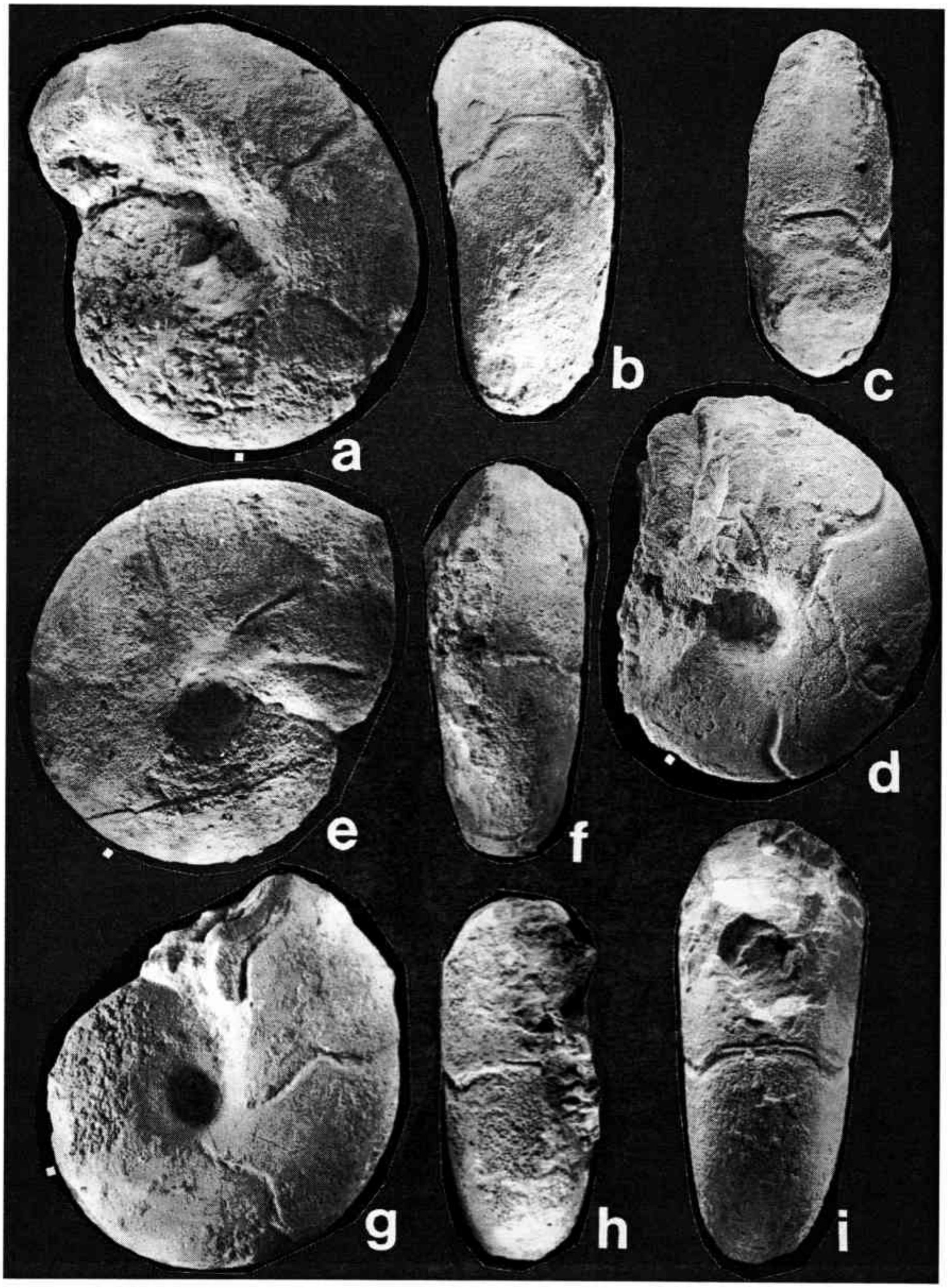

Plate 2. Sowerbyceras of the Trento Plateau, Rosso Ammonitico Veronese Formation. Sowerbyceras silenum trans. loryi. A, B : JMR2/12, lateral and ventral view, topmost Uhlandi Subzone, horizon 100 cm. C, D : 386-2SA37, ventral and lateral view, Uhlandi / Longispinum Subzone boundary, horizon 105 cm. Sowerbyceras loryi. E,F : V191-51, lateral and ventral view, Middle Longispinum Subzone, horizon 120 cm. G,H : MR77, lateral and ventral view, Loryi Subzone, horizon 140 cm. I : ME489, ventral view, topmost Loryi Subzone, horizon 147 cm. x 1. The white point indicates the beginning of the body chamber.

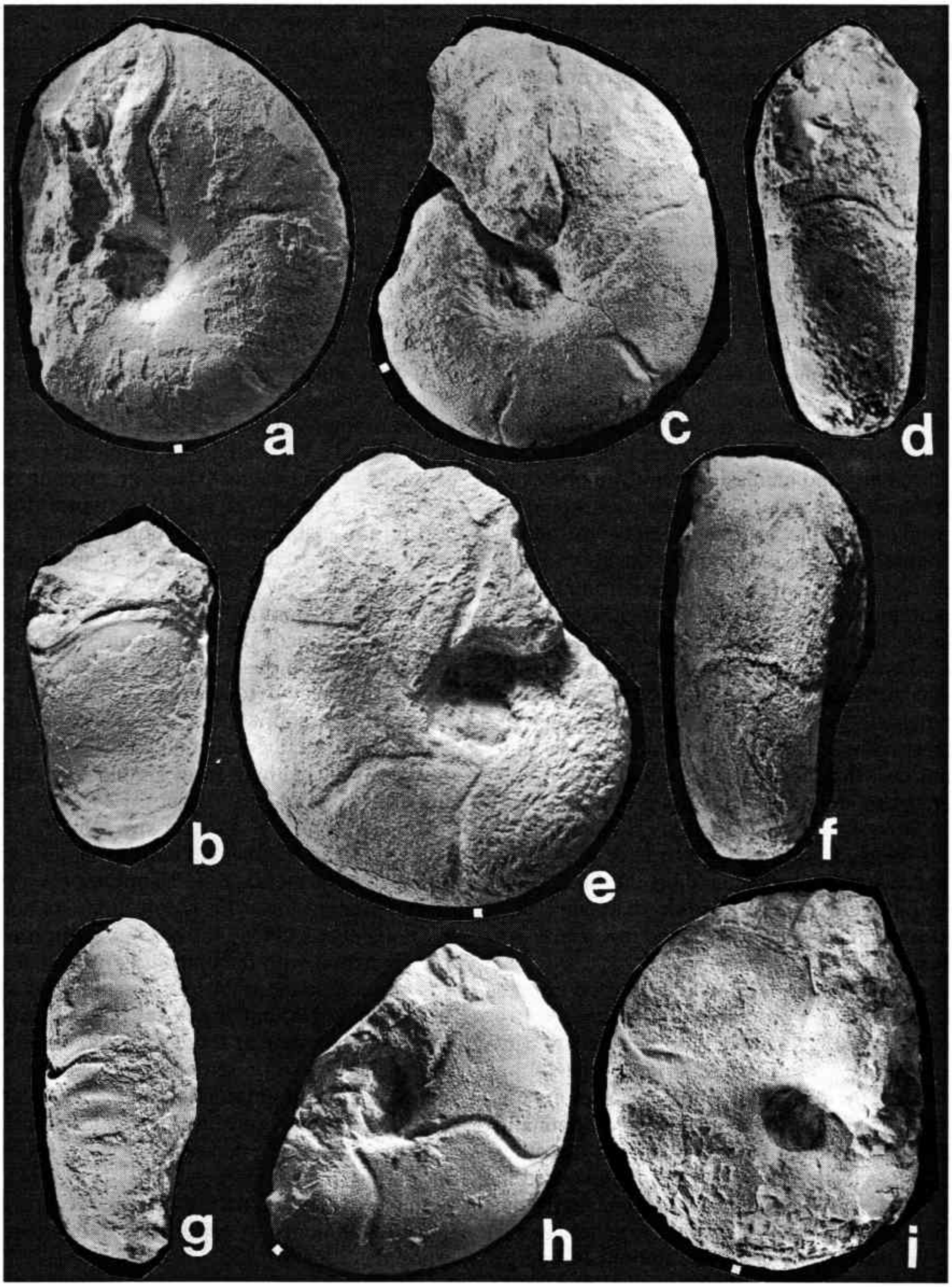

Plate 3. Sowerbyceras of the Trento Plateau, Rosso Ammonitico Veronese Formation. Sowerbyceras loryi. A, B : ME466, lateral and ventral view, lowermost Heimi Subzone, horizon 150 cm. C, D : JBPV/41, lateral and ventral view, lowermost Cavouri Zone, horizon 167 cm. G : JMR2/23, ventral view (note the teratological venter with flares), middle Cavouri Zone, horizon 180 cm. Sowerbyceras pseudosilenum. E,F : JMR1/26, lateral and ventral view. Upper Beckeri-Pressulum Zone, horizon 230 cm. H : LU63, holotype, lateral view, uppermost Beckeri-Pressulum Zone, horizon 255 cm. I : VI46, lateral view, Lower Hybonotum Zone. x 1. The white point indicates the beginning of the body chamber.

S. silenum to *S. loryi* took place by hypomorphosis, while the phyletic change from *S. loryi* to *S. pseudosilenum* is not simply a heterochrony: *S. pseudosilenum* is more like the ancestral form of its ancestor than a juvenile of its immediate ancestor.

Notwithstanding Boletzky (1981) has observed that r-K paradigm is not applicable to modern Coleoids, in the case of ammonoid taxa the concept of r-selection and K-selection can provide an explanation. Hallam (1978) proposed a model based on the r-K dichotomy, in which times of sea level transgressive pulse are characterised by K-selected regimes, and regressive intervals favour r-selected species. Times of relatively low sea-level signify times of restriction and deterioration of neritic habitat, typified by increases in temperature variability and increasing salinity of bodies of extremely shallow water. The r-selection would be favoured in unstable, contrasting and constraining environments, or in course of colonization. Since "r-selected" species tend to be environmentally tolerant and widespread (e.g.Vermeij, 1978), this suggests that periods of regression will exhibit reduced endemism (Jablonski, 1980). In terms of familiar ecological parlance, the increased environmental stress favours r-selected organisms, which is recorded by the small size of new ammonite taxa that have evolved rapidly from their larger, more stenotopic ancestors; hence speciation occurs, as well as extinction (Hallam, 1987). The "r-selected" species tend to have high fertility, precocious maturation, short life time, shortened ontogeny (smaller adult diameter) and large amount of energy devoted to sexual reproduction.

Regression of sea level would then be accompanied by a paring process, with the more stenotopic, localized faunas being eliminated due to environmental deterioration and, perhaps, increased competitive interactions. The more tolerant, widespread taxa would become dominant, resulting in a decline in endemism. On the other hand, a K-selective regime would be favoured in stable and previsible environments where the competition is strong. A K-strategy generally has the following attributes: small amount of energy devoted to sexual reproduction, extended ontogeny, longer life time (larger adult diameter).

K and r strategies are the extreme points of a continuum and therefore have been rarely perfectly realized in natural setting. As a matter of fact, hypomorphosis seem to correspond with an r-selective regime, whereas deceleration (sensu Reilly et al., 1997) correlates with a K-selective regime.

The opposite is seen in the epioceanic environment of the Trento Plateau. Here, the more important changes took place during transgressive phases and not during regressive phases. It is worth of note that during transgressive episodes the Trento Plateau was still more distal, and that, in actualistic ecology, the fact is that the more isolated the environments are, the more these areas are occupied by highly specialised species and only a small number of individuals belonging to species which are the less specialized and the most adaptable.

The example of *Sowerbyceras* shows that these Cephalopods, exposed to an apparently less favourable environments (= lesser number of individuals), reacted with a strategy typical for opportunistic colonisation (hypomorphosis). The result is a size reduction, and it is important that (as also noticed by Mignot, 1993, for the Liassic *Hildoceras*), hypomorphosis involves an active not passive reaction of these ammonites to the ecological stress. On the other hand, the stress is not necessarily related to decrease of feeding rate. Taking into account the scarce density of population, the trophic production could be sufficient, the constraint coming from simple instability of one of its components (Mignot, 1993).

On the contrary, a regressive phase on the Trento Plateau fragmented marine habitats to the extent that an increase of competition was produced, tending toward a K-selection. As noticed by Oloriz et al. (1993a), the oceanic environments, in comparison with the epicontinental ones, have undoubtedly an enormous volume of the ecospace at their disposal, but the distal plateau environment, such as that of the Trento Plateau in the Kimmeridgian, represented restricted environments, for those ammonites that are epibenthic and therefore very sensitive to sea-level changes.

In this picture, the demographical strategies r-K allows us to comprehend the respective advantages of the heterochronic types according to the environments to which the individuals are exposed.

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