

# Ammonoid Abundance Variations Related to Changes in Trophic Conditions Across the Oceanic Anoxic Event 1d (Latest Albian, SE France)

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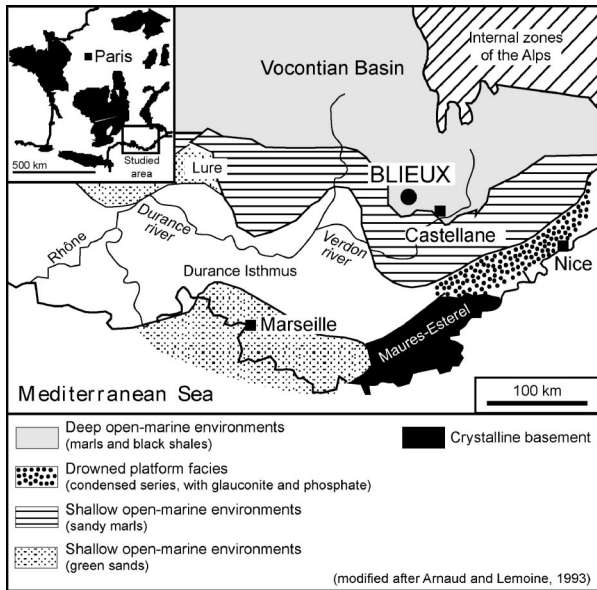
## INTRODUCTION

Macrofauna abundance has been quantified across the Breistroffer interval (OAE 1d, Latest Albian) in the Vocontian basin (southeast France). This interval is characterized by a high abundance of ammonoids showing significant morphologic disparity. Twenty ammonoid genera are recognized and assigned to seven morphostructural groups. The aims of this study are to: (1) interpret abundance variations of ammonoid taxa in terms of taphonomic processes, sedimentary dilution, and paleoenvironmental factors; and (2) discuss the habitat and mode of life of some Late Albian ammonoids with respect to their morphology and abundance variations.

Most variations in ammonoid absolute abundance are not the result of post-mortem shell transport. High abundance within the Breistroffer interval is due partly to a low accumulation rate, which is related to a maximum-flooding stage. The different trends observed among ammonoid taxa can be interpreted partly in terms of response to changes in trophic conditions inferred from the study of calcareous nannofossils. Heteromorphs, which are dominant during mesotrophic conditions, could have been more competitive than involute/evolute planispirals (normal coiling) when paleoenvironmental conditions become more unstable. Lechites (orthocone), the most abundant taxon, probably inhabited epipelagic, distal paleoenvironments. This genus, interpreted as a vertical migrant in the water column, would have been able to move up when trophic conditions were good in surface waters, and down in order to avoid oligotrophic surface waters and to exploit food-rich layers in deeper waters. Turrilitoides and Mariella (torticones) may have been quasiplanktic, and inhabited mainly neritic paleoenvironments. These forms could have occupied more distal paleoenvironments when mesotrophic conditions prevailed in the surface water column. Anisoceras and Hamites (quasiplanktic U-shaped heteromorphs) mainly lived in distal, epipelagic habitats, and could have been more competitive compared with the torticones when oligotrophic conditions prevailed in surface waters. Among involute/evolute planispiral ammonoids, Mortonicerias probably had a deep-nektonic mode of life and inhabited the lower part of the epipelagic zone. A stylized panorama of some Late Albian ammonoid habitats is proposed.

Neumayr (1883), Uhlig (1911), and, more recently, Scott (1940), Ziegler (1967, 1981), Kennedy and Cobban (1976), and Westermann (1990, 1996) have emphasized the relationships between ammonoids and ecological factors such as bathymetry, temperature, and food. Dynamics of the biogeography of ammonoids and changes in their shell morphology and assemblages generally are related to sea-level and paleoclimatic fluctuations (Enay, 1980; Enay and Mangold, 1982; Marchand and Thierry, 1986, 1997; Lominadze and Sakharov, 1988; Wiedmann, 1988; Cecca, 1992; Bulot, 1993; Rawson, 1993; Hantzpergue, 1995; Reboulet and Atrops, 1995; Reboulet, 1996; Enay and Carou, 1997; Pucéat et al., 2003). Only a few authors have discussed changes in ammonoid assemblages, such as adult-size variations and evolutionary events (appearance of heteromorphic ammonoids, radiation), as resulting from trophic opportunities (Elmi and Alméras, 1984; Reboulet, 1996, 1998, 2001; Reboulet and Atrops, 1997; Cecca, 1997, 1998; Lehmann, 2000; Guex, 2001). However, these works are not well constrained by detailed data on trophic conditions, and could appear speculative (for instance, see Lehmann, 2000). More recently, a quantitative and integrated approach including high-resolution analysis of macrofauna, nannofossils, microfacies, trace fossils, and total organic carbon allowed Reboulet et al. (2000, 2003) to interpret, in part, the absolute abundance variations of some Early Valanginian ammonoids as an important response to trophic resources. However, in that study, the ammonoid assemblages consisted of only six ammonoid families representing just two morphostructural groups (involute/evolute planispiral ammonoids and orthocones).

The aims of the present work are to quantify the absolute abundances of ammonoids, and to interpret variations and changes in assemblages with respect to the paleoenvironmental context, particularly in terms of trophic conditions in the oceanic waters. Considerations of ammonoid abundances generally are based on percentages (Marchand, 1984, 1992; Company, 1987; Reboulet et al., 1992; Cecca et al., 1993; Reboulet, 1996; Reboulet and Atrops, 1997; Cecca, 1998) and the study of absolute abundance variations is a poorly understood aspect of ammonoid paleoecology (Reboulet et al., 2000, 2003). In the present work, results and their interpretation are based on the study of Late Albian ammonoids and benthic macrofauna. Ammonoid assemblages of this stratigraphic inter-



**FIGURE 1**—Location of the Blieux section (Alpes de Haute-Provence) and paleogeographic map of the Vocontian Basin (southeast France; Lower Cretaceous).

val are characterized by high diversity, and numerous genera have been identified (Gale et al., 1996; Wright et al., 1996). Morphologic disparity also is large—from involute/evolute planispirals (normal coiling) to U-shaped heteromorphs. This wide range of ammonoid morphology may indicate distinct modes of life (swimming, buoyancy, trophic habits; Westermann, 1996; Cecca, 1997; Klug, 2001).

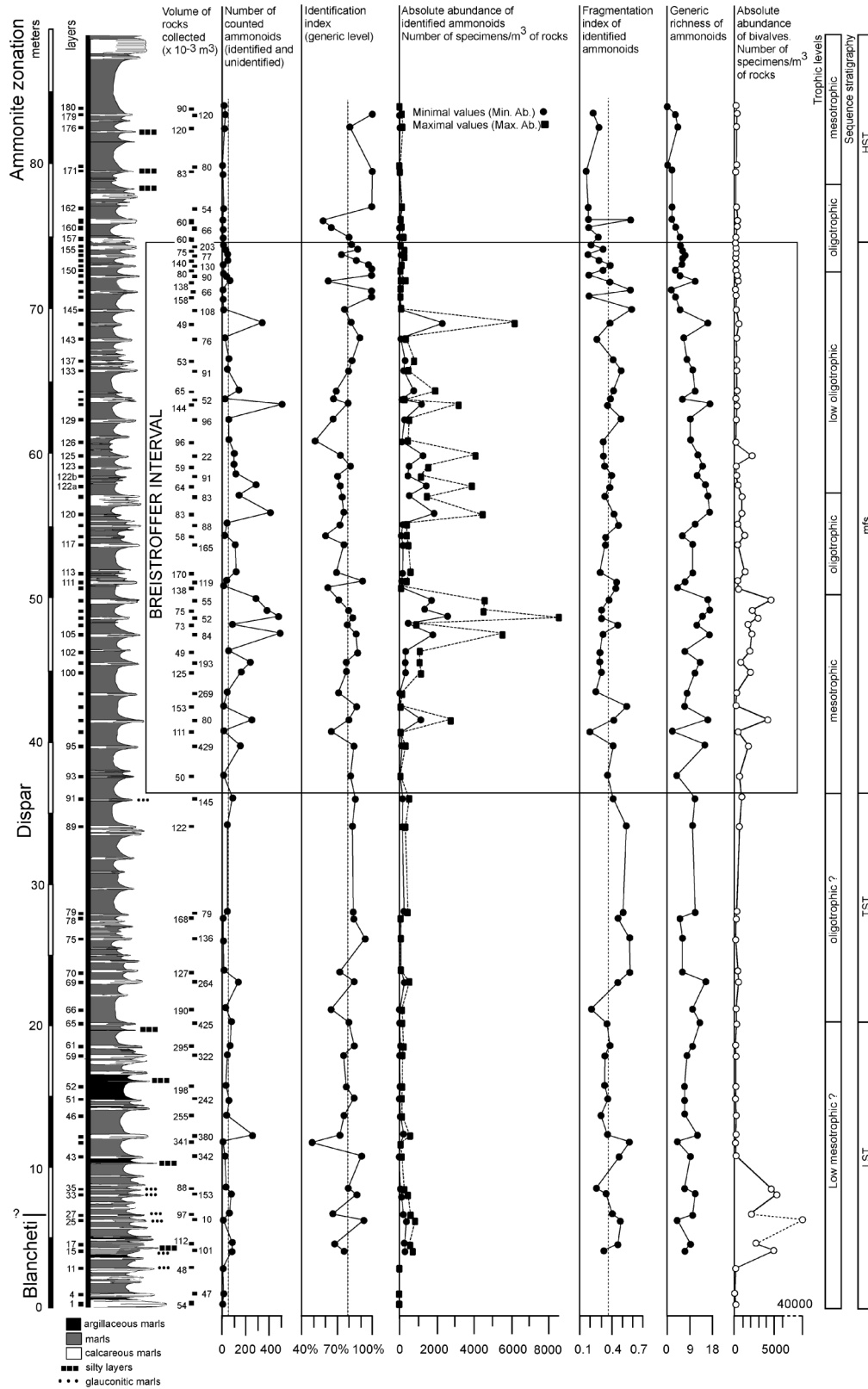
The Blieux section (Alpes de Haute-Provence; Fig. 1), located in the southern margin of the Vocontian basin (southeast France), is in a key position to record paleoenvironmental changes between proximal areas (platform environments) and the pelagic realm (open-marine water column). As described by Cotillon (1971), Blieux is one of the rare outcrops where ammonoids are abundant. Benthic macrofauna are also well represented and bivalves sometimes are abundant (Bréhéret, 1997). The Latest Albian sediments deposited in the Vocontian basin record the Oceanic Anoxic Event (OAE) 1d, named the Breistroffer interval by Bréhéret (1988). The paleoenvironmental conditions prevailing during deposition of this event (in particular, changes in surface-water fertility as well as in oxygenation in the water column and on the sea floor) have been established in the Blieux section by Giraud et al. (2003). They have shown that the OAE 1d is not recognized as a major anoxic event in the Vocontian basin. The Breistroffer deposits do not record an eutrophication of the marine surface waters associated with expansion of the oxygen minimum zone, but record changes from mesotrophic to more oligotrophic conditions in surface waters. The oxygenation conditions in the water column were always good, as demonstrated by the abundant ammonoids and benthic macrofauna. The enrichment in organic carbon is weak and mainly due to good preservation under dysoxic conditions within the sediment. In the present study, the dependence of ammonoids is discussed in relation to trophic conditions, partly based on the comparison between

macrofauna and calcareous nannofossils. This contribution was introduced during the 6<sup>th</sup> International Cretaceous Symposium (Vienna) (Reboulet et al., 2000).

#### GEOLOGICAL SETTING: THE BLIEUX SECTION

The Vocontian basin is a hemipelagic intrashelf basin of the European Tethyan passive margin. During the Albian, uplift of all the basin margins was responsible for emergence of the Durance Isthmus, to the south, on the Provence platform (Fig. 1). Consequently, strong differential subsidence occurred between shelf and basin, and increasing exposure of the hinterland enhanced terrigenous sediment supply to the Vocontian basin. The carbonate shelves surrounding the Vocontian basin are characterized by low accumulation rate, and carbonate production by benthic organisms decreased as a siliciclastic regime commenced (Ferry and Rubino, 1989). Sections generally are characterized by phosphatized and glauconitic sands, as well as sedimentary gaps (Latil, 1996). In the Gard, Vercors, and Alpes-Maritimes areas, ammonoid assemblages of the zone of *Stoliczkaia* (*Stoliczkaia*) *dispar* (Appendix 1) mainly occur in condensed levels (Breistroffer, 1936, 1940; Scholz, 1973; Latil, 1996). This period of severe platform crisis is recognized on different platforms in Tethys such as Switzerland (Renz, 1968; Delamette, 1988), Italy (Graziano, 2000), and Hungary (Scholz, 1979), as well as in the Pacific and the Atlantic Oceans (Grötsch et al., 1993), and indicates a sea-level rise of even higher amplitude in the Late Albian *Rotalipora appenninica* Zone. Following this rise, black-shale deposits are recorded in the Vocontian basin (Breistroffer interval), the Atlantic Ocean, and Canada (Grötsch et al., 1993). The Aptian–Albian interval of the Vocontian basin is characterized by a thick marly sequence of the Marnes Bleues Formation, consisting of about 800 meters of homogeneous grayish dark-blue marls and shales. Nine laminated horizons containing 1–2% TOC (Total Organic Carbon) have been identified in the 30-meter-thick latest Albian Breistroffer interval of the Vocontian basin (Bréhéret, 1988). Because of its relatively proximal position, the Blieux section does not preserve the typical laminated black-shale horizons observed in the central part of the Vocontian basin (Bréhéret, 1997).

The 88-meter-thick Blieux section (Fig. 2) belongs to a continuous succession of nearly 500 meters of sediments consisting of late Albian bioturbated marls, below the Breistroffer interval, to mid-Cenomanian limestone-marl alternations (Bréhéret, 1997). The lower part of the studied succession is comprised of 20 meters of alternating silty calcareous beds and marls. Upward, the succession becomes more marly, and is capped by a silty layer in which glauconite grains are abundant (layer 91; Fig. 2). This glauconitic bed, which can be correlated at a regional scale (Bréhéret, 1997) and marks the beginning of the Breistroffer interval, consists of 38 meters of dark argillaceous marls interrupted by thin, centimeter-scale gray marls. The Breistroffer interval is capped by silty marls intercalated with coarser, sandy layers. The biostratigraphic subdivisions are based on the occurrence of various species of *Stoliczkaia* (Hoedemaeker and Bulot, 1990; Latil, 1996). The zone of *Stoliczkaia* (*Stoliczkaia*) *dispar* of the Mediterranean Region is divided into a lower subzone



**FIGURE 2**—Argillaceous marls and marls succession of the Blieux section, location of the Breistroffer interval; ammonite biostratigraphy and trophic conditions from Giraud et al. (2003); sequence stratigraphy from Bréhéret (1997); LST, Lowstand System Tract; TST, Transgressive System Tract; mfs, maximum flooding stage; HST, Highstand System Tract. The position of the 81 macrofauna sampling stations (layers 1–180) and the volume of rock collected are plotted against lithology. Number of counted ammonoids, identification, fragmentation indices of ammonoids, generic richness, and absolute abundances per volume of rocks (m<sup>3</sup>) of identified ammonoids (minimal and maximal values) and bivalves (minimal values, dashed lines indicate break in scale) are shown. The weathering profile of the argillaceous marls and marls has been enhanced to better see sampling layers.



of *Stoliczkaia (Faraudiella) blancheti* (Breistroffer, 1965) and an upper subzone of *Stoliczkaia (Stoliczkaia) dispar* (Owen, 1975). This biostratigraphic scale has been used by the different Lower Cretaceous cephalopod teams since Hoedemaeker and Bulot (1990; Hoedemaeker and Reboulet, 2003). The Upper Albian ammonoid assemblage of the Blieux section allows recognition of the Dispar Zone and Subzone (Fig. 2). Cotillon (1971) recognized three important planktonic foraminiferal events in the Blieux succession: (1) occurrence of *Rotalipora appenninica* in the upper part of the alternating silty calcareous beds and marls succession; (2) occurrence of *Planomalina buxtorfi* at the base of the marly part below the Breistroffer interval; and (3) its absence above layer 132 in the upper part of the Breistroffer interval.

## MATERIAL AND METHODS

### Ammonoid And Bivalve Assemblages

The selected interval of the Blieux section was studied in detail for its content of pelagic and benthic macrofauna. The systematic revision of ammonoids (Proux, 2001) was based mainly on the works of Spath (1923–1944), Renz (1968), Scholz (1979), and Gale et al. (1996). The ammonoid assemblage consists of twenty genera grouped into twelve families, using the supra-specific classification proposed in the *Treatise on Invertebrate Paleontology* (Wright et al., 1996; Appendix 1). No ammonoid faunal turnover or phyletic appearance or disappearance of taxa occurs in the interval studied (Gale et al., 1996; Proux, 2001). Because fossils from the Blieux section are very abundant, intraspecific variability was recognized for *Desmoceras (Desmoceras) latidorsatum*, *Puzosia (Puzosia) mayoriana* (Fig. 3A), *Discohoplites coelonotus*, *Cantabrigites cantabrigense*, *Mortonicerus (Durnovarites) perinflatum* (Fig. 3I), *Mariella (Mariella) bergeri*, and *Scaphites (Scaphites) hugardianus* (Fig. 3J) (Scholz, 1979; Cooper, 1990; Gale et al., 1996; Proux, 2001). Dimorphic pairing was established for *Stoliczkaia (Stoliczkaia) dispar* (Fig. 3F), *Hamites duplicatus* (Fig. 3C; this species is not included in the new genus *Helicohamites* (Monks, 2002) because it lacks a helical spire), *Hemiptychoceras subgaultinum* (Fig. 3H), *Anisoceras armatum* (Fig. 3K), *Lechites (Lechites) gaudini* (Fig. 3L), *Turrilitoides hugardianus* (Fig. 3B), and *Worthoceras pygmaeum* (Fig. 3E) (Scholz, 1979; Gale et al., 1996; Proux, 2001). All genera probably are monospecific in the interval studied. They correspond to well-characterized morphologic units (Fig. 3).

The Albian ammonoids of the Blieux section are assigned to seven morphologic units using the terminology proposed in the glossary of *Ammonoid Paleobiology* (Landman et al., 1996): involute/evolute planispirals (normal coiling), including *Mortonicerus* (Fig. 3I), *Cantabrigites*, *Stoliczkaia* (Fig. 3F), *Discohoplites*, *Callihoplites*, *Desmoceras*, *Puzosia* (Fig. 3A), *Kossmatella* (Fig. 3G), *Tetragonites*, *Anagaudryceras*, *Zelandites*, and *Hypophylloceras* (Fig. 3D); orthocones (*Lechites*, Fig. 3L); torticoones with *Turrilitoides* (Fig. 3B) and *Mariella*; scaphiticoones with *Scaphites* (Fig. 3J) and *Worthoceras* (Fig. 3E); ancylocones (*Anisoceras*, Fig. 3K); and hamiticoones with two distinct morphotypes (*Hamites*, Fig. 3C and *Hemiptychoceras*, Fig. 3H). Because some families are composed of many genera

with different morphologies (for instance, Hamitidae, Fig. 3), the abundance variations are presented here at a generic level, which simplifies the identification of specimens and avoids problems related to systematics. Cecca (1998) also emphasized that it would be preferable to work at the generic level for paleoecological studies. Aptychi and rhyncholites are absent.

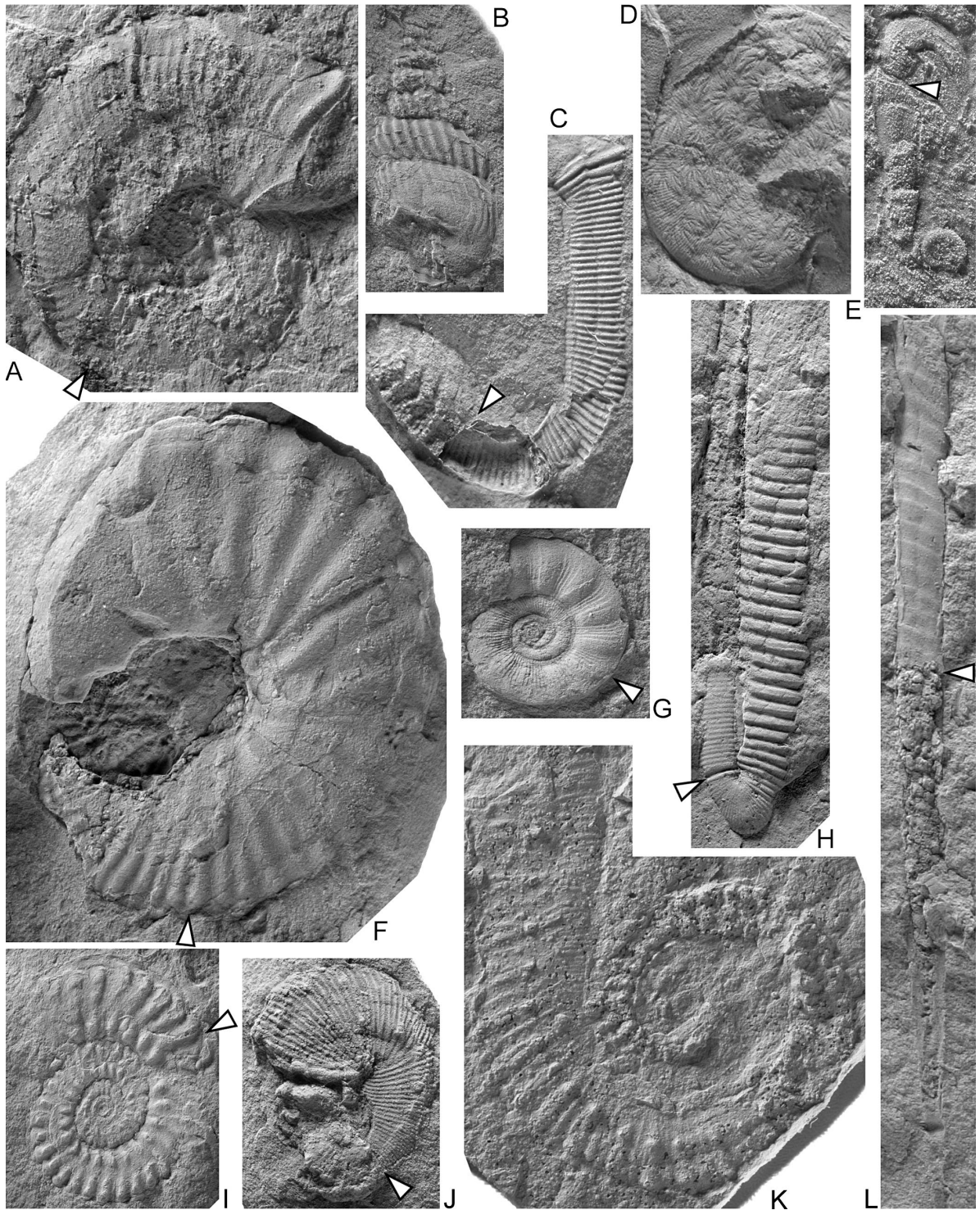
Bivalves (aucellines and inoceramids) represent 92% of the benthic macrofauna. Belemnites, gastropods, and echinoderms are rare to absent, so these three groups are not considered in the quantitative study, which is based on more than 20,000 specimens, including 8500 ammonoids. Dissolution of shells is the normal condition, and specimens are preserved as internal, generally calcareous molds. Pyritic specimens of ammonoids are observed only in a few layers, mainly in the upper part of the section.

### Quantification Of Macrofauna Abundances

Macrofaunal quantification was carried out in 81 successive sampling stations covering layers 1 to 180, including the organic carbon-rich layers (Fig. 2). Outcrop and sampling conditions were constant along the same vertical section. The lithology is homogenous (argillaceous marls and marls) and the calcium carbonate content is low (below 57%; Giraud et al., 2003), which makes sampling macrofauna easier. The rocks were broken as small (a few centimeters) and consistently as possible. The volume of analyzed rock varied from 0.010 to 0.429 m<sup>3</sup> (Fig. 2); its thickness component is generally low (~ 10 cm). The method used to quantify absolute abundances of macrofauna, proposed by Reboulet et al. (2000, 2003), allows interpretation of abundance variations with respect to the paleoenvironmental context, particularly in terms of accumulation rate and trophic conditions in the surface waters. The macrofaunal quantification takes into account the fragmentary state of the fossils. The quantity of specimens was standardized to 1 m<sup>3</sup> of sediment. Both entire individuals and fragments of macrofauna were counted using two approaches: (1) entire shells or fragments of shells were considered as one distinct specimen; and (2) entire shells were counted as one specimen while fragments were counted as a part of a specimen. Namely, a half, a quarter, a fifth of one shell were considered as 1/2, 1/4, and 1/5 of a specimen, respectively; very small fragments of the shell were counted as 1/6 of one specimen. This way, two different abundance values were obtained: (1) maximal abundance value (Max. Ab.); and (2) minimal abundance value (Min. Ab.; Fig. 2). Data based on minimal abundance values have the advantage of taking into account the fragmentary state of the fossils and minimizing the effects of variable fragmentation in the different layers. So, except for the absolute abundance of identified ammonoids (Fig. 2), only the curves of minimal absolute abundance of macrofauna are presented here, and the relative abundance (percentage) of each ammonoid taxon was calculated based on minimal values (Min. Ab.).

A fragmentation index (FI = Min. Ab./Max. Ab.; Fig. 2) was calculated for all groups of macrofauna, which enables estimation of preservation potential for different taxa. This index varies between 1/6 and 1. A value of 1 means the material is not fragmented; whereas an index of 1/6 means all the specimens are significantly fragment-





**FIGURE 3**—Photos of some Late Albian ammonoids. All specimens come from the Blieux section (Alpes de Haute-Provence), *dispar* Zone (layers have been indicated). Collection of Reboulet and Proux (UCB Lyon I, France). Arrows indicate the last preserved suture. (A) *Puzosia* (*P.*) *mayoriana* (Sowerby), x1, layer 144. (B) *Turrilitoides hugardianus* (d'Orbigny), macroconch, x1, layer 98. (C) *Hamites duplicatus* Pictet and Campiche, microconch, x1, layer 109. (D) *Hypophylloceras* (*H.*) sp. ind., x1, layer 105. (E) *Worthoceras pygmaeum* Butjor, x3, layer 97. (F) *Stoliczkaia* (*S.*) *dispar* (Neumayr), macroconch (morphotype *clavigera*), x1, layer 109. (G) *Kossmatella muhlenbecki* (Fallot), x2, layer 107. (H) *Hemiptyloceras subgaultinum* Breistroffer, macroconch, x1, layer 97. (I) *Mortoniceras* (*Durnovarites*) *perinflatum* (Spath), x1, layer 65. (J) *Scaphites* (*S.*) *hugardianus* d'Orbigny, x2, layer 97. (K) *Anisoceras armatum* (Sowerby), microconch (?) x1, layer 144. (L) *Lechites* (*L.*) *gaudini* Pictet and Campiche, microconch, x1, layer 122.



ed. An identification index (= identified specimens/total of identified + unidentified specimens) at the generic level was calculated for ammonoids, enabling interpretation of whether the identified ammonoids (Fig. 2) used for the quantitative analysis for each layer are significant. Correlation indices between distinctive variables (abundances of ammonoids, bivalves, and selected nannofossil taxa) are given. The ammonoid assemblages are characterized by absolute and relative abundance variations, and composition by generic richness. Some genera belonging to the same taxonomic family (*Turrilitoides* and *Mariella*: Turritidae; *Discohoplites* and *Callihoplites*: Hoplitidae) or superfamily (*Zelandites*, *Anagaudryceras* and *Tetragonites*: Tetragonitaceae), and with close morphology, are pooled together in counts because they are not abundant.

## RESULTS

### Comments On Identification—Fragmentation Indices And Generic Richness

The highest number of ammonoids is found within the Breistroffer interval (Fig. 2). The number of counted and identified ammonoids varies from 0 to 519 and from 0 to 461, respectively. At the generic level, the identification index (II) varies between 49% and 100% (mean = 79%). So, because less than 21% of the ammonoids were not identified, the identified ammonoids of each successive assemblage constitute significant samples. The mean value of the identification index (II) is higher (90%) when the family level is considered. Such results also are observed in the Valanginian (Reboulet et al., 2003).

The fossils rarely are totally fragmented—ammonoids often are complete (phragmocone and one-half whorl of body chamber), with rare mechanical damage except that the apertural end of the body chamber (peristome) frequently is broken or not preserved (Fig. 3). Specimens do not show evidence of breaking related to predation. The mean fragmentation index (FI) of identified ammonoids is 0.382 (Fig. 2). *Turrilitoides*, *Discohoplites*, *Zelandites*, *Callihoplites*, and *Worthoceras* show the best preservation, with a mean fragmentation index from 0.636 to 0.967. In contrast, *Anisoceras*, *Hamites*, *Lechites*, *Hemiptychoceras*, and *Hypophylloceras* are fragmented more ( $0.197 < \text{mean FI} < 0.317$ ). Other genera have an intermediate state of preservation ( $0.408 < \text{mean FI} < 0.558$ ). This variation of the mean Fragmentation Index (from 0.197 to 0.967) justifies using minimal abundances (Min. Ab.). Genera characterized by a low fragmentation index would be overrepresented if maximal abundances (Max. Ab.) were used. Bivalves often are well preserved, with a mean FI index around 0.998.

The generic richness and number of identified ammonoids are well correlated using a logarithmic regression (Fig. 4). The curve indicates that at least 50% of the maximum richness (= 20, total number of genera present anywhere in section) is recorded when more than 50 specimens are identified. However, to reach this mean richness, the number of identified ammonoids can vary from 25 to 100.

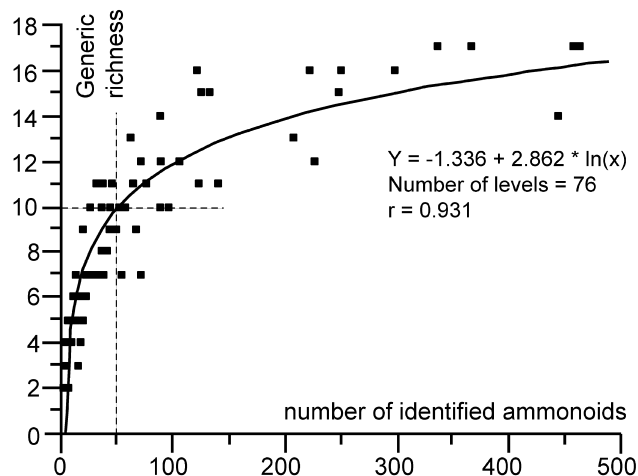


FIGURE 4—Bivariate plot of generic richness versus number of identified ammonoids for the interval 15 to 180 of the Blieux section. Horizontal dashed line indicates 50% of maximum generic richness.

### Comments On Macrofauna Abundances

The two curves of absolute abundance, “Min. Ab.” and “Max. Ab.,” were compared for identified ammonoids (Fig. 2), their different taxa, and for bivalves. There are always good correlations between “Min. Ab.” and “Max. Ab.” values ( $0.818 < r < 1$ ;  $n = 81$ ; significant at  $p = 0.05$  if  $r > 0.22$ ). This is another argument for using the minimal abundance values (Figs. 2, 5).

**Abundance Variations of Heteromorphic Ammonoids:** The absolute abundances of heteromorphic ammonoids generally are high in the lower part of the Breistroffer interval (layers 97, 105, and 107–109; Fig. 5). Among heteromorphs, *Lechites* and *Scaphites* are the most abundant. These genera can reach 1500 and 500 specimens per  $\text{m}^3$ , respectively. Their absolute abundances are correlated strongly with those of heteromorphs ( $r = 0.963$  and  $0.810$ , respectively;  $n = 81$ ; significant at  $p = 0.05$  if  $r > 0.22$ ). Other heteromorphs are less well represented and their absolute abundance never exceeds 280 specimens per  $\text{m}^3$  (Fig. 5). *Worthoceras*, *Anisoceras*, and *Hamites* show their highest abundances in layer 144. *Hemiptychoceras* presents small successive peaks in the Breistroffer interval. *Mariella* and *Turrilitoides* are present just below and in the lower part of the Breistroffer interval (Fig. 5). Only *Mariella* is present at the top of the section (layers 176 and 179).

Heteromorphs are dominant at the base (layers 45–66) and top (layers 162–180) of the Blieux section and in the lower part of the Breistroffer interval (layers 91–109; Fig. 6). They represent 50–90% of the ammonoid assemblages. Low percentages (~25%) are recorded mainly below the Breistroffer interval (layers 69–89) and in its middle part (layers 110–129). Heteromorphic and involute/evolute planispiral ammonoids are represented equally in the upper part of the Breistroffer interval (layers 130–157). *Lechites* are dominant mainly in the Breistroffer interval, where they can reach 70% of the ammonoid assemblages (layer 102). The highest relative abundances (40%) of *Scaphites* are recorded near the base of the Blieux section (Fig. 6). When *Turrilitoides* and *Mariella* are present, they

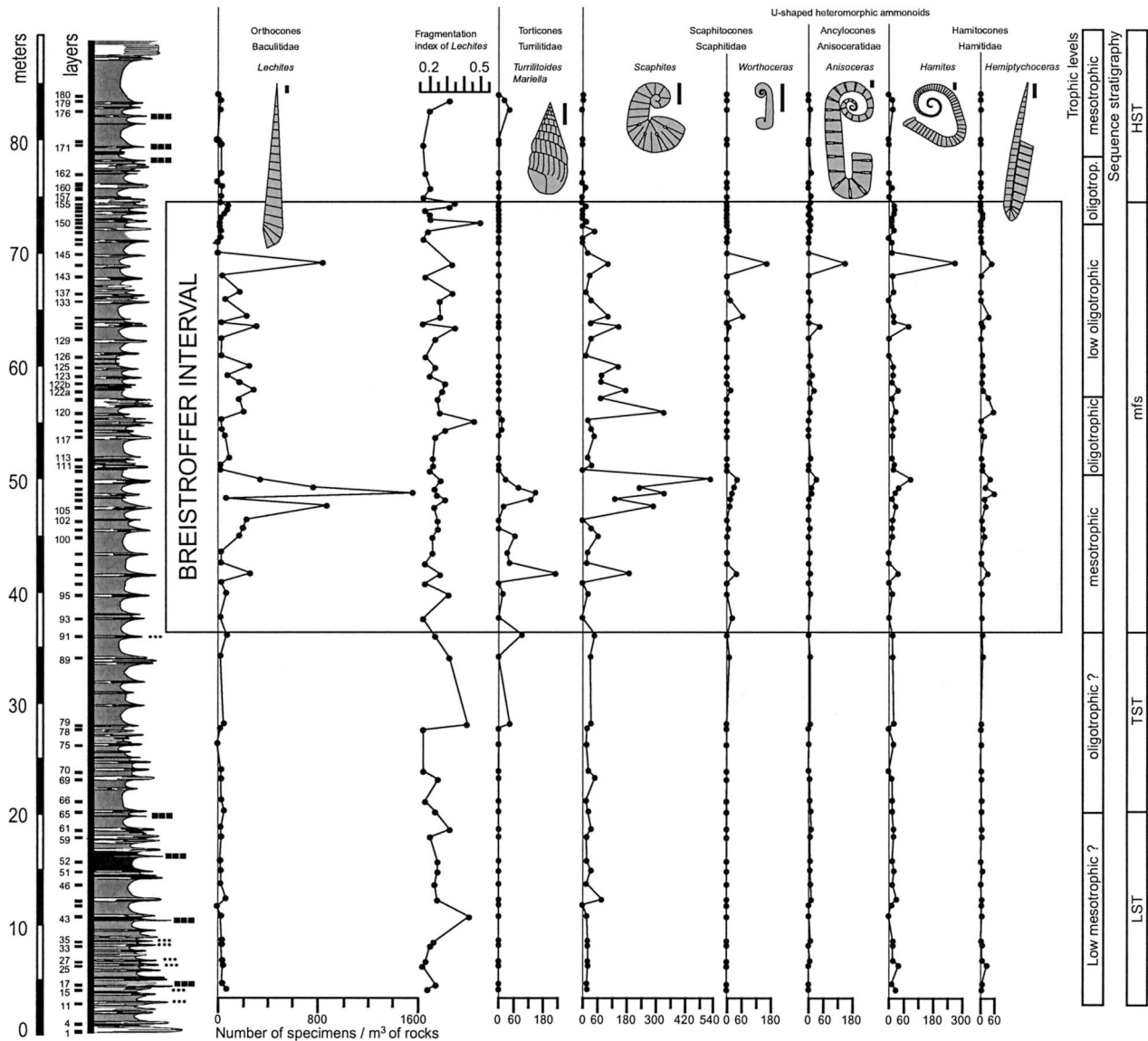


FIGURE 5—Layers 15 to 180 of the Blieux section: minimal absolute abundance and fragmentation index of *Lechites* (orthocone); minimal absolute abundances of other heteromorphs per volume of rock ( $\text{m}^3$ ). Bar scale beside ammonoid drawings = 1 cm. See Figure 2 for lithologies.

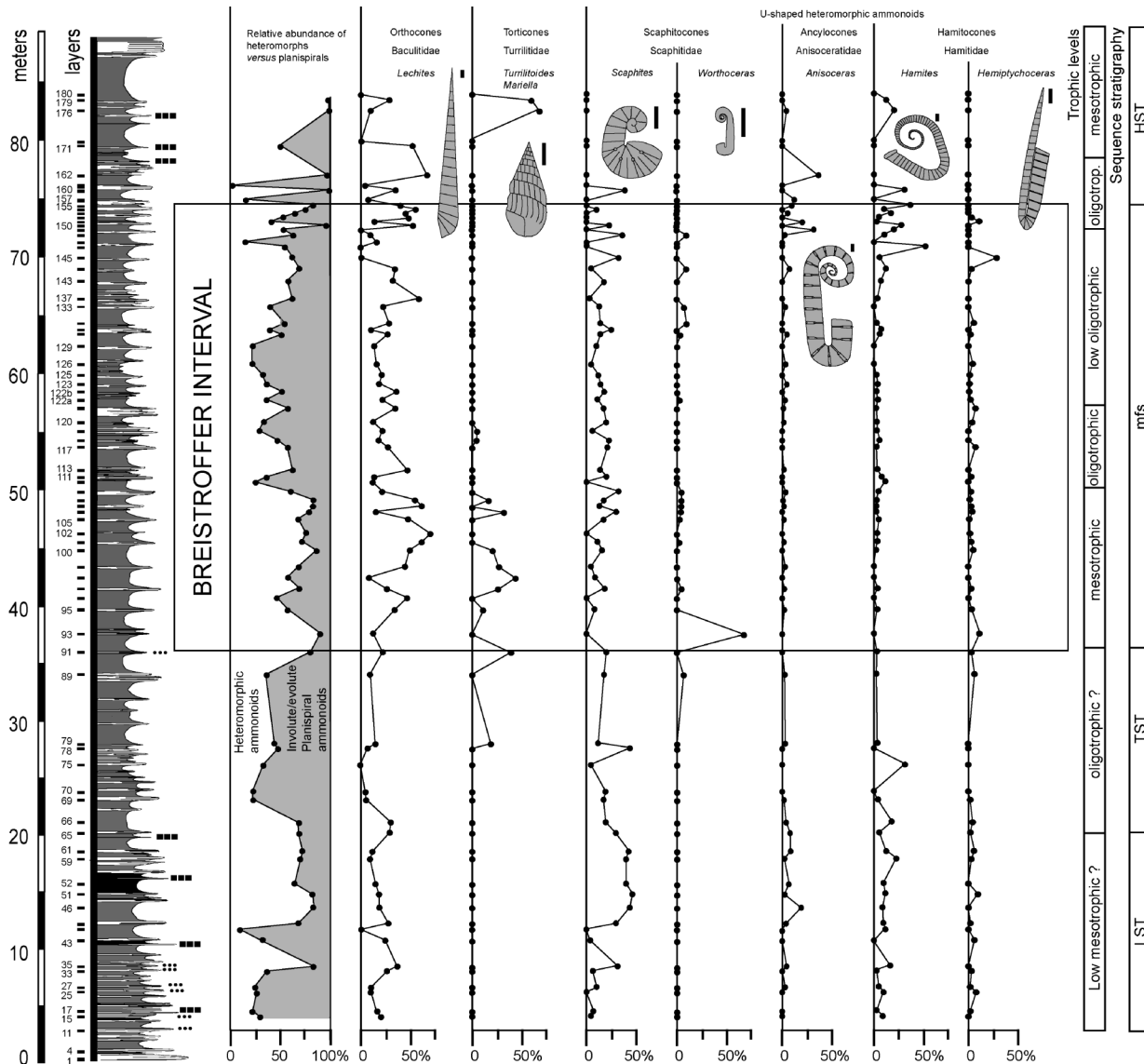
represent ~10–30% of the ammonoid assemblages. *Hamites* is the dominant genus (nearly 55% in layer 146) in the top of the Breistroffer interval. The relative abundances of *Anisoceras*, *Hemiptychoceras*, and *Worthoceras* generally do not exceed 15% of the ammonoid assemblages (Fig. 6).

**Abundance Variations of Involute/Evolute Planispiral Ammonoids:** Involute/evolute planispirals are well represented in the upper part of the Breistroffer interval (layers 120–144; Fig. 7) where they have their greatest abundance, except for *Kossmatella*, which has an important peak at the base of the section (layer 25). The variations in involute/evolute planispirals mainly are related to those of *Mortoniceras* ( $r = 0.883$ ;  $n = 81$ ), *Kossmatella* ( $r = 0.708$ ;  $n = 81$ ), and *Puzosia* ( $r = 0.694$ ;  $n = 81$ ). Other involute/evolute planispirals, such as *Stoliczkaia*, *Desmoceras*, and *Cantabrigites*, are less well represented and their absolute abundances never exceed 120 specimens per  $\text{m}^3$ . *Tetragonites*, *Anagaudryceras*, *Zelandites*, *Hypophylloceras*, *Callih-*

*oplites*, and *Discohoplites* often are represented by a low number of specimens (Fig. 7). The correlations between absolute abundances of different ammonoid taxa generally are low, except between *Hamites* and *Anisoceras* ( $r = 0.965$ ;  $n = 81$ ).

Among involute/evolute planispirals, *Mortoniceras* and *Puzosia* are dominant (Fig. 8). They frequently represent 20–30% of the ammonoid assemblages. The base of the Blieux section (0–10 m) is characterized by the dominance of *Kossmatella* (near 80%). The percentages of other genera are generally lower than 10 to 15% of the assemblages (Fig. 8).

**Abundance Variations of Bivalves:** Bivalves are very abundant at the base of the Blieux section where more than 40,000 specimens per  $\text{m}^3$  were estimated (layer 25, Fig. 2). Aucellines are dominant and constitute thin layers (1–3 cm thick; *Aucellina* beds), or are concentrated on bedding surfaces of glauconitic layers. Aucellines also are well



**FIGURE 6**—Layers 15 to 180 of the Blieux section: relative abundance of heteromorphs versus involute/evolute planispirals and relative abundances of heteromorphs. See Figure 2 for lithologies.

represented in the lower part of the Breistroffer interval (layers 95–109). Inoceramids are less abundant, except in layer 125 (2100 specimens/m<sup>3</sup>). Bivalves are rare or absent at the top of the section. Their absolute abundances do not correlate well with those of the different ammonoid taxa. A significant positive correlation ( $p = 0.05$ ) was found only between the absolute abundances of bivalves and *Kossmatella* ( $r = 0.63$ ;  $n = 81$ ).

## INTERPRETATION OF RESULTS AND DISCUSSION

### Taphonomy

Most of the variations in ammonoid abundance in the Blieux section are unlikely to be linked with taphonomic processes, such as significant post-mortem transport of the shells, re-sedimentation, or diagenetic effects.

*Post-mortem Transport:* Recent *Nautilus* provides a ref-

erence for understanding the post-mortem transport of ammonoid shells (Kennedy and Cobban, 1976; Chamberlain et al., 1981; Olóriz et al., 1996; Chirat, 2000; Reboulet et al., 2003). The ascent of the shell, which is due to a rapid gain in buoyancy following separation of the body, depends on several factors: (1) depth of the animal at the instant of death; (2) initial buoyancy of the empty shell; (3) size, weight, and morphology of the shell; and (4) rate of sea-water influx into the chambers of the phragmocone (Chamberlain et al., 1981). For these authors, the last factor appears to dominate. The post-mortem filling rate of phragmocone is a function of: (1) the permeability coefficient, surface area, and thickness of the siphuncular tube (connecting ring) through which water can enter into the chamber; (2) the length of siphuncular tissue removed when the body falls out of the shell after death of the animal (allowing flooding of the siphuncle and the first chambers of the phragmocone); and (3) hydrostatic pressure



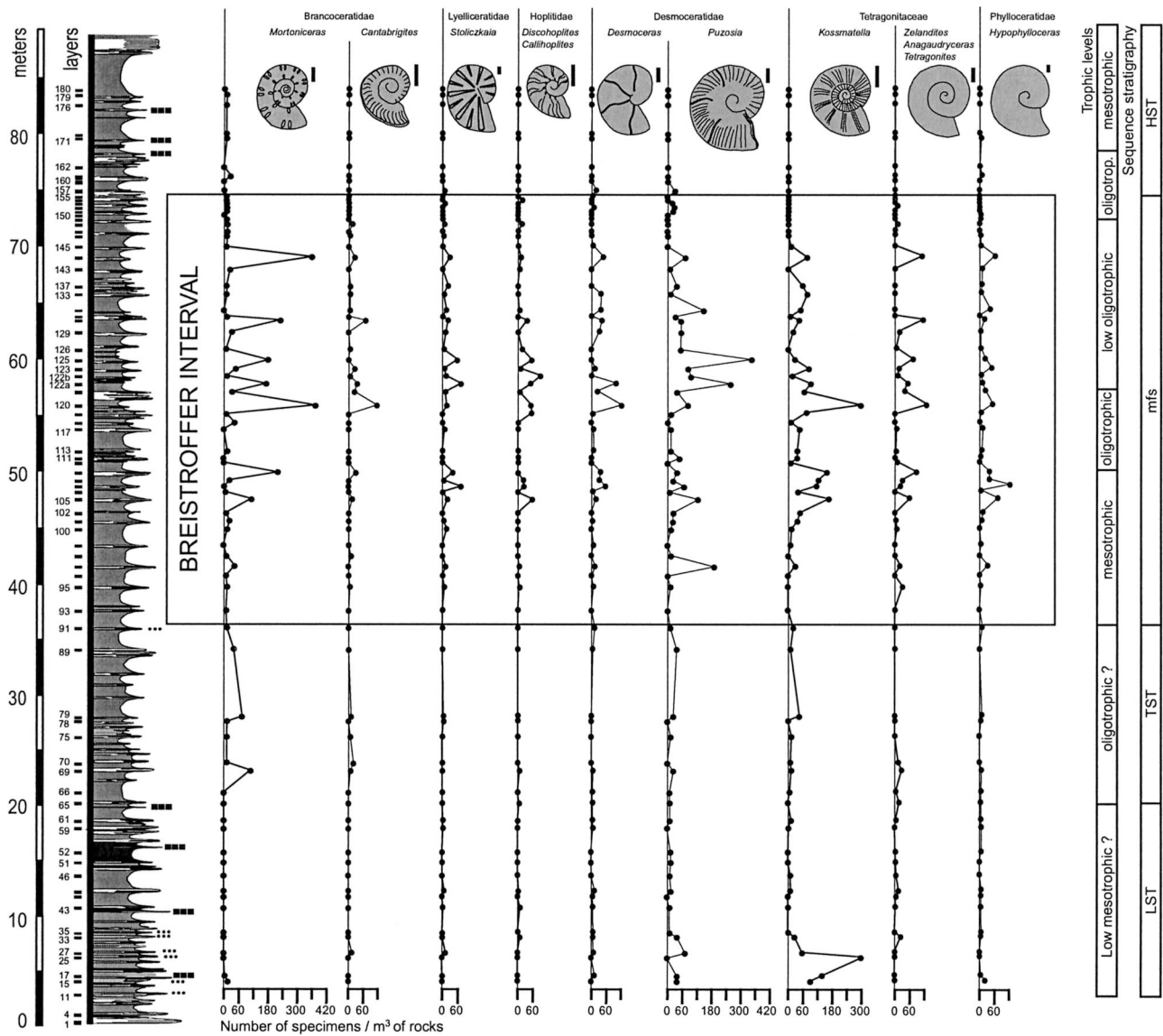


FIGURE 7—Layers 15 to 180 of the Blieux section: minimal absolute abundance of involute/evolute planispirals per volume of rock ( $\text{m}^3$ ). See Figure 2 for lithologies.

(and therefore depth), which forces water into the chamber through the connecting ring (Chamberlain, 1978; Chamberlain et al., 1981).

Chamberlain et al. (1981) concluded that extensive nekroplanktonic drifting of *Nautilus* shells occurs infrequently; after death of the animal, most shells do not reach the surface, but rather settle to the sea bottom after a short period of ascent. Except in rare cases, such as *Aturia* (Tertiary Nautilida; Chirat, 2000), the original distribution of fossil nautiloids generally is preserved, suggesting that post-mortem transport is negligible. The cosmopolitan paleogeographic distribution of *Aturia* mainly results from post-mortem transport of the shell by oceanic paleocurrents. The frequency of occurrence of this transport is due to the morphology of its siphuncle, which has a very long septal neck. This morphological feature reduces the surface area of the connecting ring, and so limits the post-mortem filling rate of the phragmocone during ascent of

the shell of *Aturia* in the water column. Contrary to the assertion of Dauphin (1979), *Spirula* cannot serve as a model for the study of post-mortem transport of fossil ectocochliate cephalopods (Chirat, 2000). This latter author notes that, in contrast to *Nautilus* and ammonoids, the post-mortem influx of water into chambers of *Spirula*, as in *Aturia*, could occur only through a very small area of the connecting ring. Assuming Chirat (2000) is correct, most ammonoids probably had a low potential for post-mortem drift, even if there are some species in nearly all suborders that possess unusually long septal necks, reducing the surface of the connecting ring and possibly delaying chamber flooding after death (Doguzhaeva, 1988; Tanabe et al., 1993). Chamberlain et al. (1981, p. 494) emphasized that “estimate of influx rates in ammonoid siphuncles indicates that many, if not most, ammonoid shells also would not become nekroplanktonic.” For these authors, nekroplanktonic drifting occurred infrequently for most of ammonoids

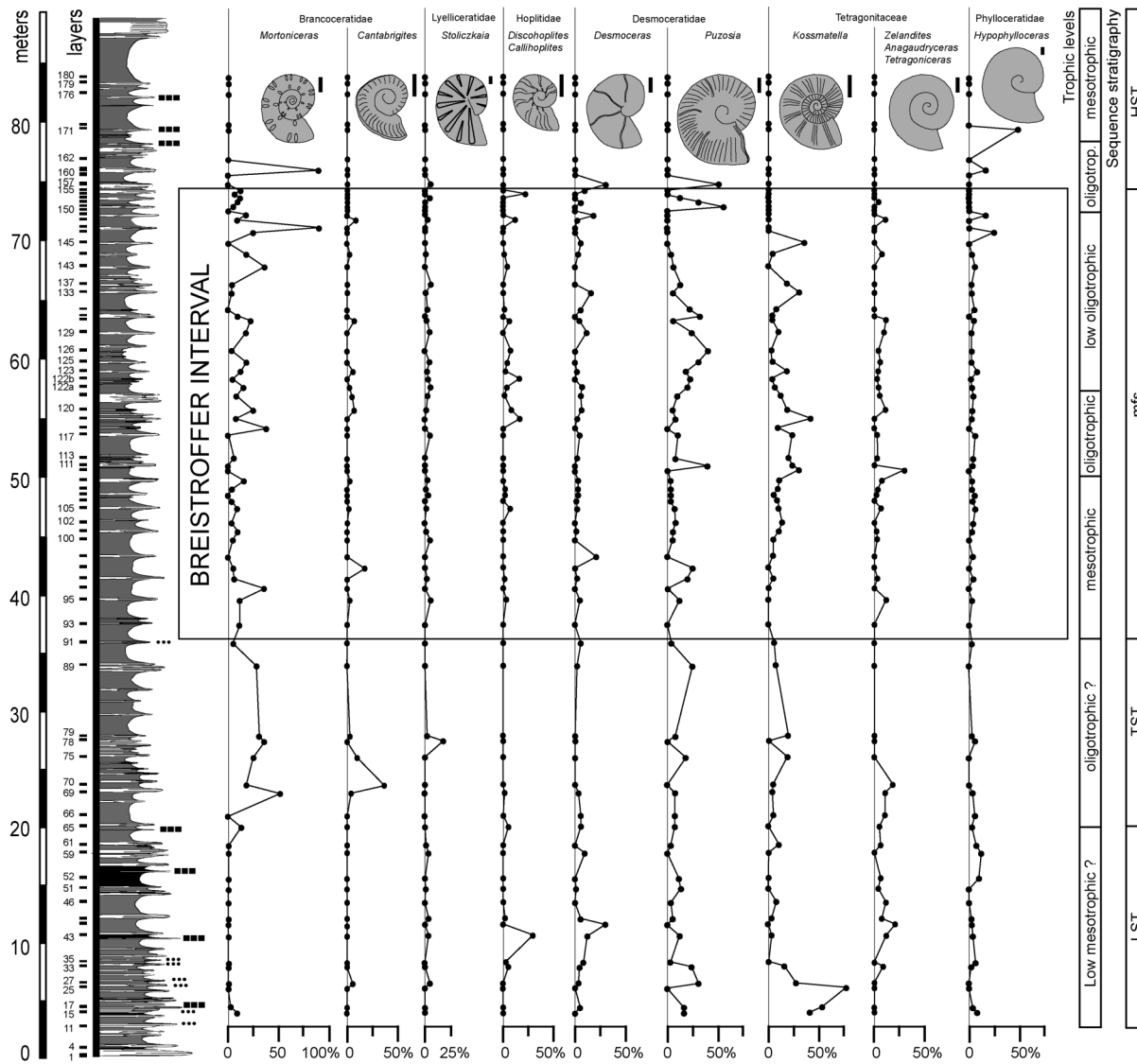


FIGURE 8—Layers 15 to 180 of the Blieux section: relative abundances of involute/evolute planispirals. See Figure 2 for lithologies.

that lived at a depth greater than 50–100 m, and especially for shells smaller than 10 cm in diameter.

All of the involute/evolute planispirals and most of the heteromorphs from the Blieux section have a small adult size that rarely exceeds 10 cm (Proux, 2001). Some Albian species, such as *M. (D.) perinflatum* and *S. (S.) dispar*, may be represented by larger specimens in shallow-platform paleoenvironments (Marcinowski and Naidin, 1976; Latil, 1996). Significant differences in adult size distribution between Valanginian assemblages from the Vocontian basin and the Provence platform suggest limited horizontal movement of adult ammonoids, and limited dispersal of ammonoids by water currents (Reboulet, 2001). Except in layer 25 (Fig. 2), the absence of large specimens in the deep paleoenvironment of the Blieux section suggests that there is no significant post-mortem transport of shells from the platform to basin. The presence of a few, large (~20 cm in diameter), unidentified involute planispiral specimens in layer 25 may be due partly to the drifting of shells from neritic paleoenvironments.

Variation of frequency of floated shells of *Nautilus* could be explained partly by different possibilities of separation of the soft parts (body extracted and consumed by a predator, body lost due to decomposition or activity of scavengers, deterioration of muscle-shell attachment areas, etc.), the length of siphuncular tissue removed after death, and the depth of the animal at time of death (hydrostatic pressure; Chamberlain et al., 1981). However, it is difficult to appreciate the impact of these factors on the post-mortem transport of shells for *Nautilus* or for ammonoids. Separation of the body from the shell would be easier in orthocones and torticocones, which were oriented vertically in life with an aperture towards the bottom, than for scaphiticocones, ancylocones, and hamiticocones, which were characterized by a hooked adult body chamber with an aperture pointing upwards. Following this hypothesis, the preservation of aptychi within the body chamber of U-shaped heteromorphs would be more favorable. However, this kind of fossil record for aptychi is always very rare as well in involute/evolute planispirals as in heteromorphs and

does not seem more frequent for U-shaped heteromorphs (Trauth, 1928, 1935, 1936; Arkell, 1957; Lehmann, 1981; Nixon, 1996), except for Aptian *Tonohamites* (Monks and Palmer, 2002) and Turonian scaphitids (Tanabe, 1979). The ammonoid/ptychi ratio provides a useful criterion for evaluating the post-mortem transport of ammonoids (Olóriz et al., 1996; Reboulet et al., 2003). No ptychi have been found in the Blieux section. Limited post-mortem dispersal of shells by water currents can explain the absence of ptychi (Maeda and Seilacher, 1996).

The great abundance of bivalves at the base of the Blieux section could be due to post-mortem transport of shells by bottom currents from proximal paleoenvironments. In fact, the mode of accumulation of aucellines and the frequent occurrence of turbiditic silty layers in this interval suggest episodic transport from platforms (Giraud et al., 2003).

**Resedimentation Processes:** Once accumulated at the seafloor, ammonoid shells can be affected by resedimentation processes (*sensu* Fernández-López, 1991), which usually generate broken specimens that are fragmented preferentially in the peristomal region (Fernández-López, 1991, 1997; Fernández-López and Meléndez, 1994, 1995; Olóriz et al., 1996; Fernández-López et al., 1999). Resedimentation does not necessarily imply significant lateral transport. The weak fragmentation of ammonoid shells of the Blieux section seems mainly related to nearly *in-situ* resedimentation by bottom currents before burial. Although original volume and shape of the living chamber often are preserved in internal molds, the phragmocones usually are compressed by diagenetic compaction (Fig. 3), which indicates a rapid sedimentary infill of the living chamber and high accumulation rate (Fernández-López et al., 2000). The residence time of the shells on the sea floor seems, therefore, to have been relatively short. The taphonomy of the specimens studied suggests rapid sinking and burial of the shells. The higher rates of fragmentation observed in some heteromorphs could be explained partly by the supposed fragility of their more open shell with respect to involute/evolute planispirals. The variations of preservation (fragmentation index) are not important enough to explain the significant changes in the absolute abundances of each taxon (Figs. 2, 5, 7). For instance, from layers 99 to 110, *Lechites* has similar fragmentation indices ( $0.255 < FI < 0.266$ ), but the absolute abundances vary strongly—from 10 to 1500 specimens per m<sup>3</sup> (Fig. 5).

**Diagenetic Effects:** Because tests of the macrofauna (except belemnites) are not preserved, the hypothesis that a different shell structure could have influenced shell preservation and modified the original composition and abundance of samples cannot be evaluated. However, the lithology of the Blieux section is mainly marls and argillaceous marls, therefore, diagenetic effects on the shells can be considered as constant for all assemblages.

#### Variations In Accumulation Rate

The absolute abundance of macrofauna specimens per volume of rock depends partly on accumulation rate (Reboulet et al., 2000, 2003). In such a case, a covariance is expected between the total abundance of ammonoids and the abundances of different ammonoid taxa as well as with the abundance of bivalves. This covariance can be ex-

TABLE 1—Correlation indices between the total abundance of ammonoids (all taxa) and the absolute abundances of selected ammonoid taxa (genus or morphotype), and the total abundance of bivalves. All correlations are based on minimum values of the absolute abundances and on a dataset of 81 samples, except the last line (80 samples).

	Total ammonoids (all taxa)
Total ammonoids (all taxa)	1.000
Heteromorphs	.949
Involute/evolute planispirals	.876
<i>Lechites</i>	.878
<i>Scaphites</i>	.859
<i>Worthoceras</i>	.605
<i>Anisoceras</i>	.534
<i>Hamites</i>	.624
<i>Hemiptychoceras</i>	.856
Torticones ( <i>Turrillitoides</i> + <i>Mariella</i> )	.356
<i>Mortonoceras</i>	.734
<i>Cantabrigites</i>	.521
<i>Stoliczkaia</i>	.786
<i>Desmoceras</i>	.730
<i>Puzosia</i>	.578
Hoplitidae ( <i>Discohoplites</i> + <i>Callihoplites</i> )	.557
<i>Kossmatella</i>	.629
Tetragonitaceae (- <i>Kossmatella</i> )	.796
<i>Hypophylloceras</i>	.882
Bivalves	.144
Bivalves (- layer 25)	.448

pressed by correlation indices between these different variables (Table 1). Total ammonoid abundance shows positive correlations with the abundances of the different ammonoid taxa—high positive correlation coefficients are found both for the most abundant taxon (*Lechites*) as well as for the taxon representing less than 10% of the assemblages (*Hemiptychoceras*). Total ammonoid abundance shows low positive correlation with the abundance of bivalves when a sample (layer 25) containing more than 40,000 specimens/m<sup>3</sup> of bivalves is considered. This great abundance of bivalves (*Aucellina* beds) in layer 25 (Fig. 2) has been related to platform input (Giraud et al., 2003). When sample 25 is removed, the correlation between total ammonoid abundance and that of bivalves is significantly better (Table 1). All these observations suggest that, in the Blieux section, the abundance of macrofauna is controlled partly (because of the variable correlation coefficients) by accumulation rate.

A decrease in accumulation rate could explain, in part, the highest abundance of ammonoids within the Breistroffer interval of the Blieux section, whereas the depletion in ammonoids below and above this interval could reflect an increased sedimentary dilution by terrigenous input and platform-derived carbonate muds, respectively (Giraud et al., 2003; Fig. 2). In the lowermost and uppermost parts of the succession, frequent turbiditic layers indicate that sedimentary dilution, and consequently, the low ammonoid abundances observed, are due to terrigenous input. Increasing accumulation rate due to enhanced carbonate



input from the shelves appears likely to have been the principal mechanism for reduction of macrofossil abundances observed in the upper part of the Breistroffer interval and just above it (layers corresponding to calcareous marls, Fig. 2; Giraud et al., 2003). For bivalves, the high abundances observed in the lower part of the Breistroffer interval (Fig. 2) partly could be explained by a reduction of the accumulation rate. However, their low abundances in the middle and upper parts of this interval cannot be explained by an increased accumulation rate, but more likely by paleoenvironmental changes (see below).

#### Paleoenvironmental Changes And Paleoecology Of Late Albian Ammonoids

Both taphonomy and dilution may have controlled some of the variations in macrofaunal abundance. Significant variations of macrofaunal abundance, and the different trends observed between benthic and ammonoid faunas (Fig. 2) and between different ammonoid taxa (Figs. 5, 7), are better interpreted in terms of response to paleoenvironmental changes and different paleoecologies of the taxa analyzed.

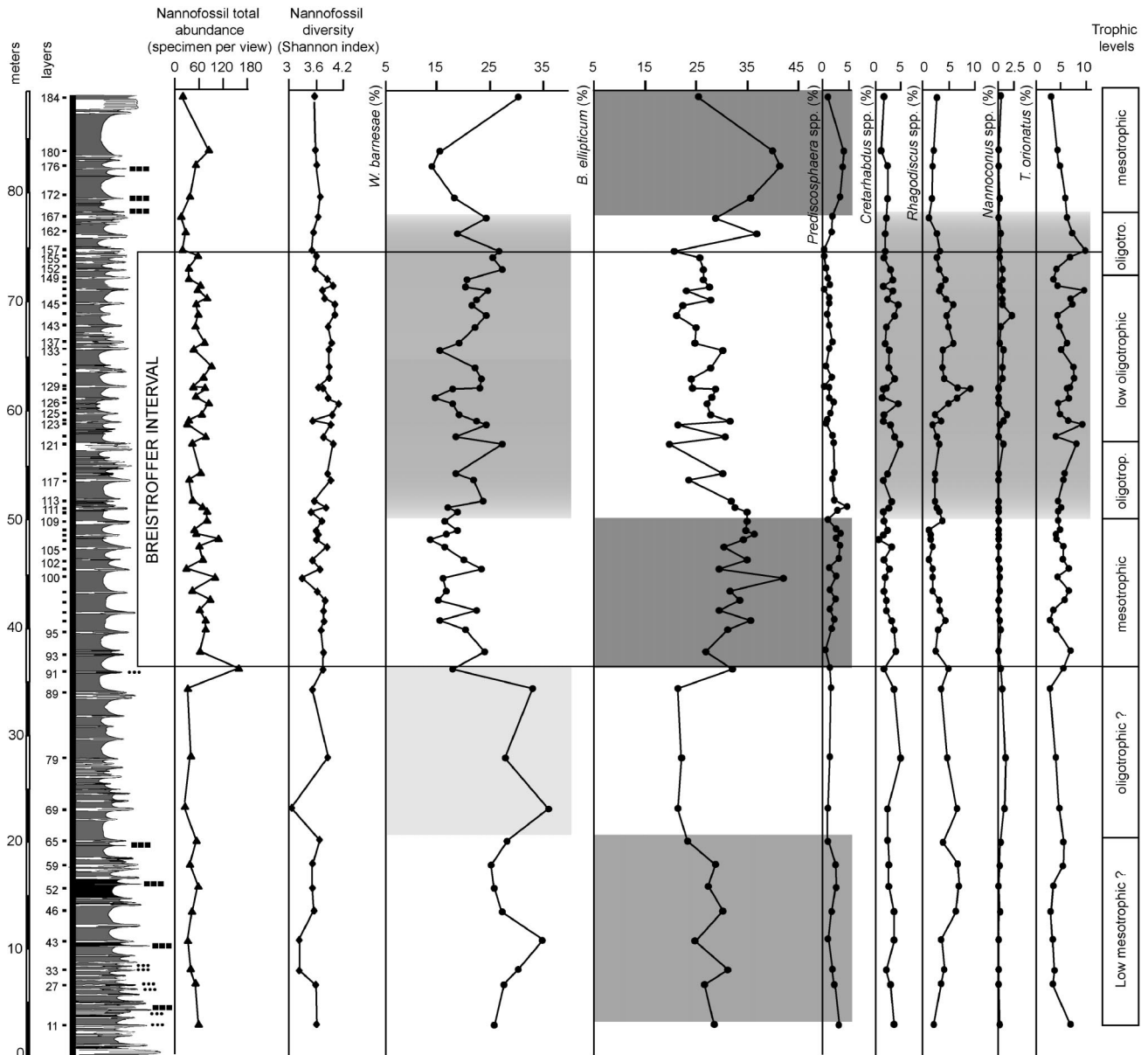
*Paleoenvironmental Changes:* A multidisciplinary approach applied to the Latest Albian Blieux succession allowed recognition of significant changes in paleoenvironmental conditions. Among these recognized changes, eustatic fluctuations strongly influenced variations in nannofossil and macrofauna abundances. In particular, during the maximum-flooding Breistroffer event, increasing distality and the associated increase in habitat space are partly responsible for the highest abundances of ammonoids and nannofossils observed with respect to the rest of the succession (Giraud et al., 2003; Figs. 2, 9). Trophic conditions in surface waters were established by analysis of the diversity and abundance variations of nannofossils. Distinctive patterns in nannofossil assemblages are recognized that reflect alternations from mesotrophic to oligotrophic conditions in surface waters (Giraud et al., 2003; Fig. 9). In Recent marine settings, mesotrophic conditions correspond to unstable environments (moderate turbulence and nutrient concentrations in surface waters), resulting in high phytoplankton production, and moderate-diversity nannoplankton assemblages dominated by small placolith-bearing species. Oligotrophic conditions correspond to stable environments (warm, stratified, nutrient-poor surface waters), resulting in low phytoplankton production, and high-to-low-diversity nannoplankton assemblages (Young, 1994). In the present paper, oligotrophic and low oligotrophic are distinguished, and refer to low- and high-diversity nannofossil assemblages, respectively. For instance, within the Breistroffer interval, mesotrophic conditions, suggested by high nannofossil abundance, low-diversity nannoplankton assemblages correlated with a high abundance of small placolith-bearing species (*Biscutum ellipticum* and *Prediscosphaera* spp.) characteristic of relatively nutrient-rich surface waters, prevailed in the lower part (layers 91–109). Oligotrophic conditions, characterized by low nannofossil total abundances, poorly diversified nannofossil assemblages correlated with the dominance of the eurytopic taxon *Watznaueria barnesae*, are recorded from layers 110 to 121. Low oligotrophic and warmer surface-water condi-

tions, shown by a slight increase in nannofossil total abundance and higher diversity nannofossil assemblages correlated with an increase in the relative abundance of non-placolith-bearing species (*Nannoconus* spp., *Rhagodiscus* spp., *Tranolithus orionatus*), prevailed in the upper part of the Breistroffer interval (layers 122–149). The slight increase in abundance of *Nannoconus* spp., considered as a deep photic zone dweller (Erba, 1994), suggests an increase in nutrient availability in the lower part of the photic zone. The increasing diversity may indicate more stable paleoenvironmental conditions in which nutrients were used by a relatively large number of species (Watkins, 1989).

Contrasting seasonal climatic conditions during the Breistroffer event (Bréhéret, 1997) probably controlled the succession of different trophic conditions in surface waters. Mesotrophic conditions prevailed during periods of increased precipitation, runoff, and introduction of associated nutrients into the marine realm, whereas oligotrophic conditions reflect low runoff and, consequently, nutrient-depleted surface waters, in times of drier climatic conditions. Following this paleoenvironmental scenario, benthic and pelagic macrofauna abundance variations are discussed mainly with respect to food availability. Variations in seawater productivity potential during marl-limestone deposition have been evoked to explain changes in abundance and diversity of Valanginian ammonoids (Reboulet, 1996, 1998; Reboulet and Atrops, 1997; Reboulet et al., 2000, 2003). The present study seems to confirm that food availability in the water column was an important factor controlling diversity and abundance of ammonoids with respect to their habitat and mode of life.

*Paleoecology of Late Albian Ammonoids:* Knowledge of the paleobiogeographic distribution of ammonoids is an important step to understanding the relationships between paleoenvironment and composition of assemblages, and it contributes to defining properly the habitat and mode of life of ammonoids (Westermann, 1996; Cecca, 1998; Reboulet, 2001; Reboulet et al., 2000, 2003). However, if the global paleobiogeographic distribution of Late Albian faunas is relatively well known (Gale et al., 1996; Wright et al., 1996), information about ammonoid distributions from proximal to distal paleoenvironments in southeast France is very scarce (Latil, 1996). Because of a severe platform crisis during the Late Albian (Grötsch et al., 1993), the succession of ammonoids on the platforms does not allow accurate and continuous correlation with the Vocontian basin sections.

Knowledge of the habitat and mode of life of Cretaceous heteromorphic ammonoids is based mainly on studies of the Valanginian–Barremian and Albian–Turonian faunal assemblages of the Mediterranean Tethys (Reboulet, 1996, 1998; Reboulet et al., 2000, 2003; Cecca, 1997, 1998) and the Western Interior Seaway (Batt, 1989, 1993; Westermann, 1996), respectively. It is suggested that heteromorphs probably had different trophic behavior than involute/evolute planispirals; the former probably could better occupy new ecological niches (Cecca, 1997; Reboulet, 1998; Reboulet et al., 2000, 2003; Guex, 2001). Recently, isotopic analyses of fifteen ammonoid shells belonging to nine Campanian species suggest a demersal (nektobenthic) habitat both for involute/evolute planispirals (some species of Phylloceratina, Lytoceratina, and Ammonitina)



**FIGURE 9**—Calcareous nannofossil abundance, diversity, and percentages of selected nannofossil taxa plotted against lithology in the Blieux section, modified from Giraud et al. (2003). The positions of the 60 samples selected for nannofossil taxa analysis are noted. Note the successive major contribution of the different species identified by the shaded bands. The color variations from pale gray to dark gray reflect changes from oligotrophic to mesotrophic conditions.

and heteromorphs (one species of Ancyloceratina; Moriya et al., 2003). With respect to the heteromorphs, involute/evolute planispirals have high abundances and dominate in intervals of the Blieux section characterized by low oligotrophic to oligotrophic conditions (Figs. 6–8). This suggests that stable paleoenvironmental conditions favored the appearance and expansion of involute/evolute planispirals. Heteromorphs, which were dominant during mesotrophic conditions (Fig. 6), would have been more competitive when paleoenvironmental conditions became more unstable (in this case, with increased runoff and fresh-water input).

The ammonoids are grouped into major morphologic types following the hypothesis that different morphologies

correspond to distinct modes of life (swimming, buoyancy, trophic habits; Batt, 1989, 1993; Westermann, 1990, 1996; Cecca, 1997; Klug, 2001; Reboulet et al., 2003). Habitat and mode of life of Late Albian heteromorphs and involute/evolute planispirals are detailed successively.

Albian *Lechites* are orthoconic forms with the whorl section slightly compressed, which is very similar to the shell shape of Cenomanian *Baculites* and Valanginian *Bochianites*. *Lechites* has a nearly cosmopolitan distribution (Gale et al., 1996; Lehmann, 2000). This is in agreement with an epipelagic habitat, allowing a wide dispersal of both eggs and adult ammonoids. However, in southeast of France, *Lechites* is rare in shallow paleoenvironments of the North-Provence platform (Pont de Peille section, Latil,

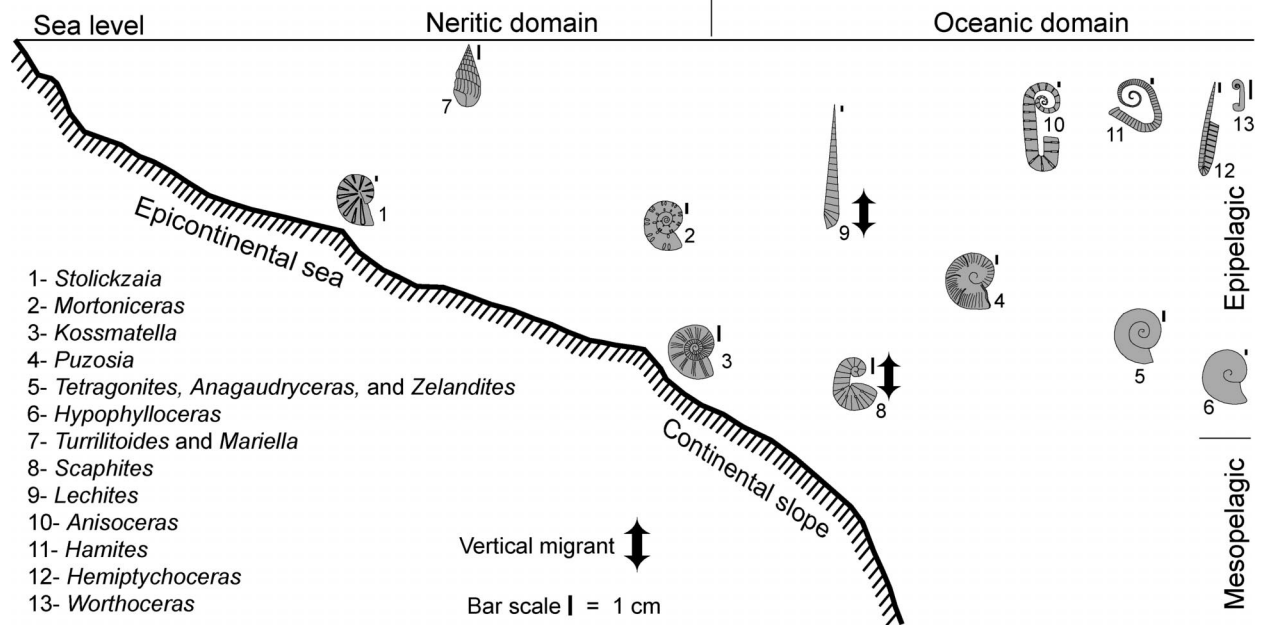


FIGURE 10—Stylized panorama of some Late Albian ammonoid habitats.

1996), but it is common (Mont Risou section; Gale et al., 1996) or abundant (Blieux section, Fig. 5) in deeper paleoenvironments of the Vocontian basin. This suggests that *Lechites* mainly inhabited epipelagic distal paleoenvironments (Fig. 10). Orthoconic forms generally are interpreted as vertical migrants (Jacobs and Chamberlain, 1996). This great capacity for vertical mobility would have permitted these forms to move up and down in the water column to exploit food-rich layers (Westermann, 1996). For instance, *Baculites* would have been quasiplanktic and a potential bottom feeder (Westermann, 1996), and *Bochianites* probably had a deep-nektonic, possibly nektobenthic, mode of life (Reboulet et al., 2000, 2003). In the Blieux section, trophic levels in surface waters alternate from mesotrophic to oligotrophic (Giraud et al., 2003; Fig. 9) and *Lechites* is always present (Fig. 5), often dominating the ammonoid assemblages (Fig. 6). This could indicate that abundance of *Lechites* is independent from fluctuations of trophic conditions in surface waters. *Lechites*, interpreted as a vertical migrant, would have been able to move up when trophic conditions were good in surface waters, and down in order to avoid oligotrophic surface waters and to exploit food-rich layers in deeper waters (Fig. 11).

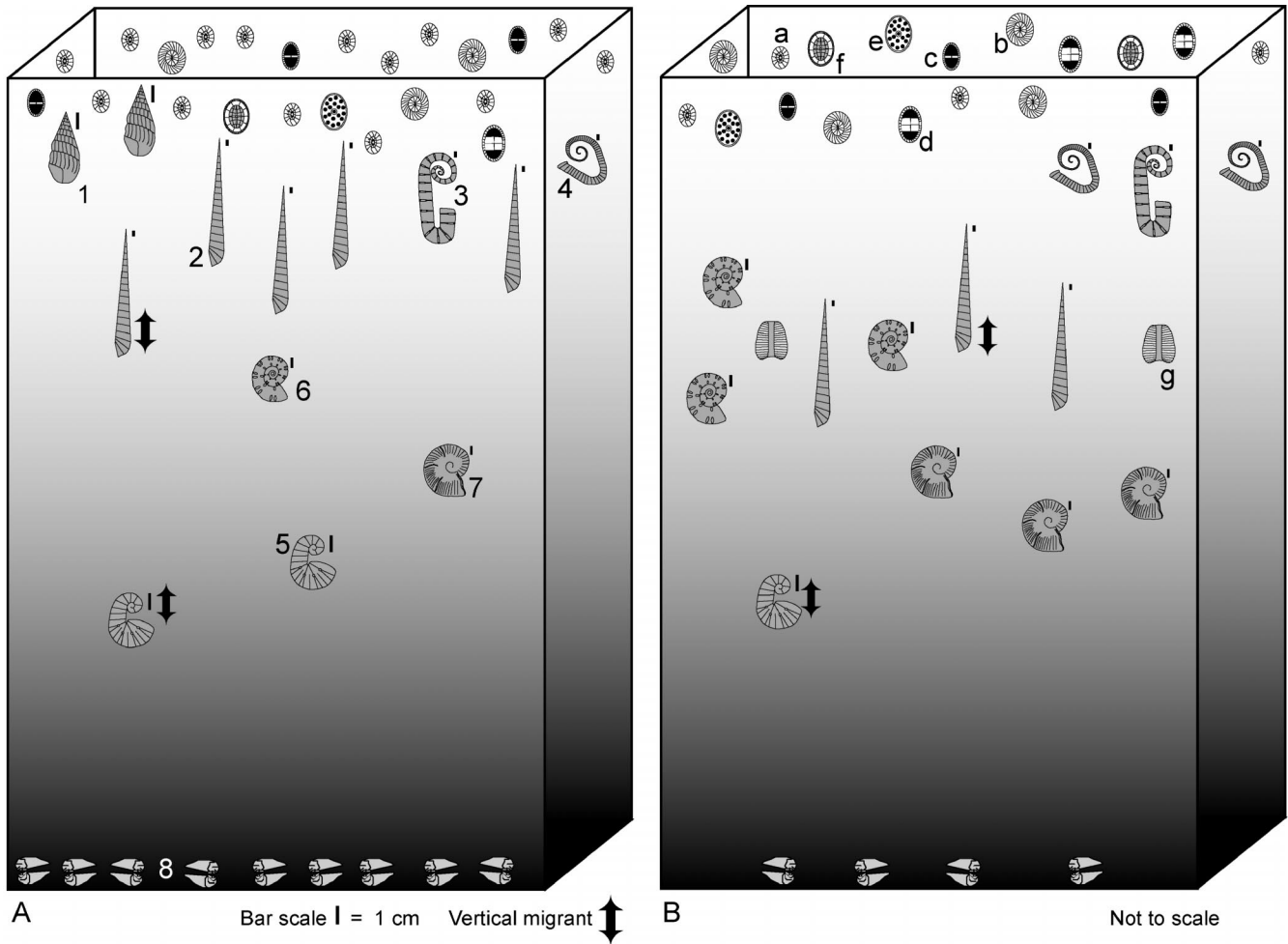
In the Blieux section, the presence of torticones (*Turrititoides* and *Mariella*) is restricted to two intervals (Fig. 5) and their relative abundance rarely exceeds 40% (Fig. 6). At the Pont de Peille section (Latil, 1996), the Late Albian ammonoid assemblage shows dominance (80%) of Turrititidae and low percentages of other heteromorph ammonoids (Baculitidae and Anisoceratidae). This suggests that *Turrititoides* and *Mariella* inhabited mainly neritic paleoenvironments (Fig. 10). Contrary to orthocones, which may have been vertical migrants, torticones might have had some difficulty in locomotion (Jacobs and Chamberlain, 1996); these forms could be interpreted as having

been weak swimmers, and a quasiplanktic mode of life may be suggested.

Batt (1989, 1993) considered Cenomanian *Turritites* (torticones) as nektobenthic, and suggested that their selective absence may indicate the extent of poorly oxygenated conditions in the water column. This hypothesis cannot explain the absence of *Turrititoides* and *Mariella* in some intervals of the Blieux section (Fig. 5). The water column always was well oxygenated, as shown by the constant presence of benthic organisms throughout the section (Giraud et al., 2003; Fig. 2). An increase of nutrients in the water column could have been favorable to the appearance and expansion of torticones in the paleoenvironment of the Blieux section (Fig. 5). In fact, the peaks of relative abundances of *Turrititoides* and *Mariella* are relatively well correlated to those of the nannofossil species *Biscutum ellipticum* ( $r = 0.409$ ;  $n = 56$ ). This species indicates mesotrophic conditions in surface waters in the Blieux section (Giraud et al., 2003; Fig. 9). These conditions, especially in the lower part of the Breistroffer interval, seem to have been favorable to bivalves and ammonoids (particularly some heteromorphs; Figs. 2, 5, 6).

Humid climatic conditions were responsible for the increased runoff from the hinterland, and introduction of associated nutrients into the marine realm. This could explain the abundance of nannoplankton taxa characteristic of relatively nutrient-rich surface waters, and thus explain the abundance of other organisms, such as ammonoids, that are higher in the food chain. An increase in fresh-water input in the marine realm could have led to episodic density stratification of the water column, resulting in high nutrient concentration at and near the sea bottom that could have favored the development of an abundant benthic community of bivalves (Giraud et al., 2003; Fig. 2). If Albian torticones were nektobenthic, good trophic resources in bottom waters also could explain their





## Ammonoids:

- 1- *Turrilitoides* and *Mariella*
- 2- *Lechites*
- 3- *Anisoceras*
- 4- *Hamites*
- 5- *Scaphites*
- 6- *Mortoniceras*
- 7- *Puzosia*
- 8- Bivalves

## Calcareous nannofossils:

- a- *Biscutum ellipticum*
- b- *Watznaueria barnesae*
- c- small *Zeugrhabdotus*
- d- *Tranolithus* spp.
- e- *Rhagodiscus* spp.
- f- *Cretarhabdus* spp.
- g- *Nannoconus* spp.

**FIGURE 11**—Sketch showing the presence/absence of some Late Albian ammonoids, their abundance variations and their position in the water column in relation to trophic conditions across the Breistroffer interval of the Blieux section: (A) Lower part of the Breistroffer interval (layers 91–109). Mesotrophic conditions in surface waters could have been favorable to the appearance and expansion of torticones (*Turrilitoides* and *Mariella*), and episodic density stratification of the water column, resulting in high nutrient availability in the lower part of the water column and at the sea bottom would have allowed appearance of deep-nektonic ammonoids (*Scaphites*) and benthic macrofauna (bivalves). (B) Upper part of the Breistroffer interval (layers 122–149). Low oligotrophic conditions in surface waters could explain the absence of *Turrilitoides* and *Mariella* as well as the relative increase of *Anisoceras* and *Hamites*, considered to have been more competitive compared to the torticones. Stable paleoenvironmental conditions favored the appearance and expansion of involute/evolute planispirals such as *Puzosia*. With respect to the lower part of the Breistroffer interval, the increasing nutrient availability in the lower part of the photic zone could have been favorable to *Mortoniceras*. The low abundance of bivalves could be explained by a reduced nutrient flux at the sea floor in times of generally more oligotrophic conditions in the water column. *Lechites*, interpreted as a vertical migrant, would have been able to move up and down in the water column, when trophic conditions in surface waters change from mesotrophic to oligotrophic, respectively.

abundance in the lower part of the Breistroffer interval. However, in the uppermost part of the Blieux section, where mesotrophic conditions in surface waters also prevailed, torticones peak in abundance (Figs. 5, 6), while bivalves are rare (Fig. 2). The relative abundance of tortico-

nes is negatively correlated with that of nannofossil taxon *Nannoconus* ( $r = -0.228$ ), which is considered to have been a deep photic-zone dweller. So, only nutrient-rich surface waters seem to have been favorable to the torticones (Fig. 11A).

These observations imply that Albian torticones were not nektobenthic, but probably quasiplanktic in the upper part of the water column. They inhabited mainly neritic paleoenvironments where trophic conditions were generally good (Fig. 10), and could occupy more distal paleoenvironments when food supplies in surface waters increased (Fig. 11A).

U-shaped heteromorphic ammonoids (scaphiticoles, ancylocones, and hamiticoles) are classically interpreted as having an adult living chamber with an aperture pointing upward (Fig. 5; Westermann, 1996). However, Kakabadzé and Sharikadzé (1993) and, more recently, Monks and Young (1998) proposed that some adult heteromorphs had an aperture tilted towards the sea floor. Most U-shaped heteromorphs probably had limited mobility (quasiplanktic mode of life; Klinger, 1981; Jacobs and Chamberlain, 1996), and lived in an oceanic epipelagic habitat (midwater?; Batt, 1989; Westermann, 1996). Cenomanian U-shaped forms from the Western Interior Seaway are common during transgression, and rare in regression, pulses (Batt, 1989). Except for a few specimens of Anisoceratidae, Albian U-shaped heteromorphs have not been found on the Provence platform (Latil, 1996). In the Blieux section, U-shaped heteromorphs are not abundant except for *Scaphites* (Fig. 5), probably because of the relatively proximal position of this section in the Vocontian basin. These forms mainly occur within the Breistroffer interval (Fig. 5), interpreted as a maximum flooding stage (Bréhéret, 1997). These observations could support an oceanic habitat (distal paleoenvironments) for most U-shaped forms (Fig. 10).

Among heteromorphs, *Anisoceras* and *Hamites* occur in low fluctuations of their absolute abundances but high variations of their relative abundances (Figs. 5, 6). These cephalopods can constitute an important part of the assemblages in intervals characterized by low oligotrophic to oligotrophic conditions in surface waters (Fig. 6). In these trophic conditions, *Anisoceras* and *Hamites* could be more competitive than torticones (Fig. 11B).

*Scaphites*, which can be distinguished from the other U-shaped forms, is the most important genus in absolute abundance, and often well represented in the ammonoid assemblages (Figs. 5, 6). These data could indicate that this form inhabited more proximal paleoenvironments than ancylocones and hamiticoles (Fig. 10), and that abundance of *Scaphites* is independent from fluctuations of trophic conditions in the water column. This last observation implies that *Scaphites* was a vertical migrant, as previously proposed by Westermann (1996). Within the Breistroffer interval, the absolute abundance of *Scaphites* correlates positively with the absolute abundance of bivalves ( $r = 0.784$ ;  $n = 35$ ). This suggests that *Scaphites* could have lived near the sea bottom. A nektobenthic mode of life was evoked for *Scaphites* by Batt (1989, 1993). Considering *Scaphites* as a vertical migrant, it would have been able to move up and down in the lower part of the water column in order to exploit food-rich layers (Fig. 11), rather than having been a nektobenthic form. The absence of *Scaphites* on the Provence platform (Latil, 1996) also is in agreement with a deep-nektonic mode of life (Fig. 10). With respect to other U-shaped forms, which mainly lived in distal paleoenvironments, the distribution of *Scaphites* seems to have been controlled further by bathymetry. *Scaphites*,

therefore, is interpreted as having been a vertical migrant in the lower part of the water column. Considered nektobenthic forms by Kakabadzé and Sharikadzé (1993) and Monks and Young (1998), in this study, distinct modes of life have been proposed for U-shaped heteromorphs.

Recent studies suggest that the majority of involute/evolute planispiral Jurassic–Cretaceous ammonoids were epipelagic, and that they generally lived in proximal paleoenvironments. The involute/evolute planispiral ammonoids were probably mainly sluggish horizontal swimmers in upper-mid waters; a few taxa are interpreted as having been nektobenthic (Westermann, 1996). A nektobenthic mode of life in shallow- to moderate depth is suggested for sculpted, inflated planorbicones with quadrate whorls, such as adult Acanthoceratidae (Westermann, 1996). Large adults of *Mortoniceras* (Acanthocerataceae) from the Provence platform have a similar morphology (Latil, 1996). Among involute/evolute planispirals, *Mortoniceras* is an important genus in both absolute and relative abundances, representing 85% of the total ammonoids in the upper part of the Breistroffer interval of the Blieux section (Figs. 7, 8). No quantified data are available for the Provence platform (Pont de Peille section), but *Mortoniceras* seems to be found frequently (Latil, 1996). Therefore, they probably inhabited the distal part of the neritic domain (Fig. 10). The adult sizes of *Mortoniceras* found in the Vocontian basin (Mont-Risou section, Gale et al., 1996; Blieux section, Proux, 2001) are smaller than those of specimens found on the Provence platform by Latil (1996). With a nektobenthic or a deep-nektonic mode of life, the smaller size could be related to a slow growth rate of the shell under conditions of higher hydrostatic pressure and/or lower water temperature in deep paleoenvironments, as was suggested for some Valanginian ammonoid assemblages (Reboulet, 2001). The absolute abundance of *Mortoniceras* does not correlate with that of bivalves ( $r = 0.005$ ;  $n = 81$ ). However, their absolute and relative abundances both correlate ( $r = 0.428$  and  $r = 0.478$ , respectively;  $n = 56$ ) with those of the nannofossil genus *Nannoconus*, which is considered a deep form, living in the lower part of the photic zone associated with a deep nutricline (Erba, 1994). This suggests that *Mortoniceras* probably had a deep-nektonic rather than a nektobenthic mode of life, and inhabited the lower part of the epipelagic zone (Fig. 11B). The very low abundance of *Cantabrigites* in the Blieux section (Figs. 7, 8) does not allow discussion of habitat and mode of life here.

After the Turrilitidae (80%), the Pont de Peille section (North-Provence platform) is characterized by *Stoliczkaia* (Acanthocerataceae), which represent ~10% of the ammonoid assemblage (Latil, 1996). Except in one layer of the Blieux section, the relative abundance of *Stoliczkaia* does not exceed 5% (Fig. 8). This may indicate that *Stoliczkaia* preferentially lived in neritic domains (Fig. 10). The adult size of *Stoliczkaia* found in the Vocontian basin (Mont-Risou section, Gale et al., 1996; Blieux section, Proux, 2001) is smaller than that of specimens found on the Provence platform by Latil (1996). As was envisaged for *Mortoniceras*, a nektobenthic or a deep-nektonic mode of life could explain this adult size variation.

Among the involute/evolute planispirals, most species of Cretaceous Phylloceratidae (Phylloceratina), Tetragonitidae, Gaudryceratidae (Lytoceratina), and Desmoceratidae

(Ammonitina) are characterized by long septal necks and relatively narrow, thick-walled siphuncular tubes that enhance the mechanical strength of the siphuncle against high hydrostatic pressure; these morphological features of siphuncle are interpreted as probable convergent adaptations to life in deep waters (Doguzhaeva, 1988; Westermann, 1990, 1996; Tanabe et al., 1993; Lehmann, 2000). Phylloceratina and Lytoceratina (the leiostraca) generally are considered to have been deep-water cephalopods (Ziegler, 1967; Cecca, 1992) that may have been able to occupy habitats below the photic zone (Kennedy and Cobban, 1976; Westermann, 1996). They probably were nektobenthic forms (Cecca et al., 1993) and were generally abundant in the deep epicontinental domain between the European and African plates (Cecca, 1998). However, their local abundance in some shallow-water deposits indicates that they were not confined to deep-water habitats; distal paleoenvironments (offshore) rather than deep waters may have been the main habitats of Phylloceratina and Lytoceratina (Kennedy and Cobban, 1976).

Valanginian Phylloceratina and Lytoceratina are found frequently in the deep paleoenvironments of the Vocontian basin, but are common (*Lytoceras*) or rare to absent (*Phylloceras*) on the surrounding platforms (Reboulet, 1996, 2001). In the uppermost Albian ammonoid assemblage of the Pont de Peille section (Provence platform), Phylloceratidae and Lytocerataceae are very rare but not absent (Latil, 1996). The very low abundances of *Hypophylloceras* (Phylloceratina), *Tetragonites*, *Anagaudryceras*, and *Zelandites* (Lytoceratina) could be related to the relatively proximal position of the Blieux section with respect to the oceanic domain. These cephalopods are more abundant during the Breistroffer interval, which is interpreted as a maximum flooding stage (Fig. 7). *Tetragonites*, *Anagaudryceras*, and *Zelandites* are slightly more abundant and frequent in the upper part of this interval, which is characterized by low oligotrophic to oligotrophic conditions (Figs. 7, 8). These stable paleoenvironmental conditions could favor their appearance. With respect to *Hypophylloceras*, which does not show significant differences in its abundance and frequency between the lower and upper parts of the Breistroffer interval, *Tetragonites*, *Anagaudryceras*, and *Zelandites* seem to have been more dependent on paleoenvironmental variations. This suggests that they had shallower habitats than *Hypophylloceras* (Fig. 10). That is also probably the case for Valanginian leiostraca; with respect to *Phylloceras*, the shallower habitats of *Lytoceras* partly could explain their greater abundance on platforms. Using stable isotopic data from specimens from the northwestern Pacific, Moriya et al. (2003) suggested a demersal habitat for some Campanian *Hypophylloceras* and *Tetragonites*. However, comparisons with the Albian genera must be made carefully because paleogeographic, paleoceanographic, and paleoclimatic conditions changed from the Late Albian to Campanian (Gale, 2000), and could explain their different habitat and/or mode of life.

Contrary to other Albian pelagic Lytoceratina, *Kossmatella* is common in the Blieux section (Fig. 7). Its dominance (80% in layer 25, Fig. 8) at the base of the section is correlated with the great abundance of benthic material (aucellines) mainly due to transport from platforms. These observations suggest that *Kossmatella* probably inhabited

more proximal paleoenvironments than other Lytoceratina (Fig. 10). The absolute abundance of *Kossmatella* has the highest positive correlation index with the absolute abundance of bivalves ( $r = 0.63$ ;  $n = 81$ ). A nektobenthic mode of life can be proposed for *Kossmatella*.

In the Blieux section, Desmoceratidae (*Puzosia* and *Desmoceras*) generally are more abundant and frequent than Phylloceratina and Lytoceratina (Figs. 7, 8). In the uppermost Albian ammonoid assemblage of the Pont de Peille section (Provence platform), Desmocerataceae also seems more frequent than Phylloceratidae and Lytocerataceae (Latil, 1996). These observations suggest that Desmoceratidae (particularly *Puzosia*, which is more abundant than *Desmoceras* in the Blieux section) inhabited more proximal paleoenvironments than *Hypophylloceras*, *Tetragonites*, *Anagaudryceras*, and *Zelandites* (Fig. 10). Batt (1989) noted that desmoceratid shells are most abundant in proximal to medial offshore facies of the Western Interior Seaway, but he interpreted these occurrences as the result of post-mortem drift from deeper areas. This author also suggested a nektobenthic mode of life in deep waters for desmoceratids, considering their narrow, thick-walled siphuncles (Westermann, 1971; Ward and Signor, 1983). In the Blieux section, because the abundances of *Puzosia* and *Desmoceras* are low or negatively correlated with those of bivalves ( $r = 0.032$  and  $r = -0.001$ , respectively), these ammonoids probably had a deep-nektonic rather than a nektobenthic mode of life. *Puzosia* is very abundant in the upper part of the Breistroffer interval, where it can constitute an important part of the assemblages (Figs. 7, 8). *Desmoceras* also is more abundant in this part of the Blieux section, which is characterized by low oligotrophic to oligotrophic conditions. These stable paleoenvironmental conditions could favor the development of Desmoceratidae. With respect to Lytoceratina (except *Kossmatella*), which show a low increase in their abundance and frequency in the upper part of the Breistroffer interval, Desmoceratidae seem more dependent on paleoenvironmental variations. This suggests that Desmoceratidae (particularly *Puzosia*) had shallower habitats than these Lytoceratina.

The very low abundance of hoplitids (*Discohoplites* and *Callihoplites*) in the Blieux section and, probably, on the Provence platform (Latil, 1996), could be explained by their paleobiogeographic distribution. The North-European province is characterized by Hoplitidae, which have been used to establish the detailed biostratigraphic scale of the Albian (Owen, 1971, 1984), but can hardly be used in the Mediterranean Province (Latil, 1996). Hoplitids generally are limited to the boreal realm and are known only as rarities elsewhere (Kennedy and Cobban, 1976).

## CONCLUSIONS

The quantitative analysis of ammonoids compared with data on bivalves and on nannoplankton across the Breistroffer interval (OAE 1d, Latest Albian) investigated for the Blieux section (southeast France) shows two major features.

- (1) Post-mortem transport of shells can be minimized in explaining ammonoid abundance variations. Taphonomy of the specimens suggests rapid sinking and buri-



al of the shells. The variation of the fragmentation index, defined to estimate the preservation state, is not large enough to explain the significant changes in the absolute abundance of the macrofauna. This variation may have been controlled partly by a dilution factor in relation to third-order sea level variations recognized in the Late Albian sediments of the Vocontian basin. Decrease in sediment accumulation rates during the Breistroffer interval, interpreted as a maximum flooding stage, partly could explain the highest abundance of ammonoids. Depletion of macrofauna below and above the Breistroffer interval in part would reflect increased sedimentary dilution by terrigenous input and platform-derived carbonate muds, respectively. However, a dilution mechanism cannot explain the different trends observed between benthic and ammonoid macrofaunas and among different ammonoid taxa.

- (2) This integrated study confirms that food availability in the water column was an important factor controlling the abundances of some ammonoids and sometimes the spatial distribution of individual genera, such as *Turrilitoides* and *Mariella*. These torticones may have been quasiplanktic and inhabited mainly neritic paleoenvironments. Colonization of more distal paleoenvironments became possible when food supplies increased (mesotrophic conditions in surface waters). *Lechites* (orthocone) probably inhabited epipelagic distal paleoenvironments. This vertical migrant would have been able to move up and down in the water column to exploit food-rich layers when trophic conditions in surface waters changed from mesotrophic to oligotrophic, respectively. Most of the U-shaped Late Albian heteromorphs (scaphiticoles, hamiticoles, and ancylocones) probably lived in an oceanic epipelagic habitat. Compared with the torticones, *Anisoceras* and *Hamites* could have been more competitive when oligotrophic conditions prevailed in surface waters. More proximal paleoenvironments are suggested for *Scaphites*, which would have been able to move up and down in the lower part of the water column in order to exploit food-rich layers. It seems that stable paleoenvironmental conditions favored the introduction and expansion of involute/evolute planispirals. *Mortoniceras* probably inhabited the distal part of the neritic domain and had a deep-nektonic mode of life in the lower part of the epipelagic zone. *Stoliczkaia* preferentially lived in neritic paleoenvironments; a nektobenthic or a deep-nektonic mode of life could be suggested for this genus. *Hypophylloceras*, *Tetragonites*, *Anagaudryceras*, and *Zelandites* inhabited mainly distal paleoenvironments. In contrast, *Kossmatella* and *Puzosia* probably lived in more proximal paleoenvironments. A nektobenthic and a deep-nektonic modes of life are proposed for *Kossmatella* and *Puzosia*, respectively.

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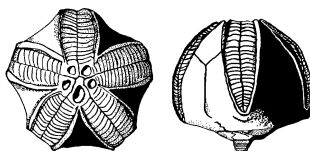
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- Anisoceratidae Hyatt  
*Anisoceras* Pictet  
*A. armatum* (Sowerby)
- Hamitidae Gill  
*Hamites* Parkinson  
*H. duplicatus* Pictet and Campiche  
*Hemiptyhoceras* Spath  
*H. subgaultinum* Breistroffer
- Turrilitidae Gill  
*Mariella* Nowak  
*M. (M.) bergeri* (Brongniart)  
*Turrilitoides* Spath  
*T. hugardianus* (d'Orbigny)
- Baculitidae Gill  
*Lechites* Nowak  
*L. (L.) gaudini* Pictet and Campiche
- Scaphitidae Gill  
*Scaphites* Parkinson  
*S. (S.) hugardianus* d'Orbigny  
*Worthoceras* Adkins  
*W. pygmaeum* Butjor
- Involute/evolute planispiral ammonoids:
- Brancoceratidae Spath  
*Mortonoceras* Meek  
*M. (Durnovarites) perinflatum* Spath
- Cantabrigites Spath  
*C. cantabrigense* Spath
- Lyelliceratidae Spath  
*Stoliczkaia* Neumayr  
*S. (Faraudiella) blancheti* (Pictet and Campiche)  
*S. (S.) dispar* (d'Orbigny)
- Hoplitidae Douvillé  
*Callihoplites* Spath  
*Discohoplites* Spath  
*D. coelonotus* (Seely)
- Desmocerotidae Zittel  
*Puzosia* Bayle  
*P. (P.) mayoriana* (Sowerby)  
*Desmoceras* Zittel  
*D. (D.) latidorsatum* (Michelin)
- Tetragonitidae Hyatt  
*Tetragonites* Kossmat
- Gaudryceratidae Spath  
*Anagaudryceras* Shimizu  
*Zelandites* Marshall  
*Kossmatella* Jacob
- Phylloceratidae Zittel  
*Hypophylloceras* Salfeld

## APPENDIX

## LIST OF AMMONOID TAXA

Taxa are grouped into twelve families, using the supra-specific classification proposed by Wright et al. (1996).

Heteromorphic ammonoids:



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