



Conch geometry, ontogeny and dimorphism in the Early Bajocian ammonoid *Stephanoceras* from Normandy, France


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A large suite of specimens belonging to the Early Bajocian *Stephanoceras* from Évreux (Normandy, France) displays wide variation in conch and sculpture. The quantitative analysis of the conch geometry and its ontogeny on the basis of more than 50 sectioned specimens reveals major problems in the separation of species within the assemblage; clear morphological boundaries between possible species cannot be established. The material shows wide variation in sculpture and conch parameters throughout ontogeny, and correlation between the characters is weak. With the study of conch ontogeny, it is possible to separate dimorphs, as microconchs show a sudden change in the conch parameters (umbilical egression, change in the shape of the whorl profile). The onset of these changes varies in the assemblage between 40 and 75 mm conch diameter. □ *Ammonoids, Bajocian, dimorphism, Jurassic, morphometrics, Normandy, ontogeny, variation.*

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Ammonoids have several properties that make them some of the best fossil organisms to study morphological changes in ontogeny and phylogeny: (1) they are highly abundant in the geological record due to their presumably high population density during their lifetime (Kennedy & Cobban 1976); (2) they had a very rapid morphological evolution during their existence from the Early Devonian throughout to the Late Cretaceous; and (3) the most impressive feature is that they retained all of their ontogeny within their conchs as they grew in a (usually) logarithmic spiral. The latter property is in contrast to vertebrates, for example, in which adult bones hardly allow any conclusions to be drawn about the original size and shape of the juvenile ones; or in arthropods, in which juvenile characters are lost when moulting. The three characters make them extremely suitable for studies on conch morphology and ontogeny.

We studied an assemblage of early Bajocian (Middle Jurassic) stephanoceratid specimens (Fig. 1) from Évreux (Normandy, France) and in order to consider the following questions: (1) how many and which species does the assemblage contain? Which morphometric patterns are visible? This work attempts to show how measured conch parameters, ratios and rates vary between the specimens in the assemblage; (2) what does the ontogeny of individual specimens show with regard to the key conch parameters? How

do these ontogenetic trajectories vary between the stephanoceratid specimens over the stratigraphical range of the sample; and (3) in which specimens can maturity be identified? Are there any sexual anti-dimorphs in the assemblage and how can they be characterized with regard to ontogenetic change in the conch geometry?

Aspects of ammonoid research

Ammonoid morphometrics

With regard to morphometric studies, Roth & Mercer (2000) provided an elegant definition of the term morphometrics: ‘Morphometrics is the quantitative characterization, analysis and comparison of biological form’. They proposed it as an instrument for extracting information about biological material and biological processes.

Although theoretical concepts for measuring and analysing the spiral growth of ammonoid conchs existed already in the 19th century (e.g. Sandberger 1858), it was not until the work of Raup & Michelson (1965) and Raup (1967) that it was demonstrated how ammonoid conchs could be measured and analysed in an elegant, quantitative manner. These studies defined the principal conch parameters that

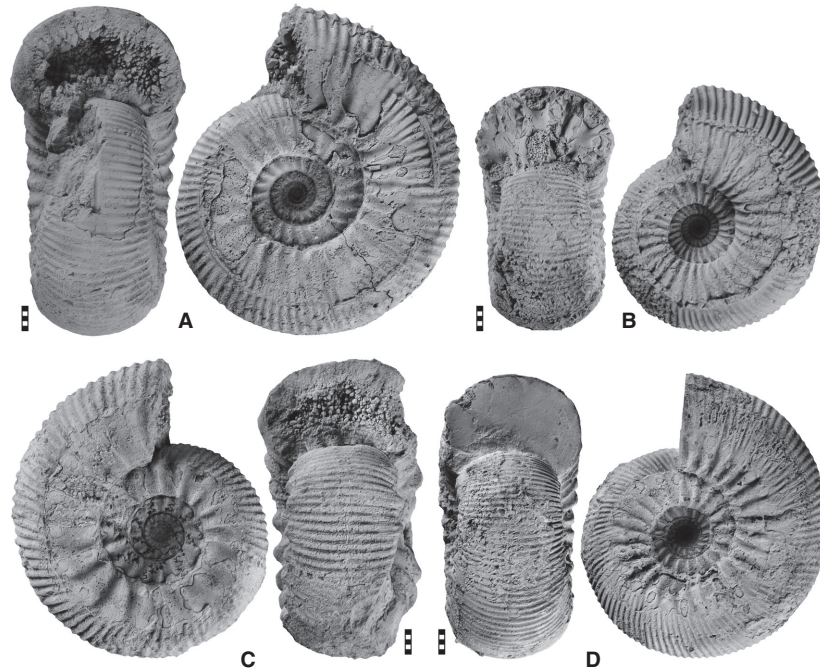


Fig. 1. Specimens of *Stephanoceras* from Évrecy. A, *Stephanoceras* sp. 1; specimen MB.C.30159 with broad, crescent-shaped whorl profile and fairly wide umbilicus. B, *Stephanoceras* sp. 1; specimen MB.C.30160 with higher aperture and narrower umbilicus. C, *Stephanoceras* sp. 1; specimen MB.C.30161 with coarse primary ribs, trapezoidal whorl profile and fairly wide umbilicus. D, *Stephanoceras* sp. 2; specimen MB.C.30162.

became so-called ‘Raupian parameters’, that is the conch radius, the whorl width and the whorl expansion rate, which reveal the data for defining a morphospace for the ammonoids within that of coiled mollusc conchs. The concept was then adopted by several authors (e.g. Saunders & Swan 1984; Saunders & Work 1997; Korn 2000) in order to analyse the dynamics in the succession of ammonoid assemblages. It has to be noted that Korn & Klug (2003) and Korn (2010) modified these conch parameters by using the conch diameter instead of the radius and a different equation for the whorl expansion rate (Fig. 2A).

Ammonoid ontogeny: growth stages and allometry

The ontogeny of an ammonoid conch is an important feature for investigating its lifetime morphology. Ontogeny refers to the change of size and shape during the development of an individual and was known worldwide after Haeckel (1866) proposed his largely discredited biogenetic law, often referred to as the ‘theory of recapitulation’. Haeckel professed this in its most famous form: ‘ontogeny recapitulates phylogeny’, which is now rejected by the majority of scientists (e.g. Gould 1977). Nonetheless, ammonoids are excellent organisms for studying ontogenetic

changes and differences between species. In the past, several authors have outlined the theoretical framework for ontogenetic research in ammonoids (e.g. Trueman 1922; Alberch *et al.* 1979; Bucher *et al.* 1996). In addition, studies were carried out with a focus on ontogenetic changes in both Palaeozoic (e.g. Kullmann & Scheuch 1972; Kant 1973; Korn 2012) and Mesozoic taxa (e.g. Gerber *et al.* 2007). According to Westermann (1958, 1996) and Klug (2001), the ontogeny of an ammonoid can be divided into four stages: (1) embryonic stage (embryonic conch, ammonitella); (2) neanic stage (neanoconch); (3) juvenile stage (juvenile conch); and (4) adult stage (adult conch).

In contrast to the living *Nautilus*, which grows with very weak allometry (except for the pre-hatching and terminal stage) (Korn 2012; Tajika & Klug 2020; Tajika *et al.* 2020), ammonoids almost always have a well-developed allometry. Isometric growth would mean that all ontogenetic trajectories run linear with the same value (allometric coefficient = 0) during ontogeny; this has apparently not been realized in the ammonoid development, at least never in the case of Palaeozoic species (Korn 2012). Allometric growth in particular, and allometry in general, can be defined in different ways. Gould (1966) referred to it in a broad sense and wrote ‘[It is a term] to designate the differences in proportions

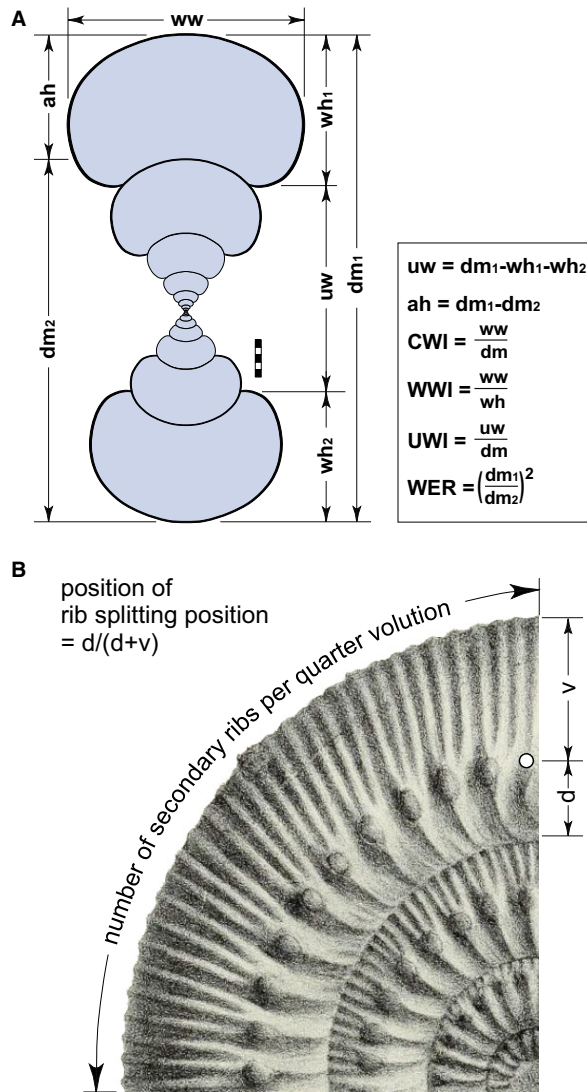


Fig. 2. A, conch dimensions obtained from ammonoid conch cross sections (using specimen MB.C.30163) and cardinal conch parameters as used in the analyses. B, sculpture data obtained from ammonoid conchs as used in the analyses. The image shows part of the lectotype illustration of *Stephanoceras humphriesianum* (Sowerby 1825) by Buckman (1908).

correlated with changes in absolute magnitude of the total organism or of the specific parts under consideration [...], or in simpler terms: '[It is] the study of size and its consequences'.

Korn (2012) described different modes of allometry that can occur in ammonoid conchs: (1) monophasic, which can occur as linear with a stable allometry coefficient $\alpha < 1$ or non-linear with a decreasing or increasing allometry coefficient; (2) biphasic, which can occur as linear with the succession of two stable allometry coefficients or non-linear with the succession of a decreasing and an increasing allometry coefficient; and (3) triphasic or polyphasic (Fig. 3).

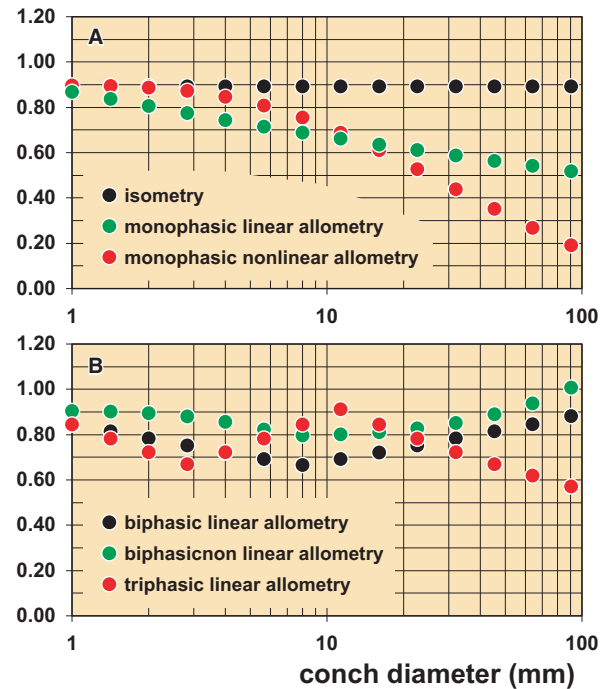


Fig. 3. Modes of isometry and various modes of allometry expressed in an ammonoid conch. A, isometry and monophasic allometry. B, biphasic and triphasic allometry.

Ammonoid macroconchs and microconchs

An hypothesis that ammonoids had sexes which differ in adult size, has a long tradition (e.g. de Blainville 1840; d'Orbigny 1842-1851). All these authors referred to dimorphic pairs that were assumed to be sexual antidimorphs while working on certain genera and species with bipolar size distributions. Callomon (1963) as well as Makowski (1962, 1971, 1991) contributed solid evidence for sexual dimorphism in Mesozoic taxa; his articles were complemented by studies on other Mesozoic cases (Brochwicz-Lewinski & Rozak 1976; Dzik 1994; Neige *et al.* 1997; Parent *et al.* 2008).

Callomon (1955) analysed assemblages that were collected from finely discriminated horizons. He introduced two terms to refer to different ammonoid sexes. He called the larger specimens 'macroconchs' and the smaller ones 'microconchs' because they occurred together in the same stratigraphical horizon and showed no difference in ontogeny. Although some authors suggested to add additional terms due to certain extraordinary big ('megaconchs'; Ivanov 1971) or exceptionally small ('miniconchs'; Matyja 1986) specimens, the vast majority of scientists agree with the proposal of Callomon (1955).

The decision as to whether two specimens belong to one species represented by macroconchs and microconchs or to two discrete species requires

clarification. Following initial works by Makowski (1962), Callomon (1963, 1981) and Davis *et al.* (1996), which were summarized by Klug *et al.* (2015), antidimorphs should show (1) differences in adult morphology, (2) fairly similar ontogenetic stages, (3) an occurrence in the same stratigraphical bed, (4) geo-geographical occurrences that overlap and (5) they should have had the same ancestor. Another point (6) considers the sex ratio, which should be stable over time and the evolution of the particular taxon. As mentioned earlier, the adult morphology should differ between the two sexes and several features must exist to detect and state the maturity of an ammonoid.

Numerous studies have focussed on mature modifications of ammonoids (e.g. Davis *et al.* 1996; Westermann 1996). The best features to proclaim the maturity of specimens are, apart from septal crowding: (1) changes in coiling in the terminal whorl; (2) a more or less sudden reduction of the surface of the whorl profile; (3) a change in the sculpture and ornament; and (4) the most conspicuous modifications: lateral lappets of microconchs. The change in coiling is marked by the term ‘umbilical egression’ and means an increase in the umbilical width ratio close to maturity. Lehmann (1981) used the term ‘retraction’ for this. A change of the sculpture at the end of somatic growth is mostly achieved by a decrease in rib density. In the macroconchs and in particular in stephanoceratids, there is often a strong constriction followed by a raided collar directly before the peristome.

Material and methods

Approximately 3,000 ammonoid specimens were available for study; more than 1,000 specimens

belong to the genus *Stephanoceras*. They were assembled by the fossil collectors Michael Heimann (Tecklenburg) and Reinhard Schmode (Rheurdt) from rock material ploughed from fields and collected from building sites in the vicinity of Évrecy (near Bayeux, Normandy, France) (Fig. 4A) and donated to the Museum für Naturkunde, Berlin. All specimens are from the lower part of the ‘Oolithe Ferrugineuse de Bayeux’ Formation, but the precise horizon cannot be determined. This oolite is a highly condensed formation of 20-cm to 3-m thickness (Pr at *et al.* 2000; Pavia & Martire 2009; Pavia *et al.* 2013, 2015), of which a very fossiliferous portion belongs in the *Humphriesianum* Zone (e.g. Maubeuge 1951; Rulleau 2011). Pavia *et al.* (2013, p. 142) concluded, for the neighbouring Maizet section, that ammonites from several biochrons can be found in the same sample.

A separation of the oolite into sub-units with finer stratigraphical resolution was not possible by our *ex situ* collected material from  vrecy; time averaging can play an important role in this ammonoid assemblage. All specimens examined here come from a rusty-yellow packstone with very numerous limonite ooids up to 2 mm in size. Specimens of the genus *Stephanoceras* (Fig. 1) outnumber all other co-occurring ammonites. According to the close similarity to the occurrence at Bretteville (Pavia & Martire 2009), it is likely that the assemblage comes from the *Humphriesianum* Chron (Fig. 4B). The close resemblance to the middle *Humphriesianum* Chron of bed 5 in the neighbouring Maizet section (Pavia *et al.* 2013) may provide an even finer stratigraphical attribution. However, it cannot be excluded that the assemblage from  vrecy contains ammonites of different chrons. At the same locality, but in somewhat

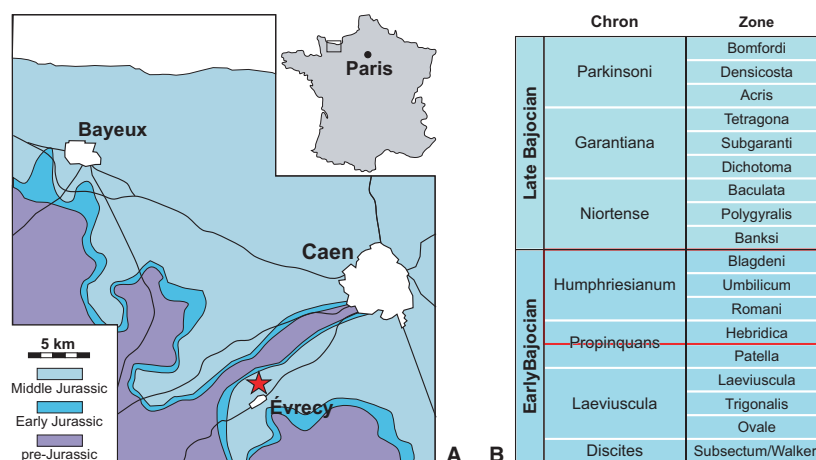


Fig. 4. A, geographical position of the locality of  vrecy in Normandy (France). B, stratigraphical subdivision of the Bajocian in Normandy with the position of the *Stephanoceras* assemblage in the *Humphriesianum* Chron.

finer-grained oolites, *Chondroceras* occurs in large numbers (analysed by Walton & Korn 2017). Pavia *et al.* (2013) concluded that four different ammonite chrons are represented in bed 5 of the Maizet section (*Propinquans* Chron to late *Humphriesianum* Chron). This corresponds to the upper *Sauzei* Zone and the *Humphriesianum* Zone in the Inferior Oolite of southern England (Chandler *et al.* 2017) and southern Germany (Dietze *et al.* 2013).

For the analysis presented here, we chose the genus *Stephanoceras* because of the large number of specimens available. A taxonomic revision of the *Stephanoceras* species within our studied sample is outside the scope of our investigation. Such a revision would require in situ collected material in finest stratigraphical resolution. Since our study focusses on the ontogenetic development of conch morphology, we first distinguished two groups of stephanoceratids based on shell sculpture (in a growth stage above 40 mm conch diameter).

A small subset of *Stephanoceras* specimens has 29 or more secondary ribs per quarter volution; these specimens are clearly separated from all others, which have rib numbers between 17 and 24. We have concentrated on the latter group, which is kept in open nomenclature here (*Stephanoceras* sp. 1). It may belong to the long-known species *Stephanoceras humphriesianum* (Sowerby, 1825).

We sectioned a total of 55 specimens for the study of the conch ontogeny. Since none of the specimens have preserved the terminal aperture, all of them are sections at a random angle. 23 of them are complete in terms of preservation of the initial whorls including the protoconch (Figs S1–S4). However, the diameters of the specimens range from 44 to 110 mm. Since most of them lack characteristic adult modifications, this means that different ontogenetic stages are represented in these sections. Adulthood can therefore only be detected when sudden changes in the conch are visible.

After grinding and polishing with the aim of meeting the protoconch at its maximum diameter, the surfaces were scanned in high resolution (600 dpi; 2400 or 4800 dpi for the inner whorls) and digitized. The resulting vector images do not exactly reproduce the scanned surface; asymmetries caused by ribs or damages were extrapolated, resulting in symmetrical cross section drawings. Care was taken to ensure that the morphometric properties were not affected by this procedure. By using cross sections, continuous data per half-volution could be obtained (Fig. 2A; supplementary material).

The 23 sectioned specimens with complete ontogeny including initial volutions were analysed for the description of ontogenetic trajectories and

quantification of ontogenetic change (Korn 2012). Another 32 sectioned specimens do not show the inner whorls and were therefore excluded from some analyses including the quantification of ontogenetic change. They were used for the morphospace analysis and partly for the correlation analysis.

We analysed two features of the sculpture: (1) the density of the secondary ribs; and (2) the position in which the primary ribs split into the secondary ribs (Fig. 2B). We counted the number of secondary ribs over a quarter of a volution to get a size-independent rib index.

For the analysis of the successive stages of conch development, we subdivided the ontogeny between 1 and 100 mm conch diameter of the specimens into 20 log intervals (Table S1). These bins were then used to calculate medians and quartiles for distinct growth intervals and also to quantify the variation within the samples. The specific methods of analysis relating to sculpture, conch morphology, conch ontogeny, variation and morphospace are explained at the beginning of the relevant sections. The analyses were performed using the PAST 4.03 software (Hammer *et al.* 2001).

The cardinal conch parameters used in the analyses and throughout the text are as follows (Fig. 2A):

CWI = conch width index ($ww/dm = \text{whorl width/conch diameter}$)

WWI = whorl width index ($ww/wh = \text{whorl width/whorl height}$)

UWI = umbilical width index ($uw/dm = \text{umbilical width/conch diameter}$)

WER = whorl expansion rate: increasing rate of the conch diameter during one volution

All raw data (measurements of conch parameters, rib counts etc.) are presented in the Supplementary Material.

Results and discussion

*Morphological range and sculpture patterns of the *Stephanoceras* assemblage*

Species of *Stephanoceras* are usually separated by differences in various conch and sculpture characters, such as (1) the ratio of whorl width and conch diameter, (2) the ratio of umbilical width and conch diameter, (3) the shape of the whorl profile (e.g. crescent-shaped or trapezoidal), (4) the strength of the nodes on the flank, (5) the position of the nodes (closer or more distant to the umbilicus), (6) the number of

primary and secondary ribs, (7) the number of secondary ribs in relationship to the primary ribs and (8) the course of the ribs on the venter.

It is necessary to say that all of the characters listed above change during ontogeny and thus depend on the size of the specimens. Changes in the sculpture, for example, can be observed in the lectotype of *S. humphriesianum* (e.g. Buckman 1908), in which the ribs become denser during the last volution between about 68 and 122 mm conch diameter (increase from 25 to 30 secondary ribs per quarter volution) and the splitting point of the ribs is shifting towards the umbilicus (from about 50% of the whorl height to 40% during the last volution). As shown below, the cardinal conch parameters do also change during ontogeny, so only comparisons between specimens with very similar conch diameters are reasonable.

For an analysis of the sculpture patterns, we selected the sectioned specimens; we counted the secondary ribs and measured the position of rib splitting in a growth interval between 40 and 50 mm conch diameter. In this material, the number of secondary ribs per quarter of a whorl ranges between 17 and 30.

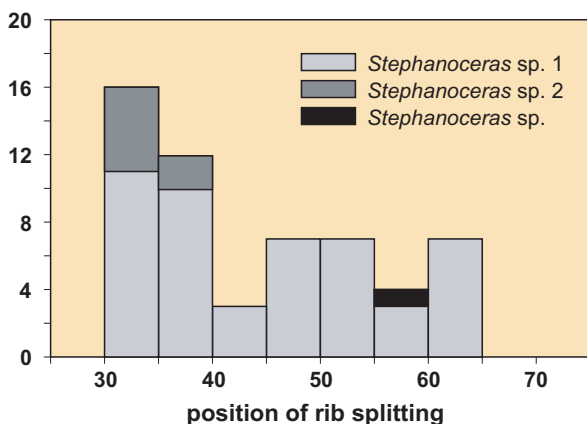
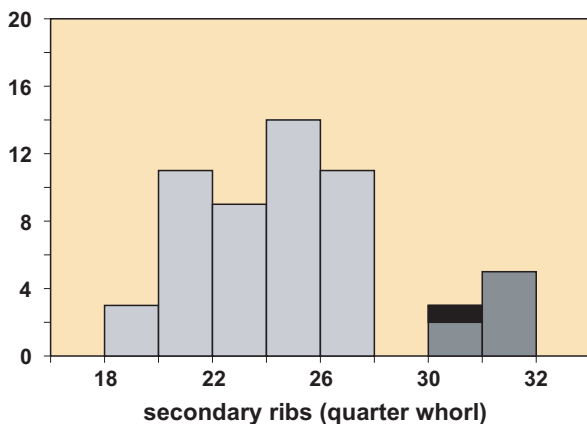


Fig. 5. Histograms showing the frequency distribution of the number of secondary ribs in a growth stage between 40 and 50 mm conch diameter.

There is not a random distribution of the numbers of ribs; a larger group of specimens ranges between 17 and 25, separated by a gap from a smaller number that has 29 or 32 ribs (Fig. 5).

The position in which the primary ribs split into secondary ribs ranges between 0.30 and 0.65 of the whorl heights. This is closely related to the shape of the whorl profile; rib splitting is more distant from the umbilicus in trapezoidal whorl profiles.

Nevertheless, distinct species represented in the *Stephanoceras* assemblage can be separated only incompletely by using the sculpture characters. In the following, we thus separate only three species groups, which differ in the number of secondary ribs:

- 1 *Stephanoceras* sp. 1 – Specimens with 17–25 secondary ribs, a varying position of the rib splitting point (dorsolateral, lateral or ventrolateral) and a varying conch morphology. These may, at least partly, belong to *S. humphriesianum* (Sowerby, 1825). It is the group that is the main focus of this study.
- 2 *Stephanoceras* sp. 2 – Specimens with 29–32 secondary ribs and a dorsolateral position of rib splitting; these are included in the analyses for comparison.
- 3 A third group is represented only by the single specimen MB.C.30164, which is characterized by 30 secondary ribs and a splitting point in the ventrolateral area.

The study of the morphological spectrum of conch geometry in the assemblage reveals that, at 40–50 mm conch diameter, the average specimen of *Stephanoceras* sp. 1 is thickly discoidal (CWI = 0.55) and subevolute (UWI = 0.40) with a moderately depressed whorl profile (WWI = 1.60) and a moderately high coiling rate (WER = 1.88).

Covariation

For an analysis of a possible covariation of conch and sculpture parameters in the specimens of *Stephanoceras* sp. 1, we used the conch parameters of the sectioned specimens (CWI, UWI and WER), data of ontogenetic change (quantified ontogenetic change) and sculpture characteristics (number of secondary ribs, position of splitting point of the primary ribs in the last quarter of a whorl before the respective diameter). We calculated the Pearson correlation coefficient (cc) (Pearson 1896) and the Spearman rank correlation coefficient (Spearman 1904) using these characters and found that there is only little correlation between most of the characters (Fig. 6).

- There is weak correlation between the number of secondary ribs and the position of the rib splitting (correlation coefficients of -0.31 in both methods).
- Correlation between CWI and UWI as well as UWI and WER shows a moderate negative correlation (cc about -0.40 to -0.50), while correlation between CWI and WER is very weak (cc below 0.20).
- There is almost no correlation between the number of secondary ribs and the CWI and WER (cc below 0.10) and only weak correlation between the number of secondary ribs and the UWI (cc = 0.20).
- The quantified ontogenetic change (D_{cumul}/dm_{log}) is weakly correlated with any of the other characters.
- As expected, there is negative correlation in the characters of the contribution of CWI, UWI and WER to the total ontogenetic change. This is not surprising, as these three represent proportions

(to produce a ternary diagram). It is also not surprising that the UWI-WER correlation is better as an increase of the coiling rate is, because of geometric relationships, causing a narrower umbilicus.

These data show that a clear separation of possible morphospecies within the material of *Stephanoceras* sp. 1 from Évrecy is not possible. Application of the traditional characters (number of ribs, position of the splitting point, shape of the whorl profile) does not give results that allow the recognition of clear morphological boundaries between species.

Ontogenetic trajectories

Ontogenetic trajectories can be described using two-dimensional cross sections with preservation of the inner volutions (Korn 2012) or three-dimensional scans (Tajika *et al.* 2015). The analysis of the cardinal conch parameters conch width index (CWI; w/w

	n sec. ribs	node at wh %	CWI	UWI	WER	Dcumul/dmlog	CWI contr.	UWI contr.	WER contr.	
n sec. ribs		-0.308	0.035	-0.207	0.005	0.279	0.187	-0.068	-0.098	Pearson's cc
node at wh %	-0.306		0.122	0.259	0.070	-0.033	-0.214	0.251	-0.074	
CWI	-0.001	0.055		-0.456	0.135	-0.278	-0.380	0.109	0.227	
UWI	-0.204	0.247	-0.455		-0.502	-0.008	0.430	0.109	-0.505	
WER	0.017	0.180	0.170	-0.412		-0.111	-0.447	0.116	0.278	
Dcumul/dmlog	0.307	-0.042	-0.287	-0.048	-0.081		0.332	-0.045	-0.252	
CWI contr.	0.149	-0.238	-0.417	0.466	-0.464	0.427		-0.496	-0.374	
UWI contr.	0.052	0.105	0.162	-0.102	0.277	-0.028	-0.524		-0.620	
WER contr.	-0.085	-0.018	0.171	-0.498	0.127	-0.257	-0.318	-0.571		

Fig. 6. Pearson's correlation coefficient (cc) (Pearson 1896) and the Spearman rank correlation coefficient (Spearman 1904) the specimens of *Stephanoceras* sp. 1, using conch parameters of the sectioned specimens (CWI, UWI and WER), data of ontogenetic change (quantified ontogenetic change) and sculpture characteristics (number of secondary ribs, position of splitting point of the primary ribs in the last quarter of a whorl before the respective diameter).

dm), whorl width index (WWI; w/w_h), umbilical width index (UWI; uw/dm) and whorl expansion rate (WER) was done to get a picture of the entire assemblage and the ontogenetic trajectories of distinct specimens. To analyse most accurate data, only complete cross sections (i.e. starting with the protoconch) were used (23 specimens).

CWI: The total plot shows an undulating, triphasic ontogeny: The median begins with 0.72 in the 1st bin (1.00–1.25 mm dm), is low with 0.61 in the 9th bin (6.2–8.0 mm dm), raises up to 0.64 in the 11th bin (10.0–12.5 mm dm) and eventually decreases to 0.46 in the 20th bin (80–100 mm dm).

UWI: As in the CWI, the UWI also has a triphasic ontogeny, but this does not show the same timing. The median begins with 0.35 in the 1st bin (1.00–1.25 mm dm), is high with 0.45 in the 8th bin (5.0–6.2 mm dm), decreases to a broad depression of 0.40 in the 15th to 17th bin (25–50 mm dm) and eventually increases to 0.43 in the 20th bin (80–100 mm dm).

WWI: The triphasic ontogenetic trajectory is largely following the CWI trajectory, meaning that changes in whorl width are not compensated by changes in whorl height.

WER: It is the fourth parameter with a triphasic ontogeny, but it does not parallel, in timing, the other three. The median begins with 1.83 in the 1st bin (1.00–1.25 mm dm), is low with 1.72 in the 8th bin (5.0–6.2 mm dm), raises up to a plateau of nearly 1.90 in the 13th to 17th bin (16–50 mm dm) and eventually slightly decreases to nearly 1.80 in the 19th band 20th bin (64–100 mm dm).

The plots of all of the 24 sectioned specimens show that each of the four cardinal conch parameters shows an undulating course that can be described by the succession of three ontogenetic phases. The turning points separating these phases do not occur simultaneously, and the length of the individual phases differs between the parameters.

The regularly undulating trajectories with the dots arranged in bands of nearly constant width throughout ontogeny may suggest that such a regular undulation also occurs in the single specimens. This is not always the case, as demonstrated in some of the trajectories.

To illustrate this, we selected six representative specimens, which were chosen as representatives for marginal positions, in at least one of the conch parameters, in the ontogenetic trajectory band (Figs 7–9). These six specimens are those with widest and narrowest conch, widest and narrowest umbilicus and highest and lowest coiling rate. These six specimens alone show that there appears to be no obvious covariation between the characters.

For example, specimens MB.C.30166 (with the widest umbilicus at 45 mm dm; Fig. 8A) and MB.C.30167 (with the narrowest umbilicus at 45 mm dm; Fig. 8B) are almost identical in the CWI trajectory throughout ontogeny, where they have a position in the centre of the morphological spectrum (Fig. 8D). They also show only minor differences in the WER trajectory with specimen MB.C.30166 being in the centre of the morphological range. Both specimens show almost identical conch proportions up to a conch diameter of 5 mm with a subsequent deviation with respect to the umbilical width that causes differences in the whorl profile shape (Fig. 8D). The difference are largest at 60 mm diameter, but towards the end of growth above 80 mm diameter, the general conch form of the two specimens closely resembles.

Specimens MB.C.30164 (with the widest conch) and MB.C.30181 (with the narrowest conch) possess nearly identical ontogenetic developments of the UWI and WER (Fig. 7). Only in some cases, such as in specimens MB.C.30168 (with the highest coiling rate) and MB.C.30169 (with the lowest coiling rate), differences in the CWI and UWI trajectories can be seen (Fig. 9).

However, this analysis shows that the four cardinal conch parameters do not allow the separation of species within the assemblage. The characters show a mosaic pattern within the sample and prevents the detection of clear morphological boundaries between groups of specimens. A similar pattern was found by Korn & Klug (2007) for the Late Devonian *Manticoceras* from Coumiac (Montagne Noire, France), where the conch parameters and also the ontogenetic trajectories were very plastic.

One has to consider that with the examined *Stephanoceras* assemblage, the morphospecies concept may be questioned. Since all the material was collected on the surface, it was not possible to investigate whether a stratigraphical sequence of different morphological features occurs. It was therefore not possible to test whether the *Stephanoceras* assemblage from Évrecy, which is most likely averaged over time, shows similar stratophenetic patterns as the Callovian material from *Virgatites* and *Quenstedtoceras* examined by Dzik (1985, 1987).

Quantification of conch ontogeny

To quantify the ontogenetic change, we calculated the cumulative value of the change of the three conch parameters CWI, UWI and WER for each half-revolution of the 24 complete cross sections using the method proposed by Korn (2012). As the cumulative values of these individual changes are size-

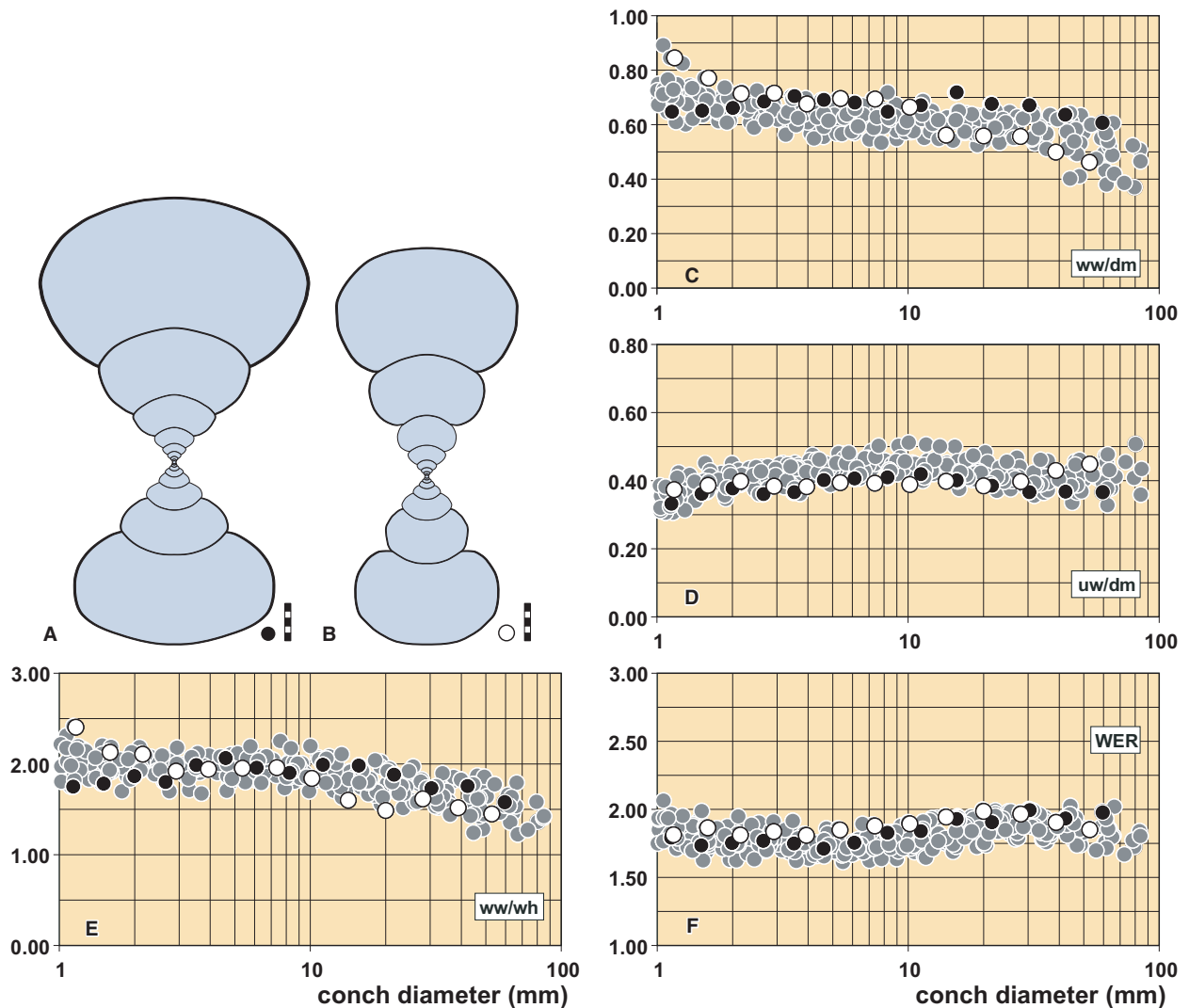


Fig. 7. Cross sections of the two specimens MB.C.30164 (A, specimen with stout conch) and MB.C.30165 (B, specimen with slender conch) as well as their ontogenetic trajectories (C–F) within the data of the entire assemblage. Scale bar units = 1 mm.

dependent, we divided the cumulative change by the log diameter (D_{CUMUL}/dm_{log}), which then leads to size-independent results (Figs 10, 11). Additionally, we calculated the contribution of each of the three conch parameters to the total ontogenetic change.

The D_{CUMUL}/dm_{log} value ranges, in the 24 sectioned specimens, between 0.73 and 1.19 and is hence comparatively low when compared with other ammonoids, particularly from the Palaeozoic (Korn 2012). The specimens are almost equally distributed within this range; there is neither a preference to lower or higher rates in ontogenetic change, nor a grouping within this range (Fig. S5).

In the ternary plot, which shows the contribution of the three conch parameters for each of the specimens, the occupied field has a position near the centre (Fig. 12). The plot explains that the variation in

the ontogenetic characters is rather high; the CWI contribution ranges from 21% to 40%, the UWI contribution from 29% to 55% and the WER contribution from 20% to 42%. These values reflect the situation in the *Stephanoceras* specimens that conchs can reach a very similar adult morphology by different ontogenetic trajectories.

Variation within the assemblage

There are differences between the terms variation and variability. According to Wagner & Altenberg (1996), variation refers to visible distinctions in a present collection or assemblage of a species, whereas variability stands for the actual potential of an individual organism to vary (in relation of certain parameters). Besides the fact that intraspecific

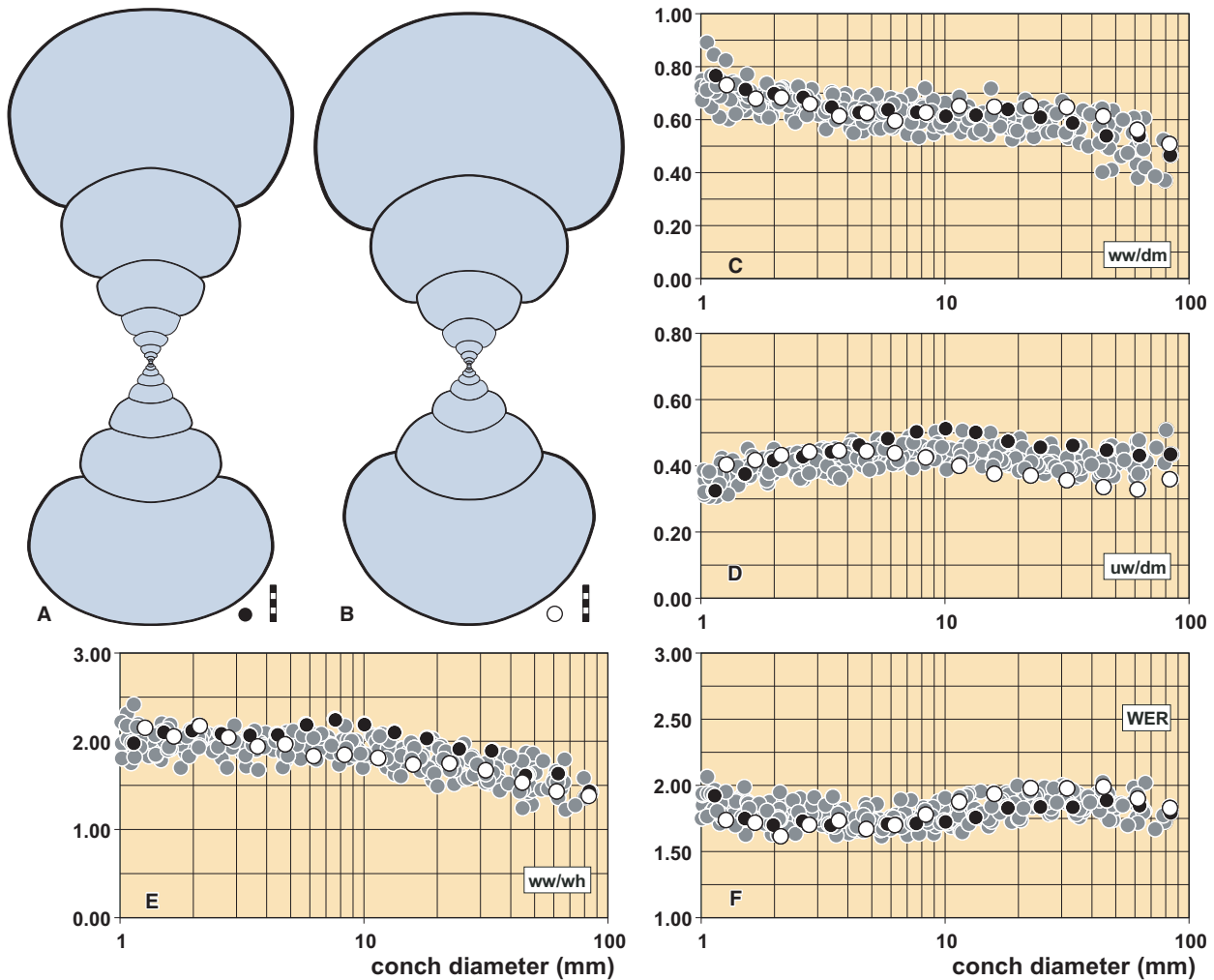


Fig. 8. Cross sections of the two specimens MB.C.30166 (A, specimen with wide umbilicus) and MB.C.30167 (B, specimen with narrow umbilicus) as well as their ontogenetic trajectories (C–F) within the data of the entire assemblage. Scale bar units = 1 mm.

ammonoid variation could depend on the environment (ecophenotypic variation) or the region (geographical variation), there are two major forms of intraspecific phenotypic variation: continuous and discontinuous variation. Continuous variation means that it follows in most cases a unimodal Gaussian distribution (Tintant 1980), while discontinuous variation refers to polymorphism (Ford 1955, 1965). A summary of variation and variability in ammonoids, including definition or terms, was provided by De Baets *et al.* (2015).

In the cardinal conch parameters, there is a wide band of dots in each of the bivariate plots, which provides evidence that variation occurs in all characters (Fig. 13). It is conspicuous that variation is, in the analysed conch parameters, similarly expressed throughout ontogeny.

The analysis of the distribution of values within certain growth intervals shows that there is only

rarely a normal or close-to-normal distribution (Fig. S6). This may, however, be due to the rather small sample size.

CWI: In the bivariate plot, the dots are arranged in a band of 0.10–0.18 width (i.e. reflecting variation at each growth stage) with exception from the early juvenile stage (possibly caused by a higher error rate) and the large stage above 40 mm conch diameter (here caused by some microconchs with an adult modification). The box plots show that the range of the middle two quartiles within the single bins is nearly always half the width of the total range.

UWI: Variation ranges between 0.08 and 0.15 and is slightly higher in the early juvenile and in the large stage. The range of the middle two quartiles within the single bins is nearly always half the width of the total range. Almost all bins show a central position of the middle two quartiles.

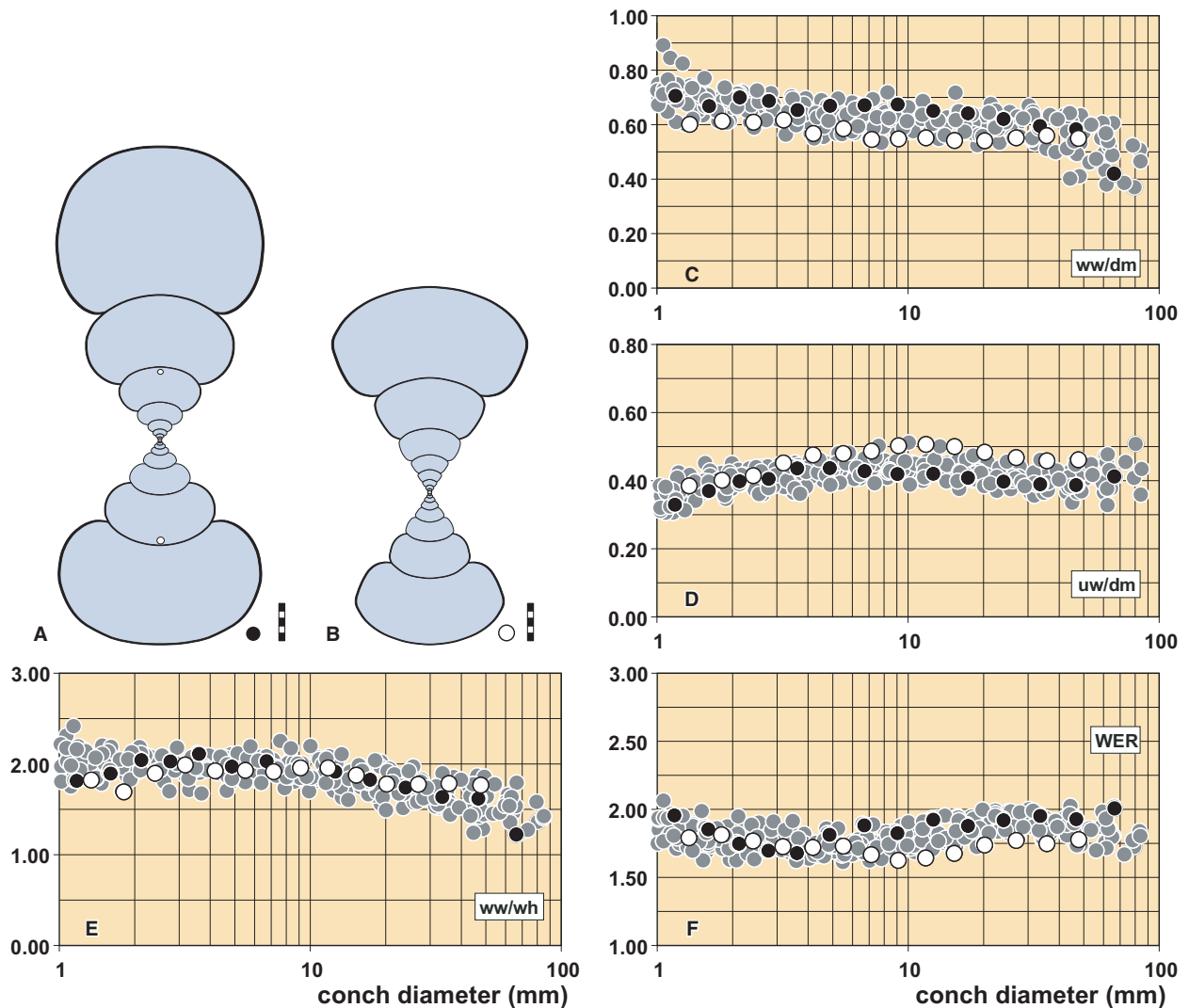


Fig. 9. Cross sections of the two specimens MB.C.30168 (A, specimen with high coiling rate) and MB.C.30169 (B, specimen with low coiling rate) as well as their ontogenetic trajectories (C–F) within the data of the entire assemblage. Scale bar units = 1 mm.

WER: The dots are, like in the other parameters, arranged in a wide band (with a width between 0.20 and 0.35). Almost all bins show a central position of the middle two quartiles.

Conch morphospace of the assemblage

We performed a principal components analysis to analyse covariation within the assemblage (Fig. 14). For this analysis, we used all cross-section data of the 55 sectioned specimens and run the analysis using the correlation mode. PC1 expresses 53.8% of the total variance and PC2 33.8%; therefore, the first two axes explain the vast majority of the variance of the specimens. PC1 mainly expresses differences in the UWI and less in the WER and CWI, while PC2

mainly expresses the CWI and the WER but not the UWI.

To depict the position of specimens with a similar conch size in the morphospace, we have highlighted the measurements of the 17th bin (40–50 mm conch diameter). The scatter plot demonstrates that specimens of this growth interval occupy only a small area of the total morphospace. Specimens with wide conch, narrower umbilicus and high coiling rate are in the upper right corner; specimens with narrow conch, wide umbilicus and low coiling rate have a position in the lower left area.

Distribution of the sectioned specimens, at a conch diameter between 40 and 50 mm, is scattered without any noticeable grouping. This reflects a more or less continuous variation within the sample; it

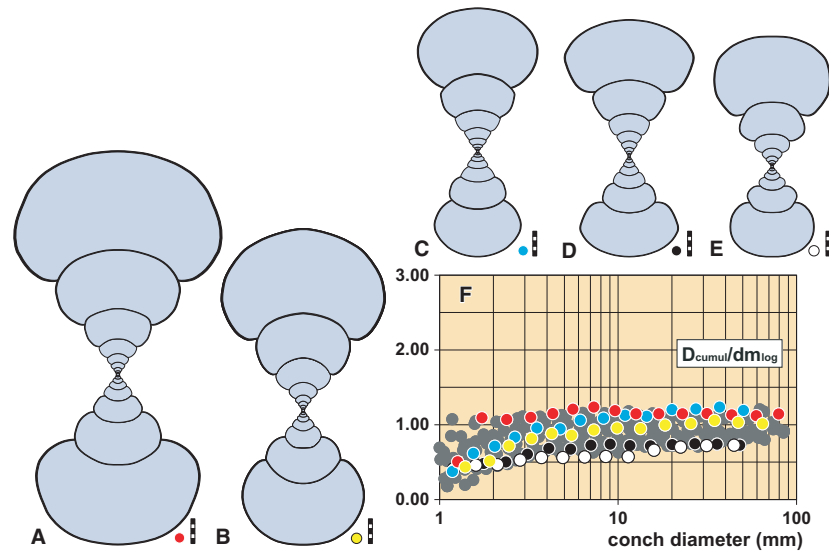


Fig. 10. Quantified ontogenetic change ($D_{\text{CUMUL}}/dm_{\text{log}}$) in selected specimens of *Stephanoceras* from Évrecy. A, specimen MB.C.30170. B, specimen MB.C.30171. C, specimen MB.C.30172. D, specimen MB.C.30169. E, specimen MB.C.30173. F, representation of the five selected specimens; all sectioned specimens represented by background dots. Scale bar units = 1 mm.

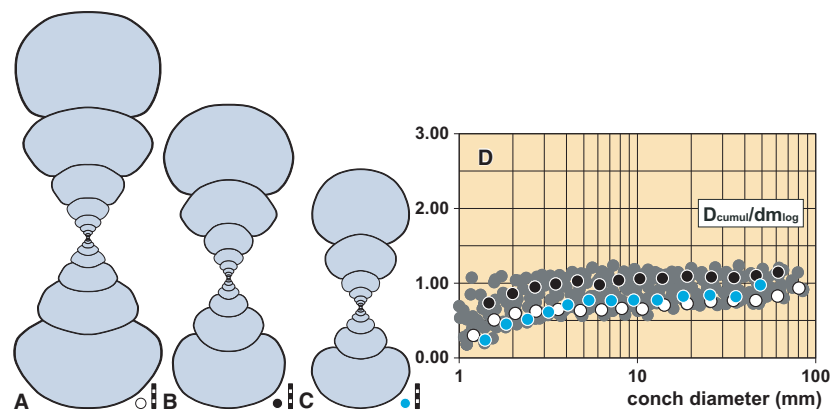


Fig. 11. Quantified ontogenetic change ($D_{\text{CUMUL}}/dm_{\text{log}}$) in selected micromorphic specimens of *Stephanoceras* from Évrecy. A, specimen MB.C.30174. B, specimen MB.C.30175. C, specimen MB.C.30176. D, representation of the five selected specimens; all sectioned specimens represented by background dots. Scale bar units = 1 mm.

appears impossible to separate distinct species. The two outliers in the lower left are the microconchs MB.C.30176 and MB.C.30179, which deviate in their adult modification (narrowing of the whorls, decrease of whorl overlap by umbilical egression).

It can also be seen from the PCA scatter plot that there appears to be no correlation between the morphometric data with the outline shape of the whorl profiles. The positions of trapezoidal and crescent-shaped whorl profiles overlap in the plot.

Dimorphism

In *Stephanoceras*, adulthood of a specimen is demonstrated by a fairly rapid change of conch

geometry: (1) by narrowing of the whorl profile, which changes from crescent shape to circular (expressed by a decrease of the WWI and consequently a decrease in the CWI) and (2) by weak uncoiling caused by umbilical egression causing an increase of the UWI and a decrease of the imprint zone rate.

Seven out of the 23 complete cross sections show obvious adult modifications and can be regarded as microconchs (Fig. S7). As the cross sections were not oriented in the specimen, they provide a somewhat random section, meaning that they represent a variable stage of adult modification and cannot be accurately compared with one another. Another problem is that some of the smaller specimens may represent

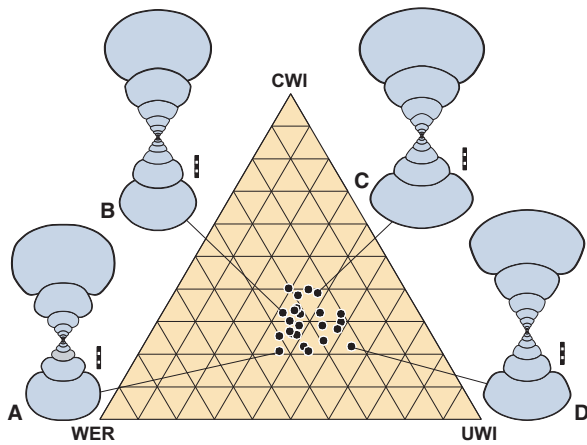


Fig. 12. Ternary diagram showing the proportional contributions of the cardinal conch parameters CWI, UWI and WER to the quantified ontogenetic change. A, specimen MB.C.30173. B, specimen MB.C.30172. C, specimen MB.C.30177. D, specimen MB.C.30169. Scale bar units = 1 mm.

the inner whorls of larger microconch specimens without modifications.

Although only seven of the 23 specimens with preserved protoconch show adult modifications and can be regarded as microconchs; they show some morphological variation. One aspect of variation, for example, is the size in which the narrowing of the

aperture begins; this ranges from around 40 mm conch diameter (specimens MB.C.30176, MB.C.30179; Fig. S7F, G) to about 75 mm diameter (specimen MB.C.30174; Fig. S7A).

The degree of adult modification is depending on the position of the section and can thus not be accurately compared between the specimens. It appears that in specimens MB.C.30168 (Fig. 9A), MB.C.30181 (Fig. 15B), MB.C.30176 (Fig. 15C) and MB.C.30179 (Fig. 15D), only the beginning of the transformation can be seen. Decrease of the CWI and increase of the UWI is only visible in the last volution, which conspicuously differs in its shape from the preceding. In contrast to this shows specimen MB.C.30174 (Fig. 15A) already a modification in the penultimate volution; the length of the interval with adult modification is hence longer than half a volution.

There is no obvious preferential position or grouping of the microconch specimens within the morphological spectrum. All that can be said is that the microconchs appear to prefer a central position in the CWI trajectory (Fig. 15E); among the seven microconchs, there are no extremely stout or slender specimens. When the quantified ontogenetic change (D_{CUMUL}/dm_{log}) is regarded, the microconchs are scattered within the range of the assemblage (Figs 11, S5).

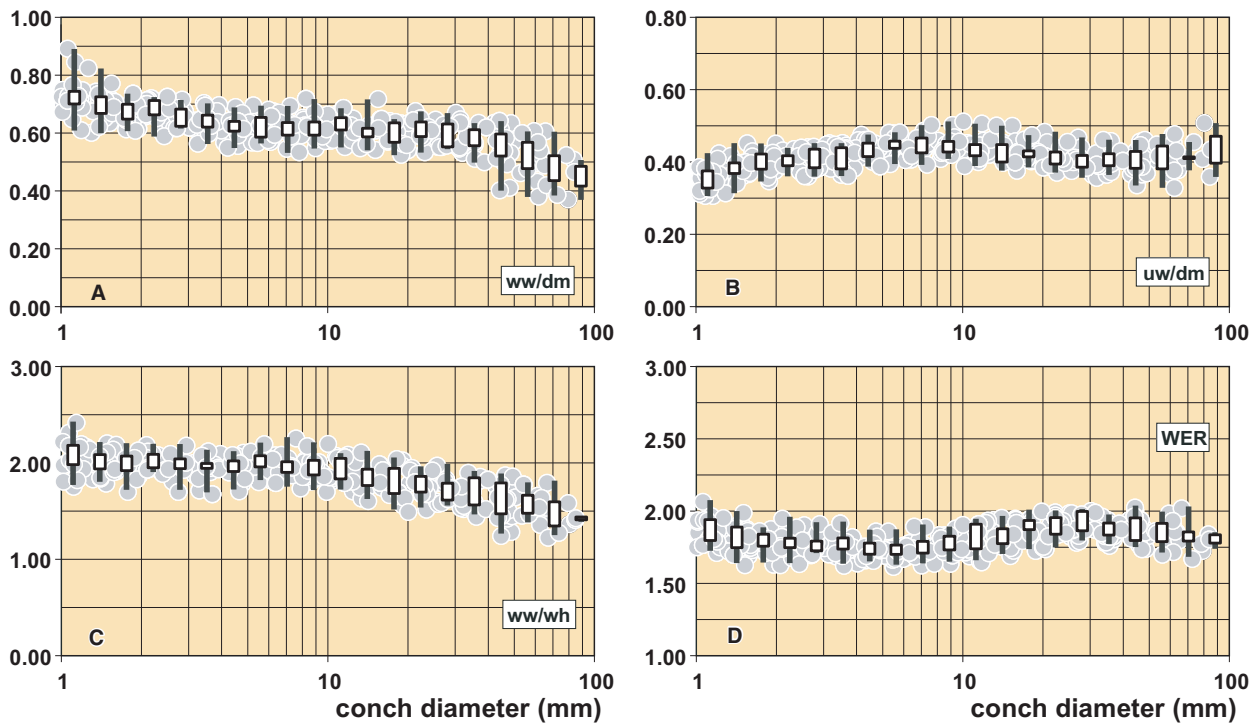


Fig. 13. Variation in the cardinal conch parameters in box-and-whiskers diagrams, showing the total range and range of the middle two quartiles for each bin.

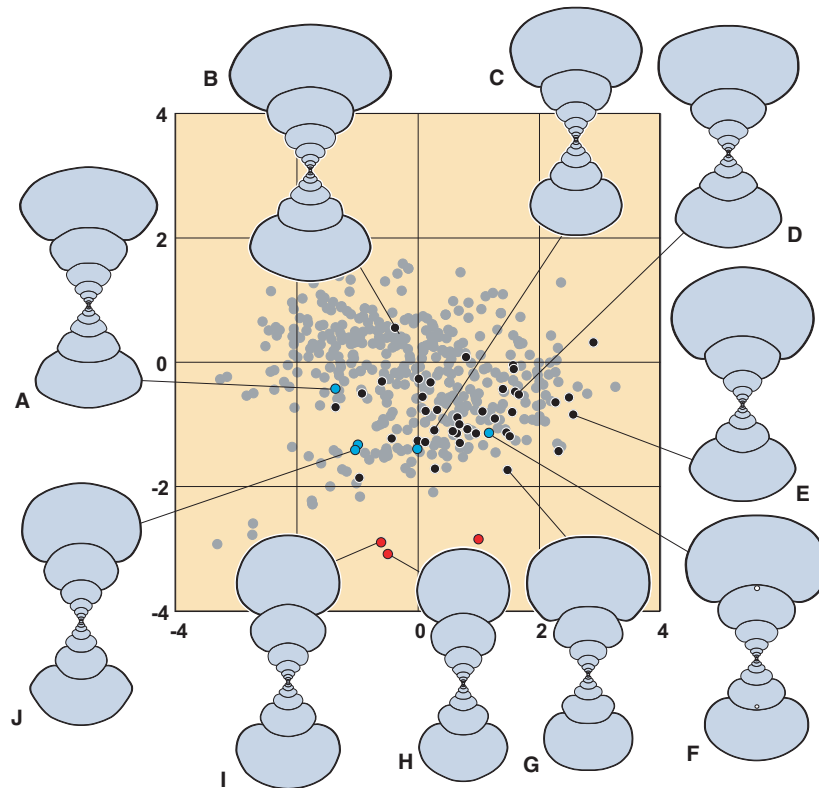


Fig. 14. The morphospace of *Stephanoceras* from Évrecy; each grey dot represents on half-volution of each of the sectioned specimens. Highlighted are the data from growth interval between 40 and 50 mm conch diameter. Grey dots = all measurements; red dots = microconchs; blue dots = microconchs, in which the adult modification occurs above 40–50 mm dm; black dots = macroconchs and indifferent specimens. A = MB.C.30174, B = MB.C.30178, C = MB.C.30170, D = MB.C.30164, E = MB.C.30167, F = MB.C.30168, G = MB.C.30173, H = MB.C.30179, I = MB.C.30176, J = MB.C.30175.

Conclusions

The large suite of specimens studied (more than 1,000) belonging to the Bajocian genus *Stephanoceras* from the lower part of the 'Oolithe Ferrugineuse de Bayeux' Formation of Évrecy (Normandy, France) enables the analysis of a number of conch and sculpture patterns for a study of palaeobiological topics.

Morphological range and sculpture patterns

The quantitative analysis of the conch geometry and its ontogeny reveals major problems in the separation of *Stephanoceras* species within the assemblage; clear morphological boundaries between possible species cannot be established. A clear separation of species appears to be impossible in the sample, which is composed of mixed assemblages. A grouping can be done by the use of the number of ribs. A group with lower number of secondary ribs (17–25 per quarter volution) is named here *Stephanoceras* sp. 1, and a group

with higher number (29–32 per quarter volution) is regarded as *Stephanoceras* sp. 2.

Covariation

There occurs weak or almost no correlation between conch geometry and sculpture in the representatives of *Stephanoceras* from Évrecy. The number of secondary ribs and the splitting point of the ribs are not influenced by the shape of the whorl profile.

Ontogenetic trajectories, quantification of conch ontogeny

For a quantitative analysis of the conch ontogeny, more than 50 specimens were sectioned. The cardinal three conch parameters (conch width index, umbilical width index and whorl expansion rate) show triphasic ontogenetic development, but the three phases of the parameters are not parallel. The analysis also shows that the ontogenetic development of conch geometry does not allow the separation of species within the assemblage.

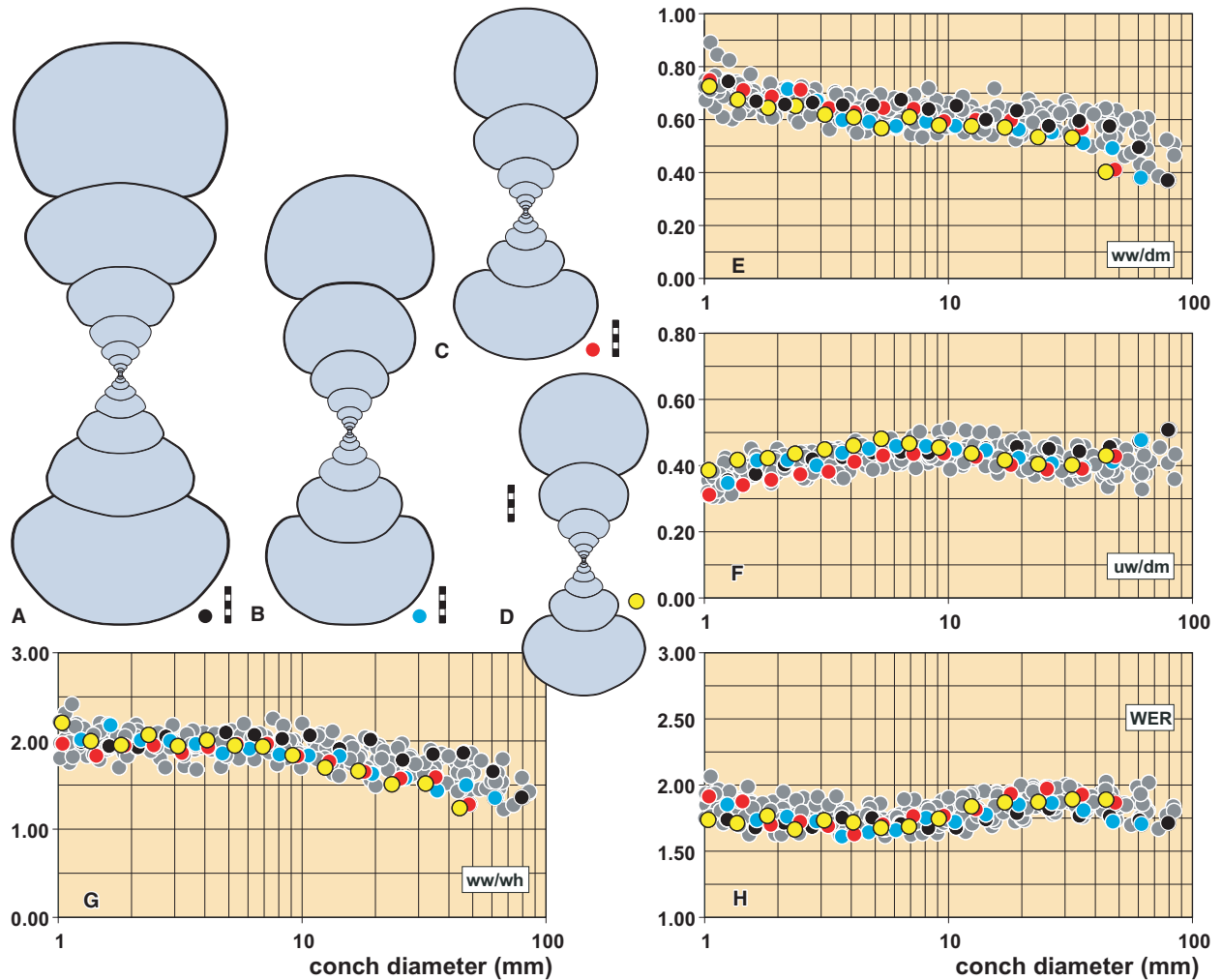


Fig. 15. Cross sections of the micromorph specimens MB.C.30174 (A), MB.C.30181 (B), MB.C.30176 (C) and MB.C.30179 (D) as well as their ontogenetic trajectories (E–H) within the data of the entire assemblage. Scale bar units = 1 mm.

Variation within the assemblage

The material shows wide variation in sculpture and conch parameters throughout ontogeny. Variation is, in the analysed conch parameters, similar throughout ontogeny.

Dimorphism

With the study of conch ontogeny, it is possible to separate dimorphs, as microconchs show a sudden change in the conch parameters (umbilical egression, change in the shape of the whorl profile). The onset of these changes varies in the assemblage between 40 and 75 mm conch diameter.

In summary, the stephanoceratids from the 'Oolithe Ferrugineuse de Bayeux' Formation of Évrecy are another example of increasing difficulties in taxonomy with increasing sample size. In the case of only a few specimens, a very clear distinction between

species would probably have been possible, but presumed species differences are eliminated by continuous transitional forms in the extensive sample. It may be possible in future investigations on the basis of material collected in greater stratigraphical detail to clarify whether the morphospecies concept is to be used or other concepts, such as the chronospecies concept, are more suitable for such assemblages.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Cross sections of *Stephanoceras* sp. 1 from Évrecy, sorted according to WWI of the penultimate whorl. A, specimen MB.C.30174. B, specimen

MB.C.30178. C, specimen MB.C.30181. D, specimen MB.C.30182. E, specimen MB.C.30169. F, specimen MB.C.30183. G, specimen MB.C.30164. H, specimen MB.C.30170. I, specimen MB.C.30177. J, specimen MB.C.30168. K, specimen MB.C.30166. L, specimen MB.C.30167. M, specimen MB.C.30176. N, specimen MB.C.30180. O, specimen MB.C.30172. Scale bar units = 1 mm.

Figure S2. Cross sections of *Stephanoceras* sp. 1, *Stephanoceras* sp. 2 (A–F), *Stephanoceras* sp. (G) and *Normannites* sp. (H) (for comparison) from Évrecy, sorted according to WWI of the penultimate whorl. A, specimen MB.C.30165. B, specimen MB.C.30173. C, specimen MB.C.30163. D, specimen MB.C.30171. E, specimen MB.C.30176. F, specimen MB.C.30183. G, specimen MB.C.30164. H, specimen MB.C.30170. I, specimen MB.C.30177. Scale bar units = 1 mm.

Figure S3. Cross sections (incomplete without inner whorls) of *Stephanoceras* sp. 1 from Évrecy, sorted according to WWI of the penultimate whorl. A, specimen MB.C.30187. B, specimen MB.C.30188. C, specimen MB.C.30189. D, specimen MB.C.30190. E, specimen MB.C.30191. F, specimen MB.C.30192. G, specimen MB.C.30193. H, specimen MB.C.30194. I, specimen MB.C.30195. J, specimen MB.C.30196. K, specimen MB.C.30197. L, specimen MB.C.30198. M, specimen MB.C.30199. N, specimen MB.C.30200. O, specimen MB.C.30201. Scale bar units = 1 mm.

Figure S4. Cross sections (incomplete without inner whorls) of *Stephanoceras* sp. 1 (A–J) and *Stephanoceras* sp. 2 (K–P) from Évrecy, sorted according to WWI of the penultimate whorl. A, specimen MB.C.30202. B, specimen MB.C. 30203. C, specimen MB.C. 30204. D, specimen MB.C. 30205. E, specimen MB.C. 30206. F, specimen MB.C. 30207. G, specimen MB.C. 30208. H, specimen MB.C. 30209. I, specimen MB.C. 30210. J, specimen MB.C. 30211. K, specimen MB.C. 30212. L, specimen MB.C. 30213. M, specimen MB.C. 30214. N, specimen MB.C. 30215. O, SPECIMEN MB.C. 30216. P, specimen MB.C. 30217. Scale bar units = 1 mm.

Figure S5. Histogram showing the frequency distribution of quantified morphological change ($D_{\text{CU-MUL/dmlog}}$) of the 24 sectioned specimens with internal whorls preserved.

Figure S6. Histograms showing the frequency distribution of conch parameters in the separated dm_{log} intervals.

Figure S7. Cross sections of microconchs of *Stephanoceras* from Évrecy. A, specimen MB.C.30174. B,

specimen MB.C.30184. C, specimen MB.C.30168. D, specimen MB.C.30175. E, specimen MB.C.30180. F, specimen MB.C.30176. G, specimen MB.C.30179. Scale bar units = 1 mm.

Table S1. The log intervals with their corresponding conch diameters used in the analyses.

Table S2. Raw data.