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A key for the description of Palaeozoic ammonoids

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Abstract

A key for the description of Palaeozoic ammonoids is presented. It contains a catalogue of descriptive terms to characterise conch morphology, ornament, and suture line particularly of Carboniferous ammonoids. A number of examples of tables and illustrations are given for the description of conch characters, their ontogeny and intraspecific variability.

Introduction

Palaeozoic ammonoids have been described for almost 200 years. Since the first nomination of the Carboniferous ammonoid "*Ammonites Listeri*" by Sowerby (1812), styles and contents of descriptions have significantly been modified and completed. The numbers of conch characteristics taken into account have increased considerably, and external as well as internal characters were evaluated to form a balance. While the early authors mainly described more or less mature stages of single individuals, later authors also included the ontogeny of specimens and or the variability within populations.

Although there is a sort of consensus among ammonoid workers about the use of the various conch characters and their importance for ammonoid description and classification, there is no agreement on how species should be characterised in terms of diagnoses and illustrations. It was particularly Ruzhencev (e.g. 1956, 1960), who in a series of monographs, developed a standard for ammonoid descriptions accompanied by illustrations of representative specimens on plates, well-drawn suture lines of mature and often of juvenile stages, and occasionally also conch cross sections. His diagnoses and descriptions of species followed a strict scheme, in which all the important characters were outlined.

Based on the study of Permian forms, Kutygin (1998) has proposed a scheme for the description of ammonoid conchs. In a bivariate diagram he showed the conch width index and umbilical width index and separated between 35 possible morphs. He named these morphs either according to their shape (e.g. 'sferokon', 'kadikon') or after ammonoid genera (e.g. 'oppellikon', 'daktilikon'); name pairs such as 'ofikon' (for very slender forms) and 'subofikon' (for moderately slender forms) lead to a reduction of descriptive terms.

The description key outlined here can be seen as a further development of the schemes proposed by Ruzhencev and Kutygin. This key is specifically coined for the Early Carboniferous ammonoids from Algeria, which will be described in monographs of this volume (Bockwinkel et al. 2010; Ebbighausen et al. 2010; Korn et al. 2010a, 2010b, 2010c); it was developed mainly for Carboniferous ammonoids of the predominant suborder Goniatitina, which has a wide morphological range but very similar suture lines.

Conch characteristics

Conch geometry

Descriptive terms of the conch characters are mainly adopted, with some modifications, from Korn & Klug (2003, 2007), who outlined the morphological spectrum for Devonian ammonoids. Cross-sections have the highest potential for providing a large data set for morphometric analysis of ammonoid conchs. With a reasonable number of cross-sections, ontogenetic development as well as in-

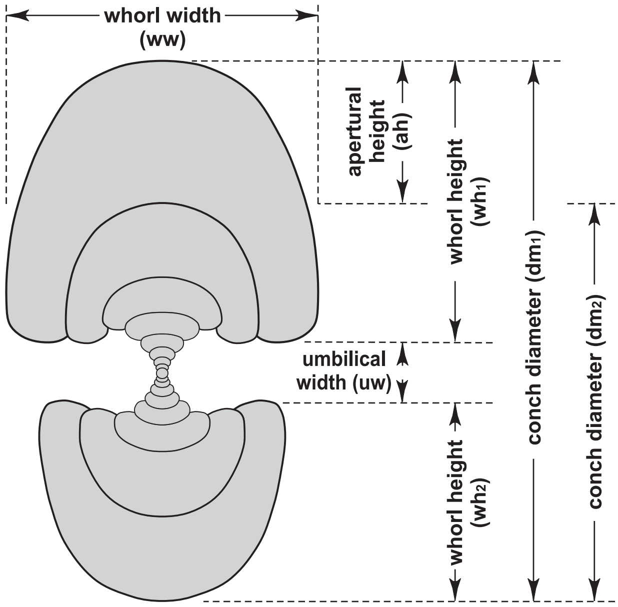

Figure 1. Descriptive terms for conch morphology of Palaeozoic ammonoids.

Table 1. Classification of the maximum conch diameters of individual specimens.

descriptive term	maximum diameter
very small	<25 mm
Small	25–50 mm
moderate	50–100 mm
Large	100–200 mm
very large	>200 mm

Table 2. Classification of the general conch shape (conch width index; ww/dm); see Fig. 2.

descriptive term	ww/dm
extremely discoidal	<0.35
discoidal	0.35–0.60
pachyconic	0.60–0.85
globular	0.85–1.10
spindle-shaped	>1.10

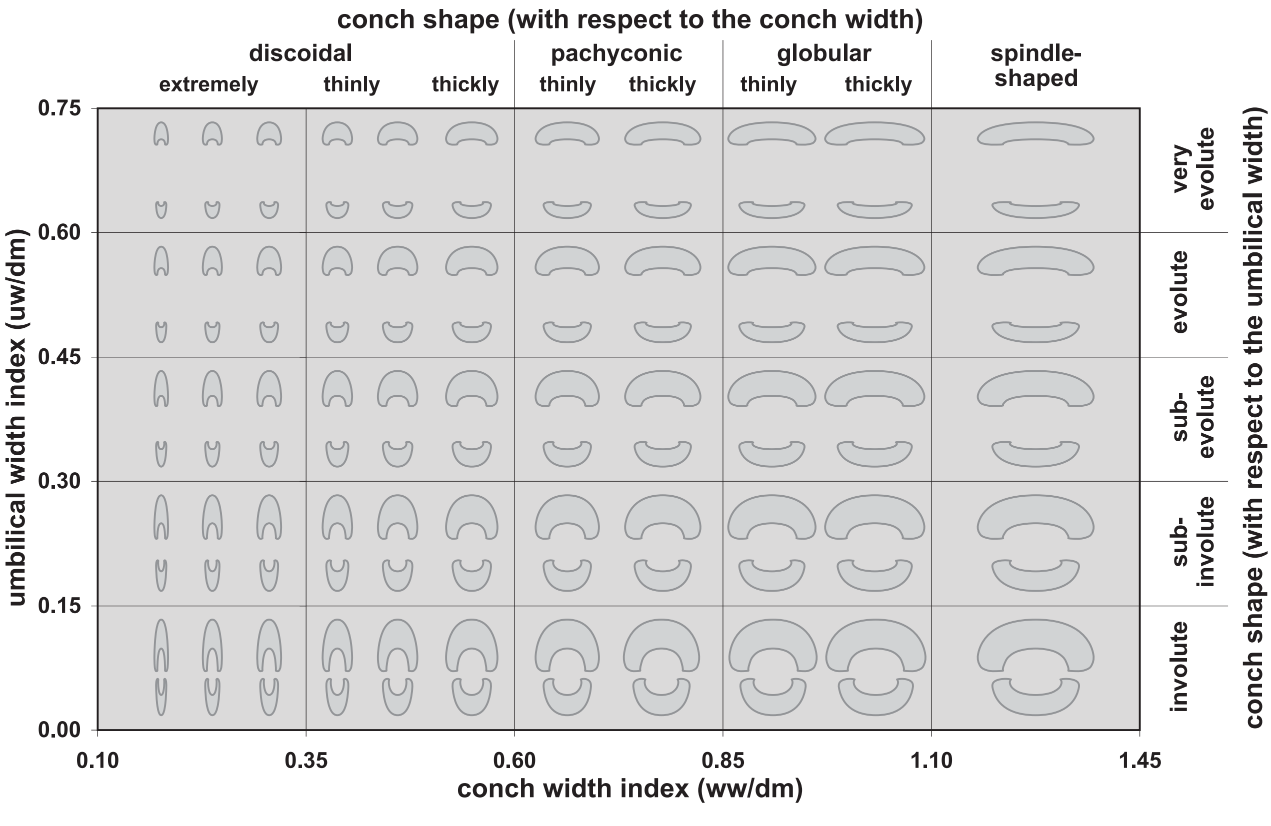

Figure 2. Bivariate plot illustrating the terminology of the conch width index (ww/dm) on the *x*-axis and umbilical width index (uw/dm) on the *y*-axis.

traspecific variability can be analysed for a number of species or complete assemblages. From computer drawings of the cross-sections, three of the basic conch parameters can immediately be obtained for each half volution (Fig. 1):

- conch diameter (dm; dm_1 is the largest diameter in a cross section and dm_2 is the diameter exactly half a whorl earlier)
- whorl width (ww; ww_1 and ww_2 as above)
- whorl height (wh; wh_1 and wh_2 as above)

Using these basic parameters, secondary parameters can easily be computed:

- umbilical width (uw) $= dm_1 - wh_1 - wh_2$
- aperture height (ah) $= dm_1 - dm_2$

- imprint zone width (iz) = $wh_1 - ah$ or $wh_1 - (dm_1 - dm_2)$

Conch proportions and expansion rates (growth rates) were calculated in the following way by using the three basic conch parameters:

- conch width index (CWI) = ww_1/dm_1
- whorl width index (WWI) = ww_1/wh_1
- umbilical width index (UWI) = uw/dm_1 or $(dm_1 - wh_1 - wh_2)/dm_1$
- whorl expansion rate (WER) = $(dm_1/dm_2)^2$ or $[dm_1/(dm_1 - ah)]^2$
- imprint zone rate (IZR) = $wh_1 - ah/wh_1$ or $-(wh_1 (dm_1 - dm_2))/wh_1$

The shape of the venter, the arrangement and the shape of the flanks, the umbilical margin and the umbilical wall can be thus described as broadly rounded, narrowly rounded, subangular, angular, and acute (Fig. 4).

Table 3. Classification of the whorl cross section shape (whorl width index; ww/wh); see Fig. 3.

descriptive term	ww/wh
strongly compressed	< 0.50
weakly compressed	0.50–1.00
weakly depressed	1.00–1.50
moderately depressed	1.50–2.00
strongly depressed	2.00–2.50
very strongly depressed	2.50–3.00
extremely depressed	> 3.00

Table 4. Classification of the umbilical width (umbilical width index; uw/dm); see Fig. 2.

descriptive term	uw/wh
very narrow	< 0.15 (conch involute)
narrow	0.15–0.30 (conch subinvolute)
moderate	0.30–0.45 (conch subevolute)
wide	0.45–0.60 (conch evolute)
very wide	> 0.60 (conch very evolute).

Table 5. Classification of the coiling rate of the conch (whorl expansion rate; WER).

descriptive term	WER
very low	< 1.50
low	1.50–1.75
moderate	1.75–2.00
high	2.00–2.20
very high	2.25–2.50
extremely high	> 2.50

Table 6. Classification of the whorl overlap rate (imprint zone rate; IZR); see Fig. 3.

descriptive term	IZR
weakly embracing	< 0.15
moderately embracing	0.15–0.30
strongly embracing	0.30–0.45
very strongly embracing	> 0.45

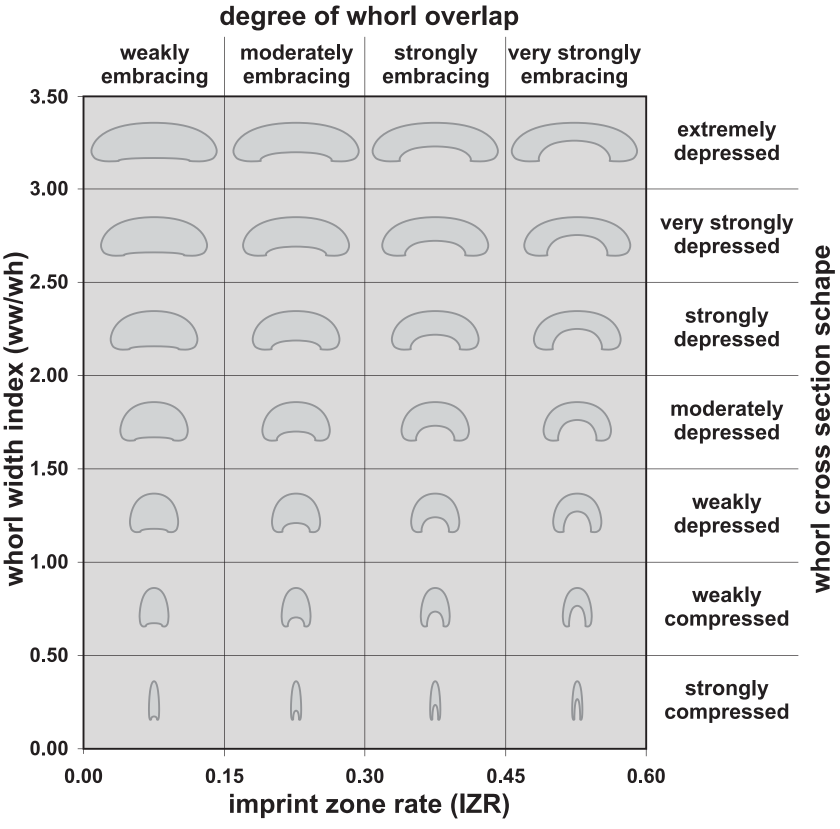

Figure 3. Bivariate plot illustrating the terminology of the imprint zone rate (IZR) on the *x*-axis and whorl width index (ww/wh) on the *y*-axis.

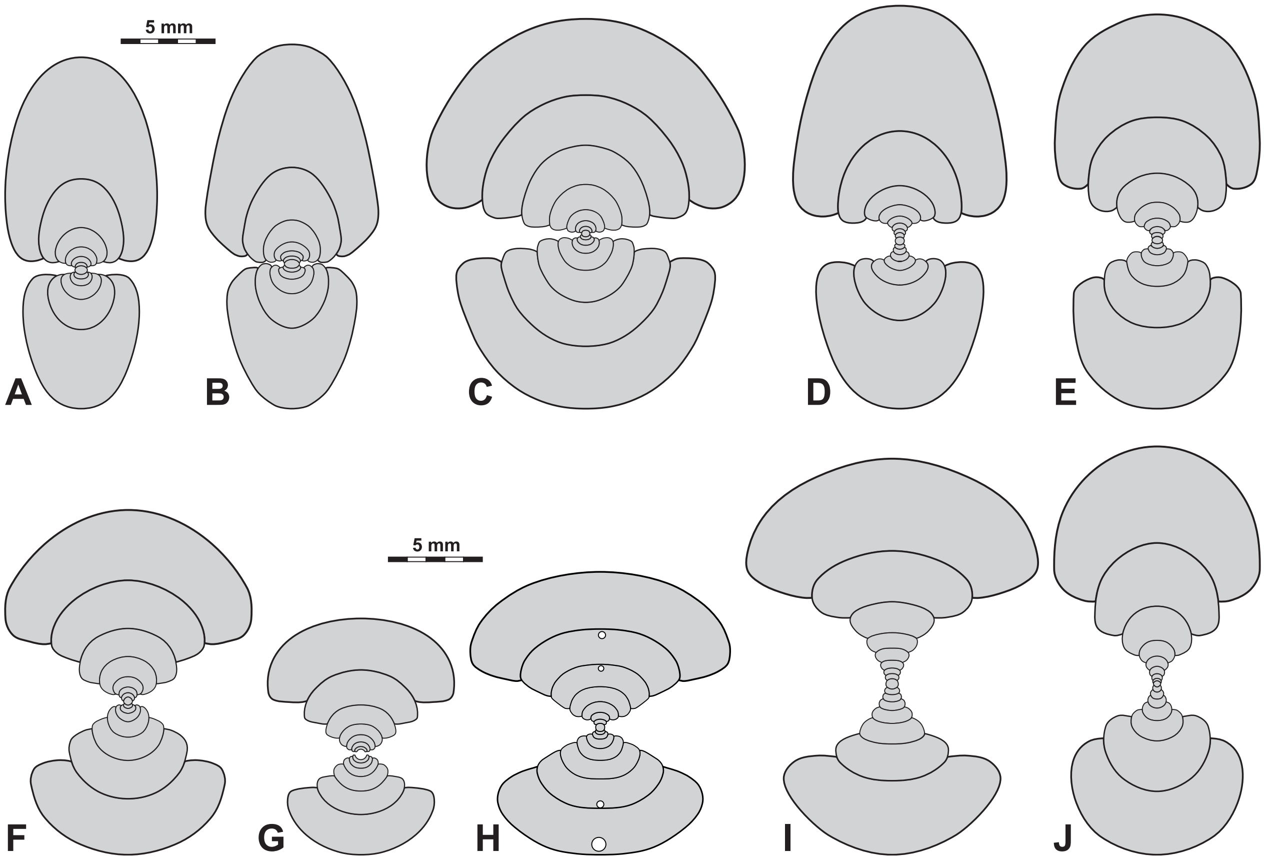

Figure 4. Various shapes of ammonoid conchs. **A.** Conch thinly discoidal, involute; venter narrowly rounded; flanks subparallel (conch widest in the midflank area); umbilical margin rounded, umbilical wall convex. **B.** Conch thinly discoidal, involute; venter narrowly rounded; flanks converging (conch widest near the umbilicus); umbilical margin subangular, umbilical wall oblique, flattened. **C.** Conch thickly pachyconic, involute; venter broadly rounded; flanks strongly converging; umbilical margin rounded, umbilical wall convex. **D.** Conch thickly discoidal, involute; venter rounded; flanks slightly converging; umbilical margin rounded, umbilical wall convex. **E.** Conch thickly discoidal, subinvolute; venter rounded; flanks subparallel; umbilical margin rounded, umbilical wall convex. **F.** Conch thinly pachyconic, subevolute; venter broadly rounded; flanks strongly converging; umbilical margin subangular, umbilical wall flattened. **G.** Conch thinly pachyconic, subevolute; venter broadly rounded; flanks subparallel; umbilical margin subangular, umbilical wall flat. **H.** Conch thinly globular, subevolute; venter very broadly rounded; umbilical margin subangular, umbilical wall flattened. **I.** Conch thickly pachyconic, evolute; venter broadly rounded; flanks strongly converging; umbilical margin subangular, umbilical wall flattened. **J.** Conch thickly discoidal, subevolute; venter very broadly rounded; flanks converging; umbilical margin rounded, umbilical wall rounded.

Shell ornament and steinkern

Growth lines, ribs, and constrictions can firstly be characterised by their direction and course across flanks and venter (Tab. 7). Therefore, the three ornament elements can be characterised by a uniform terminology.

Growth lines can occur in a wide range of strengths and consistencies, ranging from extremely fine to coarse with different spacing, they can be smooth, rough or crenulated. Strong crenulation may result in a spiral ornament, in which the spiral lines can range from fine to coarse. The number of spiral lines, counted from umbilicus to umbilicus, is often a criterion for the separation of species.

Ribs may be simple or more complex (i.e. with bifurcation and/or with intercalation of secondary ribs). They can range, in their strength, from being little more than strengthened growth lines to prominent ra-

Table 7. Classification of the direction and course of the growth lines, ribs, and constrictions (Fig. 5).

descriptive term	characteristics
rursiradiate	with a general backward direction
rectiradiate	with a general radial direction
prorsiradiate	with a general forward direction
linear	without remarkable projections and sinuses
convex	with only one wide projection on the flank (lateral projection) and a ventral sinus
concavo-convex	with a sinus on the midflank (lateral sinus), a projection at the boundary between flank and venter (ventrolateral projection), and a ventral sinus
biconvex	with two projections on the flank (dorsolateral and ventrolateral projection) and a lateral as well as a ventral sinus

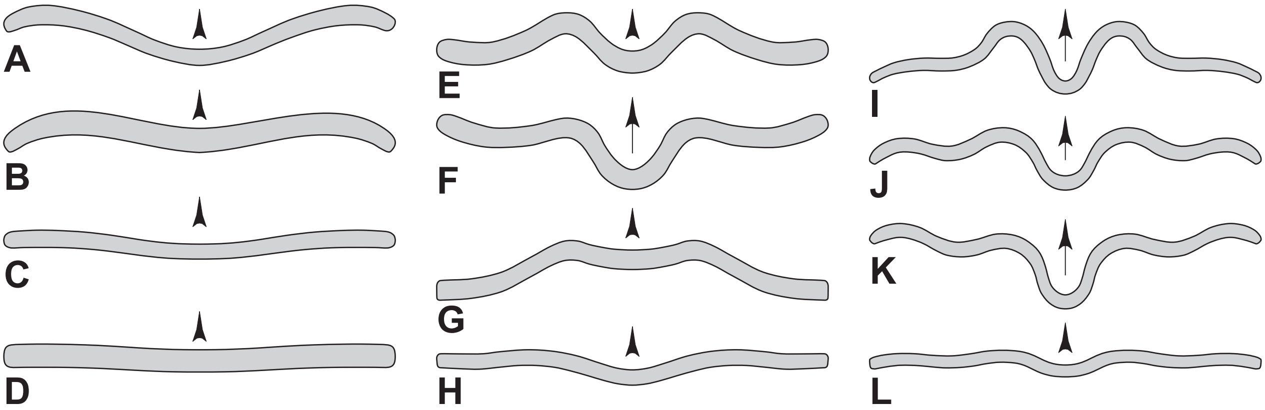

Figure 5. Various modes of constrictions. **A.** Convex with deep ventral sinus. **B.** Convex with shallow ventral sinus. **C.** Convex with extremely shallow ventral sinus. **D.** Linear. **E.** Concavo-convex with high ventrolateral projection and deep ventral sinus (direction prorsiradiate). **F.** Concavo-convex with low ventrolateral projection and deep ventral sinus (direction rectiradiate). **G.** Concavo-convex with high ventrolateral projection and very shallow ventral sinus (direction prorsiradiate). **H.** Concavo-convex with very low ventrolateral projection and very low ventral sinus (direction rectiradiate). **I.** Biconvex with low dorsolateral projection, high ventrolateral projection and deep ventral sinus (direction prorsiradiate). **J.** Biconvex with high dorsolateral projection, high ventrolateral projection and deep ventral sinus (direction rectiradiate). **K.** Biconvex with high dorsolateral projection, low ventrolateral projection and deep ventral sinus (direction rursiradiate). **L.** Biconvex with low dorsolateral projection, low ventrolateral projection and shallow ventral sinus (direction rectiradiate).

dial sculptures. Their direction and course is described as in the growth lines.

Constrictions can occur on the internal mould when they are caused by internal shell thickenings (= steinkern constrictions) or on the shell surface as well as the internal mould (= shell constrictions). Their direction and course is described as in the growth lines.

Longitudinal (spirally arranged) constrictions are described as grooves. They occur, in some groups within the Goniatitina, in the ventrolateral area and are visible on the internal mould as well as on the shell surface. Rare cases of a midventral groove are known particularly from the Prolecanitida.

Suture line

Sutural terminology (Fig. 6) for the Goniatitida is according to Wedekind (1918), and for the Prolecanitida according to Korn et al. (2003):

- external lobe (E lobe);
- median saddle (M saddle);
- ventrolateral saddle (E/A saddle; between external lobe and adventive lobe);
- adventive lobe (A lobe);
- dorsolateral saddle (A/L saddle; between adventive lobe and lateral lobe);
- lateral lobe (L lobe);
- umbilical lobe (U lobe);
- internal lobe (I lobe).

The width of the external lobe, which is an important criterion for the separation of species and genera particularly within the Goniatitina, can be described (1) by the ratio of the width (at half depth) of the external lobe and the adventive lobe (E/A as used by Korn 1988), or (2) by the ratio of width (measured at half depth) and total depth of the external lobe (EL/h as used by Korn 1997 or EL w/d as used here).

The general shape of the ventrolateral saddle can either be symmetric or asymmetric (e.g. with two strongly different flanks), it can range from being broadly rounded to narrowly rounded, subacute or acute.

The adventive lobe can be described as shallow (i.e. not as deep as the external lobe), moderately deep (about the same depth as the external lobe) or deep (deeper than the external lobe). Its general shape can be symmetric or asymmetric with incurved (concave), straight, or convex flanks.

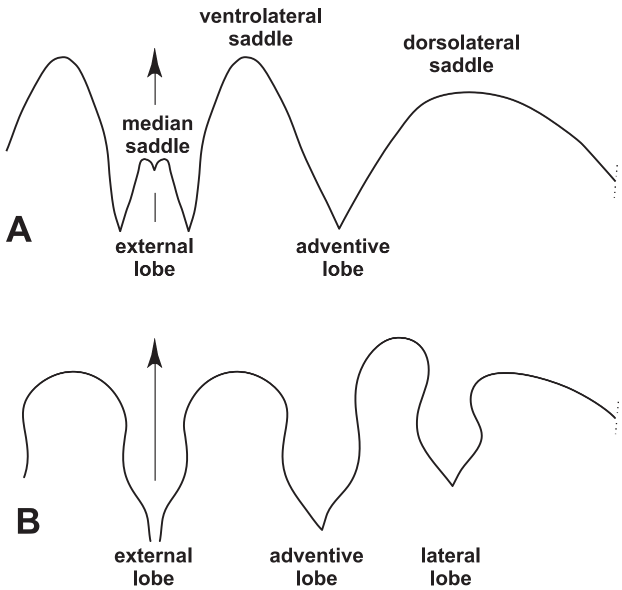

Figure 6. Descriptive terms for sutural morphology of Palaeozoic ammonoids. **A.** Goniatitid ammonoid. **B.** Prolecanitid ammonoid.

In the tables with the suture line proportions (Tab. 13), further characteristics are demonstrated, (1) the relative width of the ventrolateral saddle, calculated by its width in comparison with the external lobe (EL/VLS) or its width/height proportion (VLS w/h), and (2) the relative width of the adventive lobe, calculated by its width in comparison with the external lobe (EL/AL).

Table 8. Shape of the external lobe as an important criterion for distinguishing major ammonoid taxa.

descriptive term	characteristics
rectangular	with largely parallel and almost uncurved flanks
pouched or inflated	with more or less parallel and convexly curved flanks
V-shaped	with diverging and almost straight flanks
Y-shaped	with flanks parallel in the lower part, but diverging in the upper part
bottle-shaped	with flanks parallel in the lower part, but narrower in the upper part.

Table 9. Classification of the width of the external lobe (EL w/d).

descriptive term	EL w/d
very narrow	< 0.50
narrow	0.50–0.75
moderately narrow	0.75–1.00
moderately wide	1.00–1.25
wide	1.25–1.50
very wide	1.50–1.75
extremely wide	> 1.75

Table 10. Classification of the height of the median saddle (MS h).

descriptive term	MS h
very low	< 0.20
low	0.20–0.35
moderately low	0.35–0.50
moderately high	0.50–0.65
high	0.65–0.80
very high	> 0.80

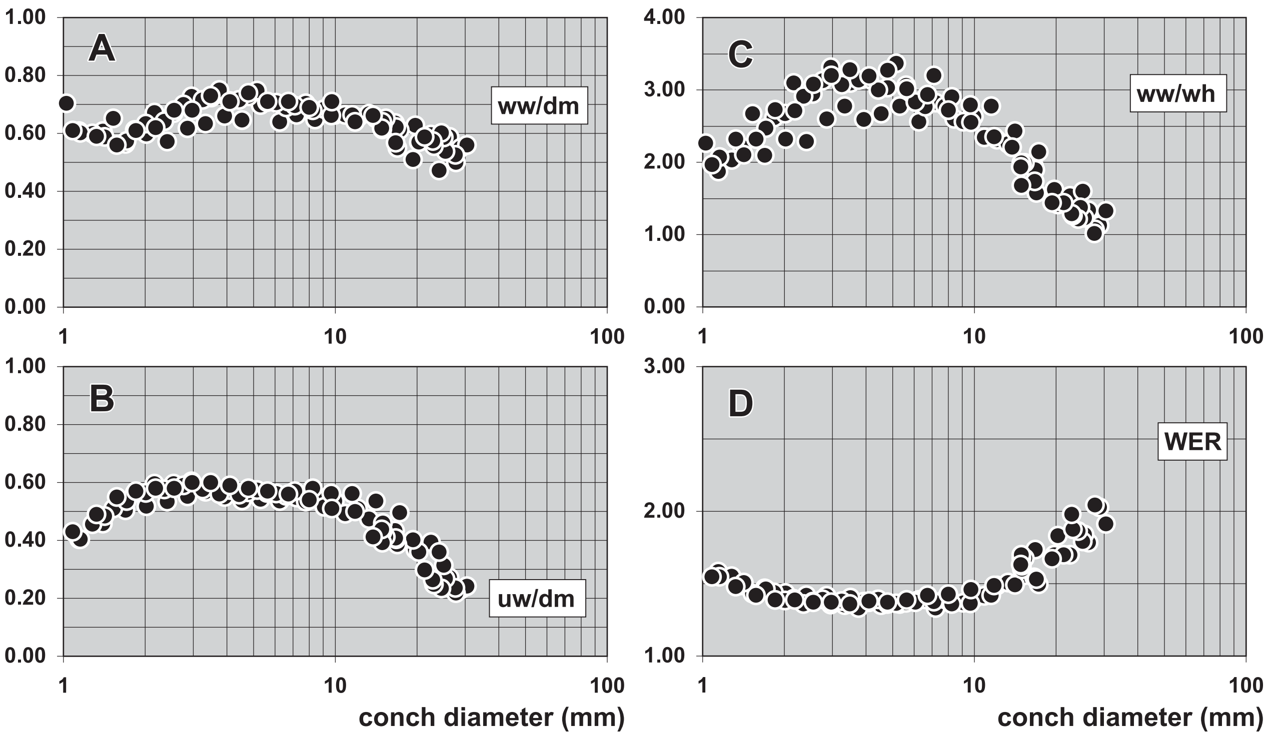

Figure 7. Example of an illustration of the ontogenetic development of the conch in ammonoids. **A.** Conch width index (ww/dm). **B.** Umbilical width index (uw/dm). **C.** Whorl width index (ww/wh). **D.** Whorl expansion rate (WER) of all available specimens of a distinct species.

Descriptions of ammonoid species

Diagnosis

Most of the Carboniferous ammonoid species are not characterised by a single or by a few apomorphic characters but much more frequently by a combination of quantitative characters. Therefore, diagnoses must often be arranged in a matrix-like matter, composed of a set of characters that allow the comparison between the species within distinct genera. Usually, the diagnosis pays attention to characters of conch morphology and ontogeny, ornament, and suture line.

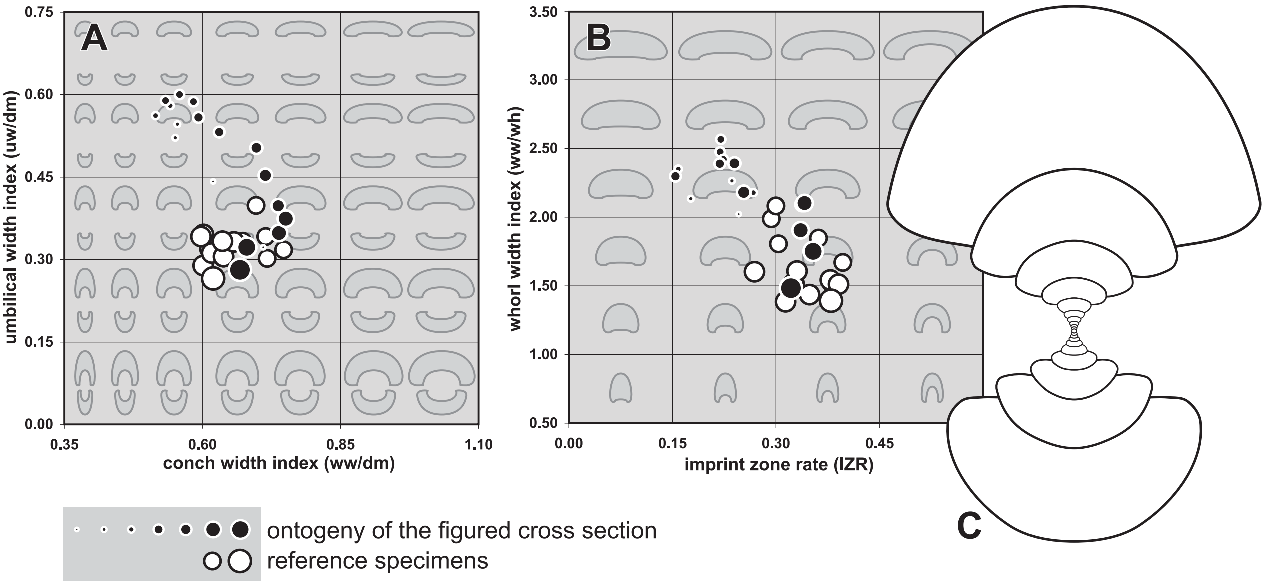

Figure 8. Example of a bivariate plot of the ontogenetic trajectories of an Early Carboniferous ammonoid (*Hammatocyclus pollex* Ebbighausen, Korn & Bockwinkel, 2010).

Description

Traditionally, descriptions are based on a number of representative specimens. In cases with a large number of specimens and rich representation by cross sections showing the conch ontogeny, the illustration of ontogenetic trajectories and intraspecific variability as well as tabular depiction with the focus on selected growth stages is much more informative.

Ontogenetic trajectories and intraspecific variability of the main conch characters i.e. conch width index (ww/dm), umbilical width index (uw/dm), whorl width index (ww/wh), and whorl expansion rate (WER) can be visualised in simple semi-logarithmic plots (Fig. 7). In these, the conch diameter is logarithmically represented on the *x*-axis and the ratio or expansion rate is on the *y*-axis.

These diagrams allow only the illustration of single characters, and therefore, bivariate plots for distinct pairs of characters were developed. In these, two related characters can be visualised. The first of these diagrams shows the conch width index on the *x*-axis and the umbilical width index on the *y*-axis (Fig. 2). The second illustrates the whorl width index on the *x*-axis and the imprint zone rate on the *y*-axis (Fig. 3). The

Table 11. Example of a table to illustrate the conch ontogeny of a Carboniferous ammonoid species, describing the conch morphology and its variation in four distinctive growth stages.

dm	conch shape	whorl cross section shape	aperture
4 mm	thickly pachyconic; subinvolute (ww/dm = 0.75–0.85; uw/dm = 0.20–0.30)	moderately depressed; very strongly embracing (ww/wh = 1.60–2.00; IZR = 0.45–0.50)	low (WER = 1.55–1.75)
10 mm	thickly pachyconic; subevolute (ww/dm = 0.75–0.80; uw/dm = 0.30–0.38)	strongly depressed; strongly embracing (ww/wh = 2.00–2.25; IZR = 0.35–0.40)	low (WER = 1.55–1.75)
30 mm	thickly discoidal; involute to subinvolute (ww/dm = 0.50–0.60; uw/dm = 0.10–0.20)	weakly depressed; strongly embracing (ww/wh = 1.00–1.50; IZR = 0.40–0.45)	moderate to high (WER = 1.90–2.10)
60 mm	thinly to thickly discoidal; involute (ww/dm = 0.45–0.50; uw/dm = 0.05–0.10)	weakly compressed; strongly embracing (ww/wh = 0.80–1.00; IZR = 0.40–0.45)	high (WER = 2.00–2.15)

Table 12. Example of a table to illustrate the conch dimensions and proportions for reference specimens of a Carboniferous ammonoid species.

	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
paratype MB.C.18610.10	59.0	27.7	32.9	3.6	18.3	0.47	0.84	0.06	2.10	0.44
paratype MB.C.18610.2	51.5	26.1	27.8	3.3	15.1	0.51	0.94	0.06	2.00	0.46
holotype MB.C.18610.1	45.8	23.5	25.8	3.5	13.6	0.51	0.91	0.08	2.02	0.47
paratype MB.C.18610.12	38.7	21.5	20.8	3.7	12.1	0.56	1.03	0.09	2.12	0.42

Table 13. Example of a table to illustrate the suture line proportions and characteristics of a Carboniferous ammonoid species. [EL w/d = width of the external lobe in relation to its depth, measured at half depth; EL/VLS = width of the external lobe in relation to the ventrolateral saddle; EL/AL = width of the external lobe in relation to the adventive lobe; MS h = height of the median saddle in relation to the depth of the external lobe; VLS w/h = width of the ventrolateral saddle in relation to its height, measured at half depth].

specimen	at dm	EL w/d	EL/VLS	EL/AL	MS h	VLS w/h	remarks
paratype MB.C.18610.10	54.5 mm	0.42	0.50	1.00	0.21	0.85	A lobe with almost straight flanks
holotype MB.C.18610.1	44.8 mm	0.39	0.43	0.79	0.18	0.89	A lobe with slightly curved flanks
paratype MB.C.18610.4	32.7 mm	0.41	0.52	0.91	0.24	0.79	A lobe asymmetric

ontogenetic stage is illustrated by the size of the dots, with small stages represented by small dots and large diameters of the specimens by large dots (Fig. 8). Using these diagrams, ontogenetic traits can be illustrated and help for the separation of species.

In the monographs published parallel to this account (Bockwinkel et al. 2010; Ebbighausen et al. 2010; Korn et al. 2010a, 2010b, 2010c), a tabular description of biometric characters of conch and suture line (Tabs 11–13) was given priority over narrative descriptions.

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