

Topics in Geobiology 43

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Ammonoid Paleobiology: From anatomy to ecology

 Springer

Topics in Geobiology

Volume 43

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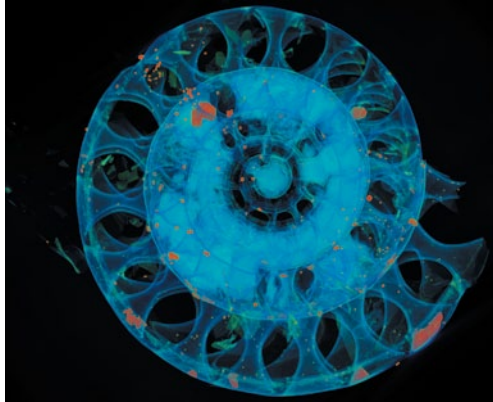
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CT-scan reconstructed by René Hoffmann (Bochum) of the Carboniferous ammonoid *Arnsbergites* (Harz Mountains, Germany). This example stands for the increase in use of non-invasive imaging techniques and 3D-visualization in ammonoid paleobiology; Image by courtesy of René Hoffmann (Bochum).

Christian Klug • Dieter Korn • Kenneth De Baets
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Image courtesy W. Gerber (Tübingen)
*To the memory of Adolf ("Dolf") Seilacher
(24. February 1925 to 26. April 2014)*

There are paleontologists, who have published hundreds of articles, but there is hardly anybody who stimulated ammonoid paleobiological research as much with insightful and innovative articles as Dolf Seilacher. Also, he published the possibly most widely cited phrase on ammonoids:

"Ammonites are for paleontologists what Drosophila is in genetics. The structural complexity of their shells, the complete ontogenetic protocol and a long and rather perfect fossil record make them the most suitable invertebrate group for macroevolutionary studies."

Seilacher (1989: p. 67)

Dolf Seilacher died peacefully on April 26th 2014 at the age of 89, short before the completion of this book. In order to acknowledge his scientific input and stimulation of research on ammonoids, we dedicate this book to his memory.

His main contributions to the field were probably the balloon-model for simple septa, the tie-point-model for complex septa, the Cartesian diver model, the use of epizoa to constrain ammonoid ecology and his works on ammonoid taphonomy and paleobiology. Below, we provide a list of his papers on ammonoids, which included ammonoid data.

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Foreword to the New Edition

This two-volume work is a testament to the abiding interest and human fascination with ammonites. As Niles Eldredge wrote in the forward to our 1996 book “Ammonoid Paleobiology” (fondly referred to as the Red Book), ammonites are “the quintessential fossils.” They have contributed to ideas about biostratigraphy, paleoecology, paleobiology, paleoenvironment, paleobiogeography, paleogeography, paleoceanography, evolution, phylogeny, and ontogeny. All of these themes are treated in the present book. The past two decades have witnessed an explosion of new information about ammonites: early life history, evolution of the buccal mass, feeding habits, soft-tissue preservation, radiation-and extinction-patterns, shell microstructure, sutures and pseudosutures, cameral membranes, mode of life, phylogeny, and habitats. Many of these discoveries have benefitted from the application of new technologies such as isotopic analysis, organic geochemistry, geographic information systems, geometric morphometrics, computerized tomography, and synchrotron imaging. They have also relied on more traditional techniques such as scanning electron microscopy and electron dispersive analysis, which continue to furnish an abundance of data. Fortunately, too, our field is constantly being re-energized by the discovery of new fossil finds that shed light on old questions and raise new ones. Given all these advances in our knowledge, this book is a comprehensive and timely “state of the art” compilation. Moreover, it also points the way for future studies to further enhance our understanding of this endlessly fascinating group of organisms.

Neil H. Landman, Kazushige Tanabe, and Richard Arnold Davis, Editors of the 1996 book “Ammonoid Paleobiology” (the original three musketeers)

Foreword to the First Edition: Ammonoids Do It All

Ammonoids are *the* quintessential fossils, seemingly covering all the major themes of paleontology. Method and theory of stratigraphic correlation using fossils? Albert Oppel, whose concepts of zonation were explicated and applied by W. J. Arkell exhaustively in his monumental works on the Jurassic System, immediately spring to mind—works based virtually exclusively on the stratigraphic distributions of ammonoid species. Evolution? W. Waagen leaps to mind, applying the term “mutation” to his ammonoid lineages, and thus introducing the word to the scientific literature well before geneticists co-opted “mutation” for their own, starkly different, use.

Extinction? Cretaceous heteromorphs were type examples of “racial senescence”—if now wholly discredited, nonetheless an important part of earlier discourse on what is one of the most compelling issues that paleobiology brings to general biological theory. I was myself stunned, when compiling data on the end-Cretaceous mass extinction in the late 1960s for a seminar conducted by Norman D. Newell, to find that the scaphitids—far from dwindling to a precious few as Cretaceous time was running out—were actually in the midst of an evolutionary radiation, an expansion of diversity cut abruptly short by whatever it was that disrupted things so badly 65 million years ago.

Indeed, though of course much remains to be learned about ammonoid phylogeny, every chart that I have seen published in the last 30 years showing the basic outlines of ammonoid evolution against the backdrop of Silurian-Cretaceous geologic time constitutes a stark object lesson on the resonance between evolution and extinction. The theme of early “experimentation” shows up amidst Devonian ammonoid diversity: the clymeniids constitute an arch example, with their siphuncle on the opposite side of the body from what proved to be the “normal” ammonoid condition—an experiment that failed to survive the late Devonian biotic crisis, thus forever depleting ammonoid morphological diversity. And are the goniatites, ceratites, and ammonites mere grades, as nearly everyone suspected back in the parallel-evolution-mad 1960s? Or are they, as now seems evident, genealogically coherent, monophyletic clades that represent radiations consequent to major biotic crises of the Permo-Triassic and Triassic-Jurassic boundaries? That grade-like patterns can come from evolutionary radiations following severe extinction bottlenecks is an aspect of evolutionary theory yet to be fully expounded. And it is the ammonoids that show such patterns best.

Biostratigraphy, evolution, extinction-not to mention biogeography, paleoecology, and functional morphology: of all major taxa in the fossil record, the ammonoids arguably do it best. But there is something more to them, a certain allure that makes them deserved rivals of trilobites as the most ardently desired and sought-after relics of the deep past. Ammonoids are at once exotic yet familiarly organic. Though nearly always simply the empty shells of long-dead animals, they nonetheless seem complete. They are almost always beautiful-and sometimes even colorful. It's probably the (nearly always planispiral) logarithmic spiral that, in spite of its mathematical precision, nonetheless casts an aura of intrigue and mystery to what is otherwise just another fossil. A few years back I published a lavishly illustrated book on fossils, using photographs of many of the finest specimens of all taxa from the rich paleontological collections of the American Museum of Natural History. And though I had skulls of a male and female Tertiary artiodactyl on the front cover, it is the photo on the back-of a pretty little pyritized specimen of the Jurassic ammonoid *Hecticoceras-that* attracted the most attention, and that has been subsequently reproduced over and over again.

I can only conclude that, over and above the prodigious intellectual contributions that continue to come from contemplation of these marvelous animals (as this present volume amply demonstrates), ammonoids also have that certain *je ne sais quoi* that will always keep them at the forefront of the paleontological realm. Ammonoids really do seem to have it all.

The American Museum of Natural History
New York, New York

Niles Eldredge

Preface

Imagine you belong to any religion and your chief deity asks you: “Could you imagine editing the new sacred book?” This is the feeling you have as an ammonoid worker, when you are offered to take care of the new edition of ‘Ammonoid Paleobiology’. Not only for us, who had the honor and burden of this gigantic task, ‘Ammonoid Paleobiology’ represented a comparably important book since we consulted it so often in order to better understand these organisms, which went extinct 65 million years ago.

Although many of the early ammonoid researchers of the nineteenth century have spent thoughts on the ammonoid organism and its mode of life, most of the major contributions to modern ammonoid paleobiology appeared roughly in the past half century. Looking at the scientific output of these decades, it appears like the first edition of “Ammonoid paleobiology” was a product of something like a golden age of ammonoid research. The two decades preceding its publication saw the first five international symposiums “Cephalopods—Present and Past” and many important articles by colleagues such as John Callomon, Antonio Checa, John A. Chamberlain, Larissa Doguzhaeva, Jean-Louis Dommergues, Jean Guex, Roger H. Hewitt, Michael House, David K Jacobs, Jim Kennedy, Cyprian Kulicki, Neil Landman, Ulrich Lehmann, Harry Mutvei, Takashi Okamoto, Bruce Saunders, Yasunari Shigeta, Kazushige Tanabe, Henri Tintant, Jost Wiedmann, Peter D. Ward. Gerd Westermann, Yuri Zakharov (incomplete list!) contributed essential data and interpretations, but they also stimulated further research in this field. Unfortunately, many important cephalopod workers and good colleagues have passed way in the last two decades. In 2014 alone, for example, Fabrizio Cecca, Adolf Seilacher, Helmut Hölder, **Hironmichi** Hirano, and Gerd E. G. Westermann passed away.

Due to fundamental changes in the structure of scientific communities including the dubious judgment of the value of scientific work by impact factors and citation rates, cephalopod research has changed as well. Additionally, the community of ammonoid researchers appears to have started shrinking. Nevertheless, the past decades still saw thousands of interesting contributions on representatives of this fantastic clade. And still, we have a lot of work ahead of us prior to becoming able to respond to all questions regarding ammonoid paleobiology.

So what is new? In terms of content, we have restructured the former into a two-volume work with the main parts shell, ontogeny, anatomy, habit and habitats, macroevolution, paleobiogeography, ammonoids through time, fluctuations in ammonoid diversity, and taphonomy. Most of these parts are subdivided into chapters. The great amount of 41 chapters reflects the panel of ammonoid workers present nowadays in academia, junior and senior scientists from many countries and a higher percentage of female authors compared to the previous edition. We aimed at being as up-to-date as possible, which had the consequence that some chapters also present unpublished specimens, data and results. We also included two chapters on the geochemistry of ammonoid shells, a field that still offers vast possibilities for new research. This is also reflected in the slightly different views presented therein.

Furthermore, we added an introductory for the definition of terms and with a recommendation for the description of new ammonoid taxa. We emphasized the next challenges in ammonoid research such as reconstructing ammonoid phylogeny, understanding their intraspecific variability or reconstructing the soft parts. Studying intraspecific variability has been widely neglected, but it offers a wealth of possible implications for life histories, ontogeny, reproduction and, most importantly, for evolution. In this context, another challenge is establishing a phylogeny for ammonoids, and thus, one part comprising five chapters is dedicated to ammonoid macroevolution. In our eyes, paleontological data yield the essential information for research on evolution. As pointed out already by Seilacher and Eldredge, ammonoids are of particular interest due to their accretionary shell, which has a good fossilization potential and hold a record of their life history, their high evolutionary rates, their wide geographic distribution, high taxonomic diversity and morphological disparity as well as their well-constrained stratigraphic (i.e., temporal) framework. In the case of ammonoids, however, countless homoplasies occurred throughout their evolution, thus hampering attempts to reconstruct ammonoid phylogeny. Nevertheless, a sound phylogenetic model for the ammonoid clade should be one of the central tasks in ammonoid research because the knowledge of ammonoid phylogeny is still patchy. Furthermore, although some quantitative approaches have been pioneered with ammonoids (e.g., Raup's morphospace, Okamoto's growing tube model), such methods are still too little used in many studies on ammonoid paleobiology and evolution; many studies restrict themselves to narrative discussions or qualitative assessments. For this reason, the application of several quantitative and statistical methods to study many aspects of ammonoid like biostratigraphy, biogeography, intraspecific variability, evolutionary trends, etc. are explained and demonstrated in several of the chapters of these two volumes, in the hope these methods will be used more widely in the ammonoid community.

Finally, we added new information obtained from tomographic data obtained both from computer tomography and grinding tomography. The field of virtual paleontology has just started to deliver ammonoid data, which are of special interest in the studies of shell morphology, ontogeny, buoyancy, mode of life, and ultimately evolution.

These two volumes would have been impossible without our wonderful authors, and especially the help of Neil Landman as well as Kazushige Tanabe. Additionally, we greatly appreciate the support of the army of reviewers, who are listed and thanked in the corresponding chapters. Naturally, our partners and families have been affected more or less from the additional time consumed by the preparation of the volumes, we apologize for that and thank them for all their patience, inspiration, and support.

Christian Klug
Dieter Korn
Kenneth De Baets
Isabelle Kruta
Royal H. Mapes

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Part I
Conch

Chapter 1

Describing Ammonoid Conchs

**Christian Klug, Dieter Korn, Neil H. Landman, Kazushige Tanabe,
Kenneth De Baets and Carole Naglik**

1.1 Introduction

Because ammonoid jaws are rare (Tanabe et al. 2015) and preserved soft parts as well as radulae (Klug and Lehmann 2015; Kruta et al. 2015) are even rarer, most paleontologists are limited in the available morphological information to the conch when describing ammonoids. Taking the great diversity and disparity as well as the over 300 Ma of the clade's existence into account, it becomes obvious that the different ammonoid clades have divergent sets of characters requiring descriptive procedures adapted to the requirements. For example, in the earliest ammonoids, details

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of the suture line and the ornamentation are often less important while conch geometry yields important information. By contrast, ornamentation and sutures can be essential for the systematics of Late Paleozoic and Mesozoic ammonoid groups, while conch shape might play a lesser role. Additionally, intraspecific variability differs strongly between ammonoid clades and thus, small differences between some forms might justify the introduction of a new species whereas in other clades, such a small difference could fall within the broad range of intraspecific variability (De Baets et al. 2015).

Nevertheless, we will try to give a guideline on the optimal features that systematic descriptions of ammonoid species should take into consideration offering some suggestions which certainly go beyond the normal framework of descriptions, but which would give them a special above average quality. At the same time we are well aware that some of our suggestions would lead to some kind of ‘de luxe’ description, presuming all our suggestions are fully implemented.

Naturally, this is not the first attempt to produce a guideline for a more uniform and intelligible mode of ammonoid description. Many pioneers, however, did not explicitly state their strategies in describing ammonoids in their monographs, although these authors commonly followed certain rules.

Miller et al. (1957) and Arkell (1957) summarized the available morphological terms in the Treatise for Invertebrate Paleontology for Paleozoic and Mesozoic ammonoids, respectively. As far as Paleozoic ammonoids are concerned, it was Ruzhencev (1960) who set the standards for the description of Paleozoic ammonoids. His descriptions are not only well-structured but also provide the same set of information in a uniform order, accompanied by photographs of lateral and ventral views as well as suture lines and often cross sectional drawings. His introduction to conch shape and terminology in the *Osnovy Paleontologii* (Ruzhencev 1962, 1974) belongs to the best that have been printed.

Branco (1879–1880) described general characteristics of the early internal conch features of some ammonoids. Subsequent works with SEM (Tanabe et al. 1979; Drushchits and Doguzhaeva 1982) have demonstrated that the study of ontogenetic development of internal structures is as important as that of suture, shape and sculpture of conchs to construct an adequate scheme of major taxonomy and systematics of Ammonoidea (Kulicki et al. 2015).

In his famous books, Lehmann (1976, 1981, 1990) presented important descriptive terms with simple line drawings. However, his main focus was on paleobiological aspects of ammonoids.

Landman et al. (1996) and Westermann (1996) also defined morphological terms in a qualitative way. They distinguished various types of conch shapes for ‘normal’, planispirally coiled, ammonoids (with touching or overlapping whorls): cadiconic, discoconic, elliptospheroconic, planorbiconic, platyconic, serpenticonic, spheroconic. They also use specific terms to refer to “heteromorph” ammonoids, which are not planispirally coiled and/or have successive whorls in contact with one another: ancyloconic, breviconic, gyroconic, hamitoconic, orthoconic, scaphitoconic, torticonic and vermiconic. For relative terms, they use ‘evolute’ for more loosely coiled conchs, ‘involute’ was used to refer to tightly coiled conchs with a large whorl overlap and ‘advolute’ was used to refer to whorls, which are touching but not overlapping.

Landman et al. (1996) and Westermann (1996) also used the terms ‘brevidomic’, ‘mesodomic’ and ‘longidomic’ to describe body chamber lengths of approximately one-half whorl, three-fourth whorl, and a whorl or more in length, respectively. Body chamber length is usually expressed as the Body chamber angle (BCA) or the

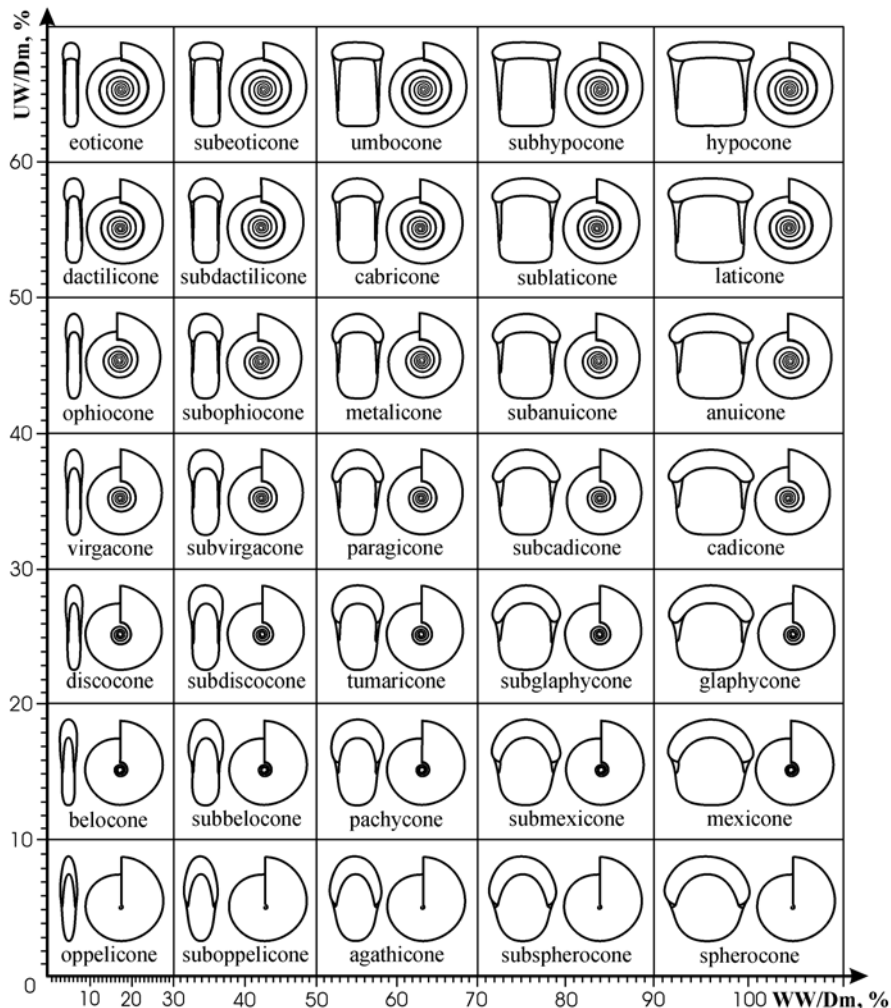


Fig. 1.1 Description of conch shapes as suggested by Kutugin (with permission, from Kutugin 1998) for Permian ammonoids. In the terminology of Arkell (1957), the following terms would be synonymous: oxycone—oppellicone; serpenticone—eoticone/dactilicone; platycone—suboppellicone/subbelocone; sphaerocone—subcadicone via mexicone and agathicone to sphericone

angular length measured from the septal neck (medial saddle of the external lobe) of the ultimate septum to the peristome (apertural edge), excluding lappets or rostra.

In several of his articles and monographs, Korn (e.g., Korn 1997; Korn and Klug 2002, 2003, 2007) quantified terms which he commonly uses to describe morphological aspects of ammonoid conchs. In order to make this more broadly known, he published “*A key for the description of Palaeozoic ammonoids*” (Korn 2010), where he listed terms, how to calculate certain ratios, and how to illustrate them properly.

Kutugin (1998) subdivided conch shapes of normally coiled ammonoids according to their umbilical width/conch diameter ratio versus whorl width/conch diameter ratio (Fig. 1.1). He outlined a theoretical morphospace of ammonoid conch-shapes, which he used to illustrate morphological change through ontogeny (Kutugin 2006).

Other examples for comprehensive definitions of terms are the monographs of Schlegelmilch (1976, 1985, 1994). He produced drawings of ribbing types, whorl cross sections, conch shapes, keels, shapes of apertures, and other conch parts.

Here, we provide an introduction to the terminology and methodology needed and/or recommended to describe ammonoids in general. There is such a wealth of terms, definitions and methods that we include only the most widely used ones.

1.2 Geometry

1.2.1 Classical Conch Parameters

Possibly, Moseley (1838) and Guido Sandberger (1851, 1953a, 1953b, 1857) were the first who described the coiling of ammonoid conchs mathematically. More recently, with the works of Trueman (1941) and Raup (Raup and Michelson 1965; Raup 1967), the quantification of ammonoid conch morphology has reached the ‘high table’ of ammonoid workers. Raup (1961, 1966) mainly used the following parameters:

- S Shape of the generating curve;
- W Whorl expansion rate;
- D Position of the generating curve relative to the coiling axis;
- T Rate of whorl translation. T equals zero in planispiral conchs and thus is of lesser interest in ammonoid research.

Instead of radii, which refer to the coiling axis, Korn (1997, 2010) began to use diameters to calculate whorl expansion rates. Diameters are much easier to measure and the coiling axis usually varies in its position through ontogeny. Accordingly, the main conch parameters (Fig. 1.2; Tab. 1.1) are:

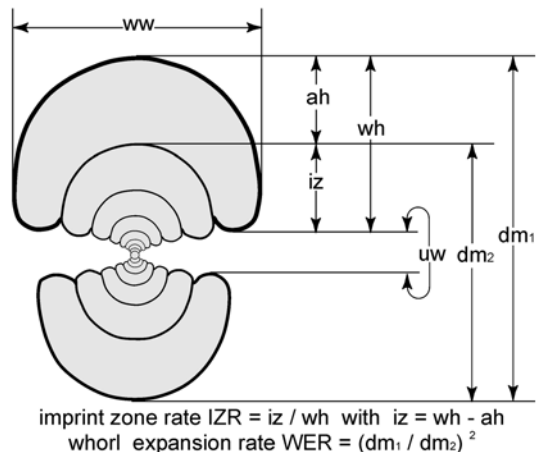


Fig. 1.2 Overview over the main conch parameters and ratios, exemplified on a cross section of the Middle Devonian ammonoid *Subanarcestes*

Table 1.1 Classification of the maximum conch diameters of individual specimens, the conch shape (ww/dm), the whorl width index (ww/wh), the umbilical width index (uw/dm), the whorl expansion rate (WER), and the whorl overlap or imprint zone rate (IZR). All values taken from Korn (2010)

Parameter	Descriptive term	Equation	Value
Max. conch diameter	Very small	dm	<25 mm
Max. conch diameter	Small	dm	25–50 mm
Max. conch diameter	Moderate	dm	50–100 mm
Max. conch diameter	Large	dm	100–200 mm
Max. conch diameter	Very large	dm	>200 mm
Conch shape	Extremely discoidal	ww/dm	<0.35
Conch shape	Discoidal	ww/dm	0.35–0.60
Conch shape	Pachyconic	ww/dm	0.60–0.85
Conch shape	Globular	ww/dm	0.85–1.10
Conch shape	Spindle-shaped	ww/dm	>1.10
Whorl width index WWI	Strongly compressed	ww/wh	<0.50
Whorl width index WWI	Weakly compressed	ww/wh	0.50–1.00
Whorl width index WWI	Weakly depressed	ww/wh	1.00–1.50
Whorl width index WWI	Moderately depressed	ww/wh	1.50–2.00
Whorl width index WWI	Strongly depressed	ww/wh	2.00–2.50
Whorl width index WWI	Very strongly depressed	ww/wh	2.50–3.00
Whorl width index WWI	Extremely depressed	ww/wh	>3.00
Umbilical width index UWI	Very narrow (involute)	uw/wh	<0.15
Umbilical width index UWI	Narrow (subinvolute)	uw/wh	0.15–0.30
Umbilical width index UWI	Moderate (subevolute)	uw/wh	0.30–0.45
Umbilical width index UWI	Wide (evolute)	uw/wh	0.45–0.60
Umbilical width index UWI	Very wide (very evolute)	uw/wh	>0.60
Whorl expansion rate WER	Very low	$[dm/(dm - ah)]^2$	<1.50
Whorl expansion rate WER	Low	$[dm/(dm - ah)]^2$	1.50–1.75
Whorl expansion rate WER	Moderate	$[dm/(dm - ah)]^2$	1.75–2.00
Whorl expansion rate WER	High	$[dm/(dm - ah)]^2$	2.00–2.25
Whorl expansion rate WER	Very high	$[dm/(dm - ah)]^2$	2.25–2.50
Whorl expansion rate WER	Extremely high	$[dm/(dm - ah)]^2$	>2.50
Imprint zone rate IZR	Weakly embracing	$(wh - ah)/wh$	<0.15
Imprint zone rate IZR	Moderately embracing	$(wh - ah)/wh$	0.15–0.30
Imprint zone rate IZR	Strongly embracing	$(wh - ah)/wh$	0.30–0.45
Imprint zone rate IZR	Very strongly embracing	$(wh - ah)/wh$	>0.45

- conch diameter: The maximum diameter is abbreviated as dm (or dm_1). In order to determine the whorl expansion rate, a second diameter value is needed, namely the diameter measured half a whorl earlier (180° behind the aperture or dm_1 , respectively; dm_2). The conch diameter has often been used as proxy for size

(and relative age). However, other properties like body chamber volume might be more suitable as a proxy for size because it better reflects the volume of the soft body than the conch diameter, especially when comparing forms with very different conch geometries (e.g., Bucher et al. 1996; Dommergues et al. 2002; De Baets et al. 2012, 2013a, 2015). In extant coleoids (Nixon and Young 2003; Boyle and Rodhouse 2005), mostly the (dorsal) mantle length (which would correspond with the body chamber length in ammonoids) is used as a measure of size. Other measures are also used such as weight (which would correspond to the weight of the soft tissue with or without the conch) or the total length (with arms as they can form a major part of the coleoid). Nevertheless, the diameter will always be an important parameter in ammonoids as it is easy to obtain and has been widely used and available in the literature (Bucher et al. 1996).

- whorl width: It is measured perpendicular to the plane of symmetry and abbreviated as ww. In ornamented forms, this parameter is commonly measured between the ornament, so it represents a kind of minimal value. If this measurement is taken from older ontogenetic stages (e.g., from cross sections) in half a whorl distance (each 180 degrees), the values are labeled accordingly ww_1 , ww_2 , ww_3 . This can also be done with the following parameters.
- whorl height: This parameter, abbreviated as wh, is measured parallel to the plane of symmetry from the umbilical seam or umbilical wall to the middle of the venter.
- umbilical width: Being a secondary parameter, it can be measured from umbilical wall to umbilical wall or it can be calculated as follows:

$$uw = dm_1 - wh_1 - wh_2$$
- aperture height: This value is measured from the dorsum of the preceding whorl to the dorsum of the whorl under consideration. It can also be calculated:

$$ah = dm_1 - dm_2$$
- imprint zone width: This parameter describes the degree of whorl overlap and is measured from the umbilical seam of the whorl under consideration to the dorsum of the preceding whorl. It may be calculated using the following equation:

$$iz = wh_1 - ah = wh_1 - (dm_1 - dm_2)$$

1.2.2 Cross Section and Ratios

An easy way to assemble a lot of morphometric data from ammonoids is to produce cross sections perpendicular to the plane of symmetry and through the initial chamber. This allows quantification of ontogenetic change in the parameters listed above and also makes changes in shell thickness and in whorl cross section visible. A peculiar aspect of conch shape, made visible by cross sections, is the umbilical lid (a continuation of the lateral conch wall partially covering the umbilicus) of the Early Devonian auguritids and the Middle Devonian pinacitids (Klug and Korn 2002; Monnet et al. 2011) as well as in Middle Devonian pharciceratids (Bockwinkel et al. 2009). In the Auguritidae and Pinacitidae, the lateral wall begins to extend over the umbilicus starting in the juvenile whorls. Although this is just an example,

such cross sections can also reveal shell thickenings at the umbilicus, keels and other morphological details (e.g., Tozer 1972).

The greatest advantage of cross sections is the access to comprehensive morphometric data throughout ontogeny. In order to assure accuracy of the cross sections, the section should optimally run through the maximum diameter of the initial chamber (protoconch) and should be perpendicular to the plane of symmetry (Fig. 1.3). The values measured on complete specimens or sections can then be used to calculate the following simple ratios (Korn 2010):

- conch width index: $CWI = ww/dm$
- whorl width index: $WWI = ww/wh$
- umbilical width index: $UWI = uw/dm = (dm_1 - wh_1 - wh_2)/dm_1$

Based on the conch width index and the umbilical width index, the conch shapes and cross sections can be classified as (Fig. 1.4):

- discoidal ($CWI < 0.60$)
- pachyconic ($0.60 \leq CWI < 0.85$)
- globular ($0.85 \leq CWI < 1.10$)
- spindle-shaped ($CWI \geq 1.10$)

According to the umbilical width, ammonoid conchs can be termed as

- involute ($UWI < 0.15$)
- subinvolute ($0.15 \leq UWI < 0.30$)
- subevolute ($0.30 \leq UWI < 0.45$)
- evolute ($0.45 \leq UWI < 0.60$)
- very evolute to advolute ($UWI \geq 0.60$)
- advolute: whorls touch but do not overlap
- heteromorphic/cricone: whorls do not touch

Cross sections also better reveal details of the conch morphology such as the vaulting of lateral or ventral walls. They help to describe the whorl cross section more correctly.

1.2.3 Expansion Rates

Due to their nearly logarithmic conch growth, most conch parameters also increase at differing rates. Caused by allometric growth, the change in certain parameters through ontogeny is not necessarily perfectly linear in a loglog-space (Kant 1973; Kant and Kullmann 1980; Klug 2001; Korn and Klug 2003; Urdy et al. 2010a, 2010b; Korn 2012; Urdy 2015). In order to quantify these changes, parameters taken from transverse cross sections or values measured in the plane of symmetry can be used.

Longitudinal (median) sections should optimally be in the plane of symmetry, i.e. the siphuncle or the siphuncular perforations should be visible completely. These sections offer the opportunity to measure parameters such as apertural height