

# Chapter 1

## Describing Ammonoid Conchs

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### 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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C. Klug et al. (eds.), *Ammonoid Paleobiology: From Anatomy to Ecology*,  
Topics in Geobiology 43, DOI 10.1007/978-94-017-9630-9\_1

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.

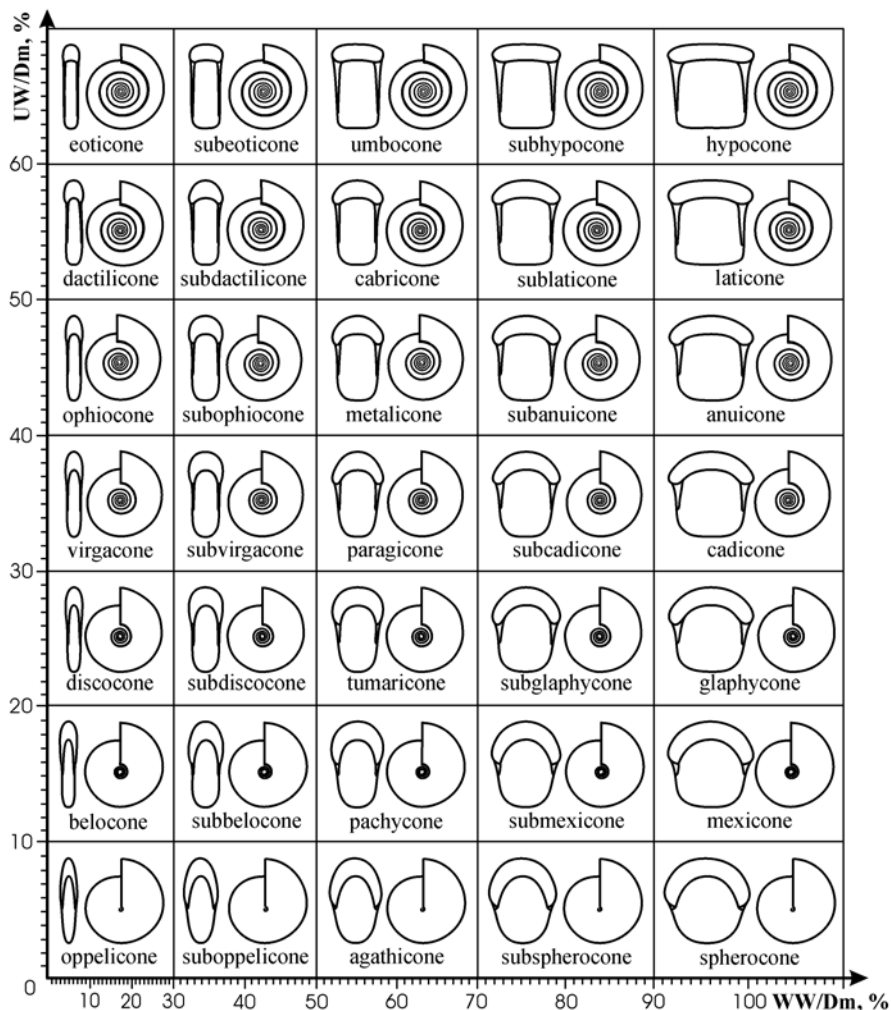
Miller et al. (1957) and Arkell (1957) summarized the available morphological terms in the Treatise for Invertebrate Paleontology for Paleozoic and Mesozoic ammonoids, respectively. As far as Paleozoic ammonoids are concerned, it was Ruzhencev (1960) who set the standards for the description of Paleozoic 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 spherocone

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.

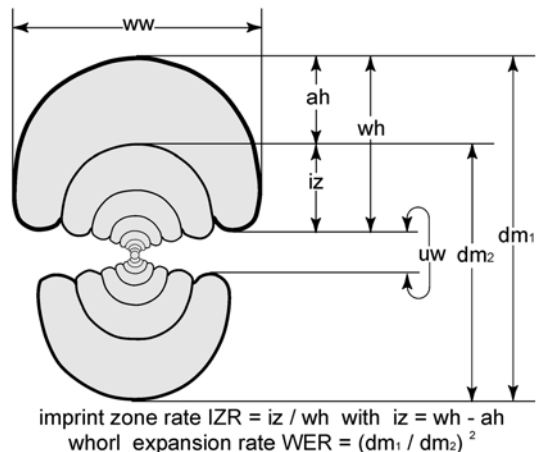
## 1.2 Geometry

### 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 ( $180^\circ$  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

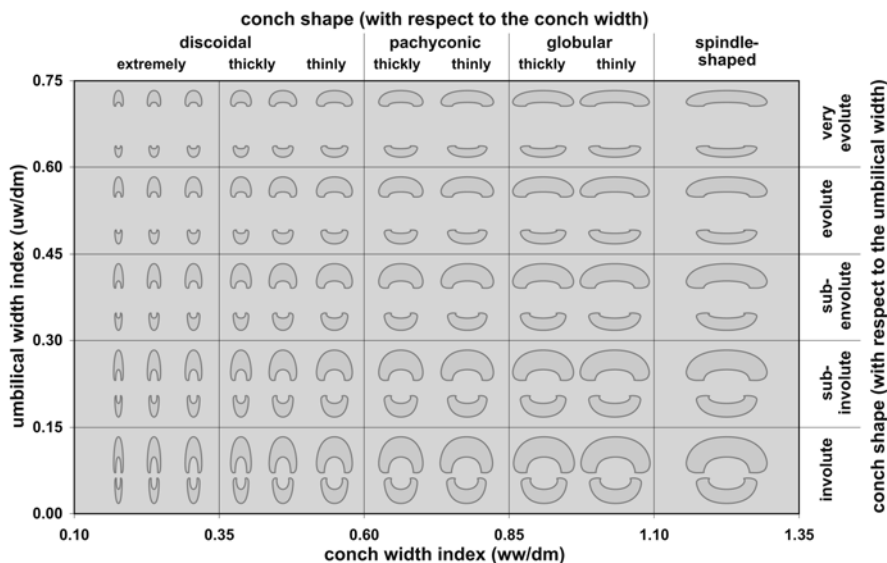
Due to their nearly logarithmic conch growth, most conch parameters also increase at differing rates. Caused by allometric growth, the change in certain parameters through ontogeny is not necessarily perfectly linear in a loglog-space (Kant 1973; Kant and Kullmann 1980; Klug 2001; Korn and Klug 2003; 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



**Fig. 1.3** Example of **cross sections** of various ammonoids: **a** *Sellanarcestes* cf. *tenuior*, late Emsian, Devonian, Filon 12, Tafilalt, Morocco; protoconch is visible, almost perpendicular to the





**Fig. 1.4** 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 (from Korn 2010)

and diameter in small increments, while whorl width, umbilical width, imprint zone width, and whorl height cannot be measured. Additionally, the angle between septa becomes measurable (Bucher et al. 1996; Kraft et al. 2008).

plane of symmetry (note the septa). **b** *Subanarcestes macrocephalus*, middle Eifelian, Filon 12, Tafilalt, Morocco; note the siphuncle. **c** *Goniatites multiliratus*, Viséan, Elm Creek, Oklahoma, USA; note the symmetry in the septa, indicating a plane perpendicular to the plane of symmetry. **d, e** *Macrocephalites* sp., PIMUZ 19078, Callovian, Jurassic, Anwil, Switzerland; note the approximately symmetrically cut septa. **Orientation of ornament:** *F. Parkinsonia parkinsoni*, Bajocian, Port-en-Bessin, France, dm 124 mm, Staatliches Museum für Naturkunde Stuttgart. *G. Lytoceras fimbriatum*, Pliensbachian, Jurassic, Fresney-le-Puceux near Caen, France, dm 209 mm, Staatliches Museum für Naturkunde Stuttgart. *H. Erbenoceras advolvens*, GPIT 1849-2002, early Emsian, Devonian, northern Tafilalt, Morocco, dm 156 mm. (all images: W. Gerber, Tübingen; A, B reproduced from Ernst and Klug 2010). **Spiral ornamentation.** I to K: Lateral structures. I, *Maxigoniatites saourensis*, Viséan, Carboniferous, near Merzouga, Tafilalt, Morocco, dm 72 mm. J, *Amaltheus margaritatus*, PIMUZ 13468, Pliensbachian, Reichenbach near Aalen, Germany. K, *Douvilleiceras mammillatum*, Albian, Cretaceous, Courcelles near Troyes, France, dm 10.8 cm, image: A. E. Richter, Augsburg. L to N: ventral structures. L, *Arietites* sp., Sinemurian, Jurassic, Mögglingen, Germany, dm 70 mm, Staatliches Museum für Naturkunde Stuttgart. (image: W. Gerber, Tübingen). M, *Euhoplites proboscideus*, PIMUZ 23108, Lower Gault, Albian, Cretaceous, Folkestone, Kent, UK, dm 40 mm. N, *Venezoliceras karsteni*, J 17830, Albian, NNE of Barbacoa, Venezuela, dm 110 mm, Naturhistorisches Museum Basel. **Ribbing patterns.** O, *Virgatisphinctes* sp., PIMUZ 16975, Unterhausen near Neuburg/Donau, Germany, dm 110 mm. P, *Pavlovia pal-lasioides*, Kimmeridgian, Jurassic, Kimmeridge Bay, Dorset, UK, dm 140 mm.

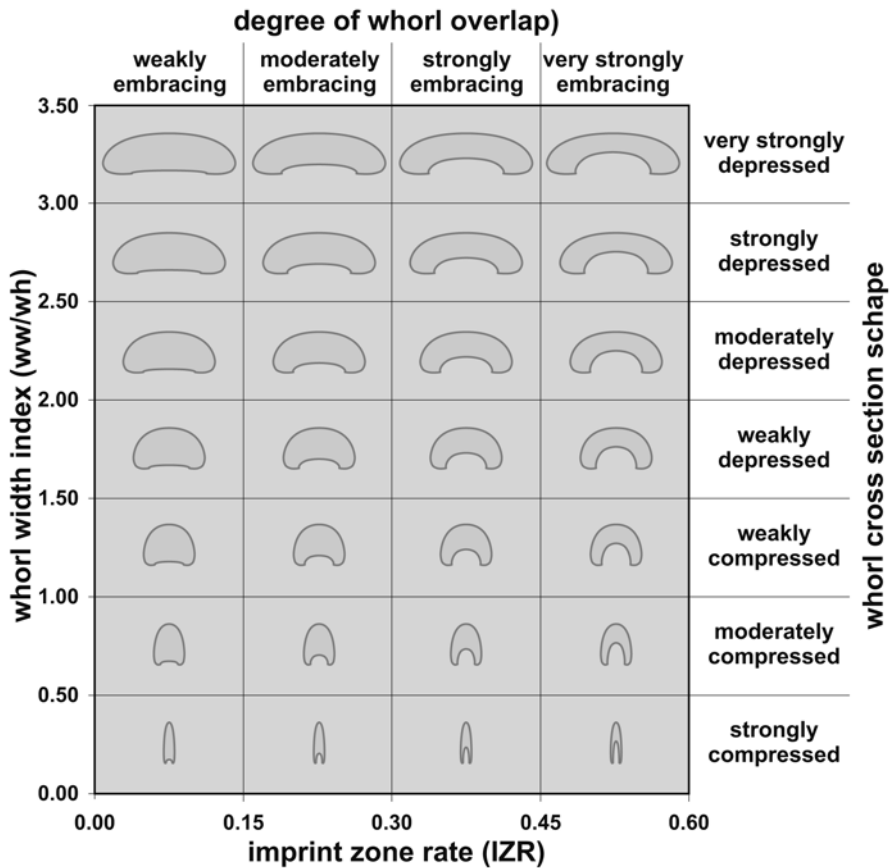


Fig. 1.5 Bivariate plot illustrating the terminology of the imprint zone rate (IZR) on the x-axis and whorl width index (ww/wh) on the y-axis (from Korn 2010)

Parameters measured through ontogeny on either kind of cross sections can be utilized to calculate the following expansion rates:

- whorl expansion rate:  

$$WER_1 = (dm_1/dm_2)^2 = [dm_1/(dm_1 - ah_1)]^2$$
- imprint zone rate:  

$$IZR_1 = wh_1 - ah_1/wh_1 = -[wh_1 \cdot (dm - dm_2)]/wh_1$$

See Fig. 1.5 and Tab. 1.1 for subdivisions of whorl expansion rates and imprint zone rates.

Korn and Klug (2002) introduced a slightly different formula for the Whorl Expansion Rate (WER) than the one used by Raup (1967), which better reflects the growth of the soft-body during ontogeny (in loosely coiled forms) and which is easier and more precisely applicable than the classical equation proposed by Raup and Michelson (1965).

Parent et al. (2010, 2011) also independently arrived at a similar formula for planispirally coiled Mesozoic forms. They slightly modified the Raup-model to also include planispirally coiled forms with non-touching whorls.

## 1.3 Ornamentation

### 1.3.1 *Radial Elements*

All ammonoids bear fine or coarse radial elements on the conch. The finest structures are commonly the growth lines (Bucher et al. 1996), which are formed during conch growth. They form when shell is secreted discontinuously at the aperture and may be spaced at distances of around 0.1 mm (Vermeij 1993; Bucher et al. 1996). Characteristically, they are interrupted and cannot be traced around the entire whorl. To examine them, well preserved original or replacement shell is needed.

Lirae are usually much stronger; they are also formed more or less regularly with distances sometimes exceeding 1 mm. Normally, lirae can be traced around the ammonoid's circumference, but the limits between growth lines and lirae are not clearly defined. Both are simply fine and coarse traces of former apertures, recording their shape through growth.

Ribs represent even larger undulations in the conch wall and are not present in all ammonoid taxa. Their shape, arrangement, strength, etc. varies broadly and significant changes during ontogeny may be observed. Rather often, ribs continue into nodes or spines. They still carry valuable taxonomic information, although the strength of the ribs often covaries with the whorl cross section (Checa et al. 1996). Their strength, spacing and orientation may be quantified for taxonomic purposes (e.g., De Baets et al. 2013a, 2013b).

Constrictions are less frequent than the previously mentioned radial elements; they usually occur in a lower number than ribs (often between one and five per whorl) and commonly are produced at growth halts (megastriae; see Bucher et al. 1996; Urdy 2015). At least on the internal mould (steinkern), constrictions are visible as furrows. Often, constrictions are internal shell thickenings which may have made interim apertures more resistant against mechanical damage by any cause during growth halts. In some cases, the shell thickening equalized the inward bent shell surface in such a way, that it is barely visible from the outside. Since they represented growth halts, the orientation of younger radial elements tend to display an orientation differing from that of the preceding ones. In some cases, these interim apertures carried collars, spines or nodes, which can be diagnostic for certain taxa.

The orientation of the radial elements (Fig. 1.3, 1.6) can be described as rectiradial (radial orientation), proradial or prorsiradial (turning toward the aperture in the ventral direction) and rursiradial (turning away from the aperture in the ventral direction). Depending on their curvature, the ribs can be concave (vaulted away from the aperture) or convex (vaulted towards the aperture); these two terms can

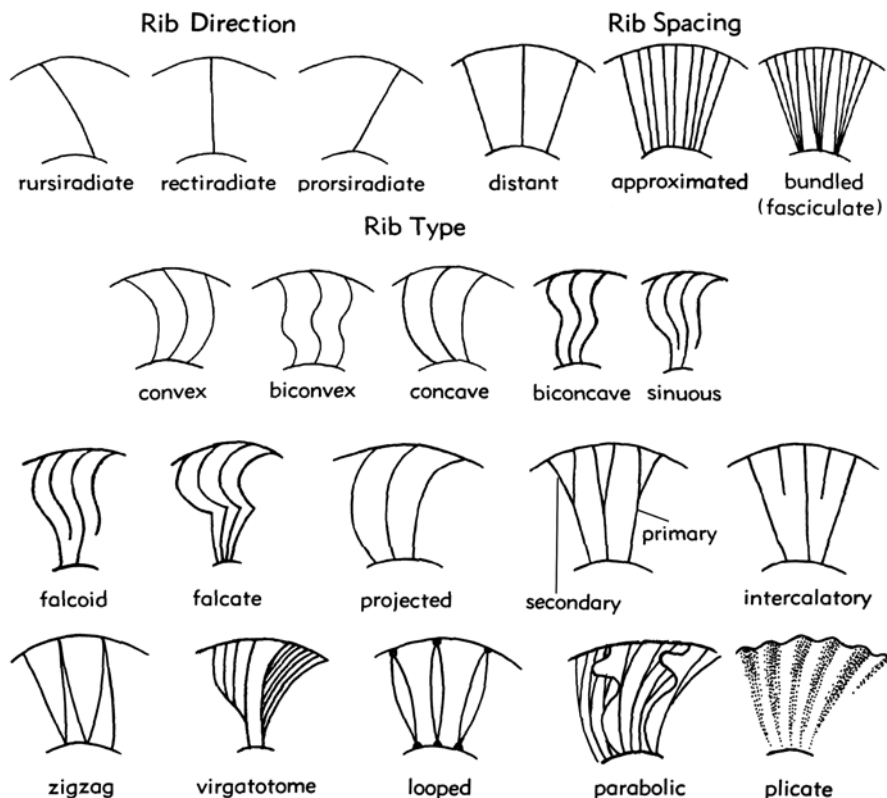


Fig. 1.6 Rib shape, spacing and course (modified from Arkell 1957)

be combined with the prefix *pro-* when they are inclined anteriorly (ventrad) and *retro-* when they are inclined posteriorly (ventrad). If the rib is partially concave and partially convex, it is called sinusoidal (sigmoid, sinusoid) and if the dorsal part of the rib is straight it is termed falcate. Ribs can split in various ways (Fig. 1.3, 1.6):

- simple (not branching)
- monoschizotomous (branching once): primary splits into two (bipartite, biplicate, dichotomous), three (tripartite) or four (quadripartite) secondary ribs
- dischizotomous (branching twice): primary splits into three (polygyrate) or four (bidichotomous) branches
- polyschizotomous (branching more than twice): branching only on one side of the primary rib (virgatipartite, virgatotomous) or branching on both sides of the primary (diversipartite)
- fibulate: ribs split and fuse again, forming a narrow ellipsis

In several Devonian and Carboniferous ammonoid species, subadult to adult specimens display the wrinkle layer (Korn et al. 2013). In all cases, these wrinkles are irregular and form a kind of fingerprint pattern on the dorsal shell. The elevation

of the wrinkles varies between a fraction of a millimetre and a few millimetres. In contrast to the wrinkle layer, Ritzstreifen extend over the entire conch and occur only in the Devonian (Sandberger and Sandberger 1850; Korn et al. 2013; compare Kulicki et al. 2015).

The spacing of radial elements is usually measured per half-whorl or demi-whorl (e.g., RDW or ribs per demi-whorl = the amount of ribs counted on a half-whorl). Other parameters such as a rib-index have also been used to quantify rib spacing more locally (or on fragments: compare Yacobucci 2004; De Baets et al. 2013a).

### 1.3.2 *Spiral Elements*

Spiral ornament can be subdivided according to position, i.e. ventral, lateral, or dorsal. Many ammonoids display spiral ornament such as spiral lines, which are usually rather weak compared to many radial structures (Fig. 1.3). Spiral lines are particularly common in Paleozoic ammonoids, where they sometimes form reticulate patterns when they occur in combination with radial lirae or ribs. Another common phenomenon is spiral rows of spines or tubercles (Fig. 1.3), which may occur laterally and ventrally.

In the Early Jurassic Amaltheidae, the dorsal conch commonly displays spiral wrinkles comparable to the radial wrinkles of the wrinkle layer known from Paleozoic ammonoids (Fig. 1.3). As far as ventral structures are concerned, keels have to be mentioned. These may be sharp or rounded, they can be connected to the flanks with a smooth transition or they can be clearly set off, they may be accompanied by a pair of furrows or a set of several parallel keels can occur (e.g. in Frasnian Beloceratidae). Families such as the Parkinsoniidae or the Hoplitidae have a midventral furrow.

### 1.3.3 *Spines, Nodes, Tubercles*

There are several kinds of ornamentation, which are neither truly radial nor spiral in orientation. Spines are pointed and elongate, while tubercles and nodes are knob-shaped. The term node is sometimes used for bigger structures, although the use is not uniform and some might consider nodes and tubercles synonymous terms. All these structures can be arranged radially and/or spirally, for example in *Douvilleiceras* (Fig. 1.3).

Some Paleozoic forms have developed deep ventral sinuses in their aperture (ventral band). At the edge of this sinus, collar-like projections developed in some genera, which formed long ventral ‘median spines’ in genera such as *Armatites* or *Kosmoclymenia* (e.g., Korn 1979, 2014).

## 1.4 Septa

### 1.4.1 *Suture Line*

The suture line is the line, where the septal mantle first attached the organic septal membrane and later the septum is formed by mineralization of the membrane. Its importance in systematics and taxonomy varies, depending on the researcher and also on the taxon under consideration. In Early and some Middle Devonian forms, differences in the suture line are sometimes so subtle that other conch characters are of greater use (e.g., Chlupáč and Turek 1983).

Nevertheless, the suture line yields valuable information on systematics and ultimately also phylogeny. In order to produce good drawings of suture lines, growth lines or constrictions, various techniques can be used.

1. A very simple procedure that can be applied to sutures, which lack microscopic detail, is the following: A sharp pencil is used to trace the suture line directly on the specimen. Afterwards, a strip of thin transparent duct tape is used to cover the entire suture line under consideration. After rubbing the surface of the tape, where the suture was colored before, the tape can be removed and attached to a sheet of paper. Next steps are scanning and tracing the suture line formerly copied on tape with any vector graphic software.
2. The classical method is to mount the specimen with modeling clay under a binocular microscope and then use a drawing mirror (camera lucida) or a grid within an ocular in order to transfer the suture on paper. In order to depict the entire suture, the specimen needs to be turned and mounted again in a new position on the modeling clay. The raw drawing can then also be scanned and traced with vector graphic software.

The convention is that the saddles (Klug and Hoffmann 2015) point with their convex sides towards the top (aperture). The plane of symmetry (the center of the E-lobe) is marked by an arrow, the umbilical shoulder (if present) can be indicated by a dotted line, the umbilical seam by a curve segment and the dorsal intersection with the plane of symmetry is indicated by either two straight dashes or two straight lines. If possible, mostly the right side of the suture is depicted, at least until the umbilicus and, if visible, the internal suture is also added.

In the case of suture lines, it is also very helpful, when more than one ontogenetic stage is depicted, because the change in complexity through ontogeny can be extreme, especially in Mesozoic species. It is also important to illustrate an adult suture, because usually, the adult sutures display the peak complexity.

### 1.4.2 *The Septum in Space*

In many publications, the third dimension of the septum is neglected. This is somewhat justified because normally, the septum displays the strongest folding at the suture line. The way in which the septum is folded, however, might yield additional

information for the discrimination of taxa or for the reconstruction of phylogenetic relationships. Accordingly, it can be rewarding to pay special attention to the morphology of the entire septum, also because it might display soft-tissue imprints (Klug et al. 2008).

To some extent, septum shape depends on the whorl cross section. For example, in strongly compressed as well as in extremely depressed forms, there are often high numbers of sutural elements (Ruzhencev 1949). Corresponding pairs of sutural elements are often linked by bulges in the septum, namely in the case of compressed forms symmetrically arranged in lateral direction, in the case of depressed forms arranged in approximately dorsoventral direction. Depending on the orientation of this bulging (see Klug and Hoffmann 2015 for illustrations), the terms central fluting (bulges are radially arranged relative to the initial chamber), lateral fluting (bulges are perpendicular to the plane of symmetry) or radial fluting (bulges are arranged radially around the center of the septum) were introduced. Additionally, ammonoid septa may be synclastically (concave toward the aperture) or anticlastically folded (partially concave and partially convex toward the aperture).

## 1.5 Discriminating New Species

Naturally, the requirements for the introduction of a new species are not uniform across all taxonomic and stratigraphic boundaries. Nevertheless, some common rules apply to most groups of ammonoids. In the following, we will highlight some important aspects that can be taken into account, when new species are described. We are well aware that not all material yields all the information to perform all the studies listed below.

### 1.5.1 *Ontogeny*

A common problem with many taxa that have been introduced in the nineteenth century is that hardly anything is known about ontogenetic changes in these taxa. However, some parts of ammonoid conchs grow allometrically (Klug 2001; Korn 2012) and in the course of their growth, variability was not uniform (Ropolo 1995; De Baets et al. 2013a). This has been more generally shown for mollusk conchs by Urdy et al. (2010a, 2010b). Variability is often the lowest in the early and the latest whorls, i.e. these are the most characteristic, but still variable (De Baets et al. 2015).

If the material permits, as many of the major ontogenetic stages (embryonic conch, neanconch, juvenile conch, preadult conch, adult conch; Westermann 1996; Klug 2001) as possible, especially of the last three stages, should be displayed and described in order to avoid that future researchers ascribe different ontogenetic stages of the same species to a different taxon.

### 1.5.2 *Intraspecific Variability and the Quality of Characters*

Discrete characters such as the absence or presence of certain structures or significant differences in numbers of lobes can be very helpful to identify species and also to justify the introduction of new species. In the case of characters, where transitions in character states between the supposedly new species and closely related species are known, intraspecific variability can be examined based on some tens of specimens of one size class in order to use such a character to explain the separation of a new species (De Baets et al. 2013a, 2015). The obvious disadvantage of the quantitative evaluation of intraspecific variability and its description as well as illustration is that they cost a lot of time and that they require a lot of printed space. Therefore, compromises are usually unavoidable and intraspecific variability cannot be examined for every single species. Nevertheless, it is a good idea to attempt to understand the intraspecific variability of the group one has to deal with, because then, the meaning of differences in any character between specimens can be more confidently interpreted with respect to its meaning, be it variation within a species or a difference in taxon.

When differences between supposedly new species in ratios such as UWI, CWI or WWI and in expansion rates such as WER and IZR (see Chap. 1.2) are evaluated, awareness of the respective intraspecific variability of the character under consideration can be of great help to both justify species separation and to avoid mistakes (e.g. by overestimating the character's meaning); however, intraspecific variability is roughly known only for a few species and genera, hampering such studies. This implies that, if time, the material, and thus the morphometric data permit, tests could be carried out to understand how the various character states are distributed through ontogeny. Are they normally distributed within a size class? Are one or several maxima present? Optimally, there should be two or more clearly separate peaks in the curve in order to make a quantitative character useful for species separation. An example, how such data can be represented, is given in Fig. 1.7. In any case, intraspecific variability of ammonoids is so poorly studied that it yields a wide array of possibilities for future studies (De Baets et al. 2015).

As stated above, intraspecific variability changes through ontogeny; it is usually the highest in middle whorls. This is partially reflected in some studies on covariation, Buckman's laws as well as in some other articles on variability (Hohenegger and Tatzreiter 1992; Dagens and Weitschat 1993; Checa et al. 1996; Korn and Klug 2007; De Baets et al. 2013a). If possible, we recommend basing descriptions on several specimens displaying several ontogenetic stages only. Furthermore, it is very helpful to include information on adult specimens, because adult conch modifications can show important diagnostic characters.

Sexual dimorphism (Klug et al. 2015) also contributes to intraspecific variability, especially in Mesozoic forms (Makowski 1962; Callomon 1963; Westermann 1964). Since dimorphism mostly applies to the last part of ontogeny, aspects of variability linked to dimorphism can be discriminated from variability within one sex.

Another poorly studied topic is differences in variability between regions; one of the inherent problems is the difficulty to reconstruct whether regional morpho-



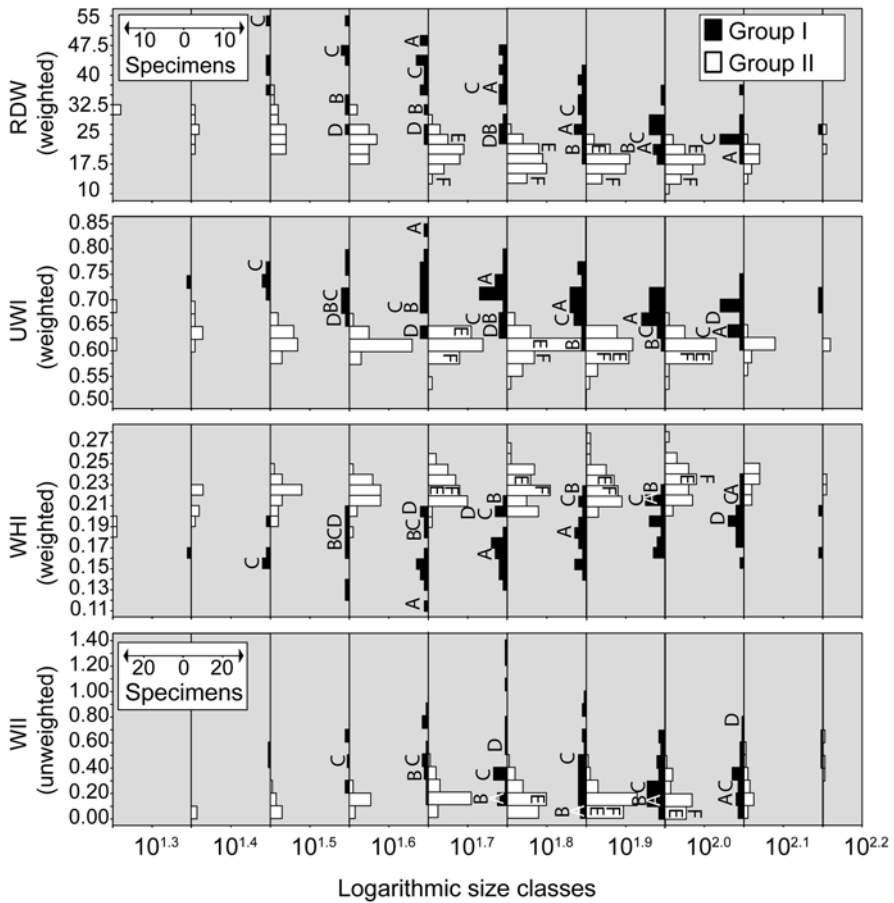
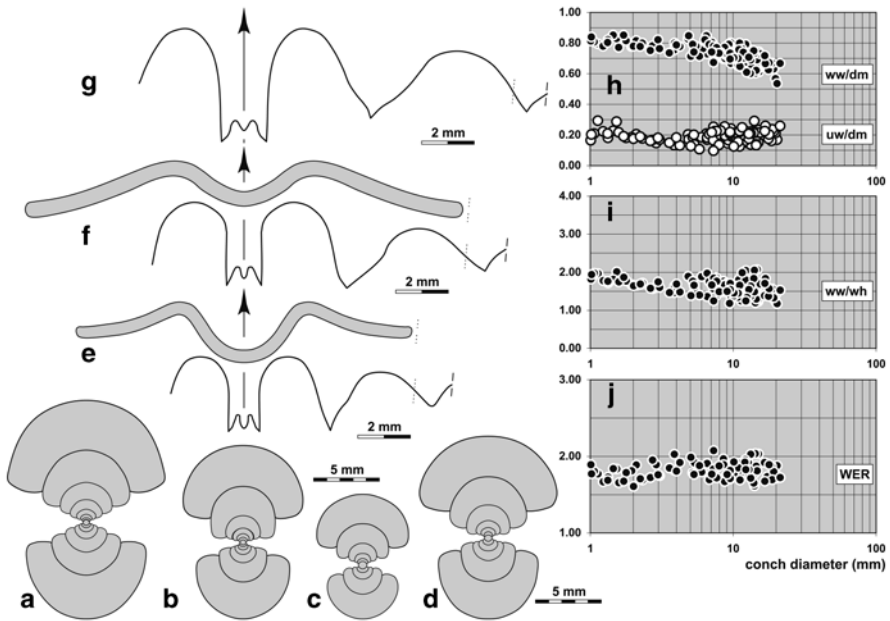


Fig. 1.7 Diagrams from De Baets et al. (2013a). Back-to-back histograms of Group I (black) and Group II (white) for ribs per half-whorl, RDW (weighted); umbilical width index, UWI (weighted); whorl height index, WHI (weighted); and whorl interspace index, WII (nonweighted)

logical differences originate in the facts that they are different species or whether these differences were caused by phenotypic plasticity or variation (Jacobs et al. 1994; Wilmsen and Mosavinia 2011). Body size may have varied geographically; intraspecific variability has certainly differed between regions, too (De Baets et al. 2015).

Although the study of intraspecific variability might appear as a nuisance, partially because it is time-consuming and partially because it is difficult to understand and describe in detail, it is actually an interesting topic for research since variation is essential for evolution, particularly heritable phenotypic variation (Hunt 2004, 2007). Furthermore, research on links between ecology and variability can also be rewarding (Jacobs et al. 1994; De Baets et al. 2015).



**Fig. 1.8** An example of how to organise an illustration when a new species is described (Korn et al. 2010): *Eurites permutus* from the early Late Tournaisian of Oued Temertasset (Mouydir, Algeria). **a** Cross section, MB.C.18849.1. **b** Cross section, MB.C.19040.3. **c** Cross section, MB.C.19040.4. **d** Cross section, MB.C.19040.5. **e** Suture line and constriction, MB.C.18835.1, at 11.0 mm dm, 7.9 mm ww, 5.3 mm wh. **f** Suture line and constriction, MB.C.18978.1, at 14.0 mm dm, 10.4 mm ww, 7.0 mm wh. **g** Suture line, MB.C.19040.1, at 19.0 mm dm, 12.5 mm ww, 9.0 mm wh. **h–j** Ontogenetic development of the conch width index (ww/dm), umbilical width index (uw/dm), whorl width index (ww/wh), and whorl expansion rate (WER) of all specimens

### 1.5.3 Number of Specimens and Figures

As ammonoids may show great intraspecific variability and since many taxa display allometric growth in their conch, it is advantageous when more than one specimen is available when a new species is described. If possible, these specimens should show the major growth stages, especially the juvenile, the preadult, and the adult stage. Similarly, it is helpful when the main allometric changes, as well as a large part of the intraspecific variability of one growth stage can be illustrated.

As far as the number of figures is concerned, we recommend producing some graphs illustrating the ontogenetic change of morphometric aspects of the ornamentation (rib spacing, ornament strength, ornament orientation etc.), UWI, WWI and WER through ontogeny of several specimens. This yields an idea of intraspecific variability and allometry. Optimally, one specimen of each growth phase should be illustrated, with the adult growth phase being possibly the most important. If dimorphism is strongly expressed, a dimorphic pair can be illustrated. Furthermore, a cross section (photograph or drawing after a photograph) may yield valuable ontogenetic information and drawings of the suture as well as of growth lines, the aperture, constrictions, etc. Some of these illustrations may be meaningfully combined (see Fig. 1.8).

## 1.6 Organizing A Species Description

Classically, a diagnosis is given first, usually combined with information on synonymies, origin of the name, type material, its provenance, other materials used and the repository. Although slightly dated, Matthews (1973) and Bengtson (1988) are still some of the best references for how best to use synonymy lists and open nomenclature, respectively. The diagnosis should be concise and contain the major characters of the taxon. It should list the main aspects of conch morphology and ontogeny, ornament, and suture line (Korn 2010).

In the detailed description, the same topics should be addressed in the same order, but in greater detail. The task and strength of such a descriptive text is to highlight important parameters and character states. Comparisons can be listed in the “comparisons” or “remarks” paragraph.

As most ammonoids underwent more or less profound changes in morphology throughout their ontogeny, it is advantageous to provide a reasonable amount of information on these ontogenetic trajectories, at least as far as such data can be obtained. Some examples for representations of ontogenetic changes can be found in the following articles: Korn (1997); Klug (2001); Monnet et al. (2012).

Although Korn et al. (2010) replaced the descriptive paragraphs in the systematic section by tables with the main morphological information, many might want to list the characters and their states in descriptions. One can order the descriptions according to

- specimen
- ontogeny (initial chamber, ammonitella, juvenile/neanic, preadult, adult/mature/gerontic)
- character (conch shape, ornamentation, suture line)

It is the easiest for the reader, when one of these orders is chosen and adhered to throughout the entire manuscript. Naturally, several aspects will vary according to the individual style.

**Acknowledgments** Some of the insights grew in the course of the research projects with the numbers 200021-113956/1, 200020-25029, and 200020-132870 funded by the Swiss National Science Foundation SNF (CK, CN, KDB). We greatly appreciate the constructive reviews of Otilia Szives (Budapest) and Christian Meister (Geneva).

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