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The morphospace of Late Permian coiled nautiloids

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Occurrences of Late Permian coiled nautiloids are widespread but they have never been analysed in terms of spatial and temporal disparity changes. Morphometric analyses using the cardinal Raupian conch parameters: conch width index, umbilical width index and whorl expansion rate with subsequent analysis by using principal components analysis and non-metric multidimensional scaling, allow the construction of a nautiloid morphospace. The analyses show that there is a stable disparity in the coiled nautiloids from the Wuchiapingian to the Changhsingian. Differences between the three major Late Permian nautiloid occurrences (Salt Range, South China and Transcaucasus-NW Iran) are considerably small; the South Chinese occurrences, however, are characterized by many endemic genera. The most important variation in morphospace occupation is caused by environmental differences such as water depth. ☐ *Changhsingian, disparity, morphospace, Nautilida, palaeogeography, Wuchiapingian.*

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It is well known that the ammonoids underwent profound evolutionary changes during the Late Permian (e.g. Ruzhencev 1962; Ruzhencev & Shevyrev 1965; Shevyrev 1965; Zhao *et al.* 1978; Leonova 2002; Villier & Korn 2004; Barskov *et al.* 2008; Korn *et al.* 2016), before they experienced one of several near-complete extinctions at the end of the Phanerozoic (e.g. Schindewolf 1953; House 1981; Teichert 1986; Erwin 1994; Brayard *et al.* 2009; Korn *et al.* 2013). Such a pattern is not known for nautiloids, which in general show much lower evolutionary rates during the Carboniferous, Permian and Triassic (e.g. Miller *et al.* 1933; Miller & Youngquist 1949; Kummel 1953, 1964; Ruzhencev & Shimansky 1954; Shimansky 1965, 1967). Differences in evolutionary patterns between the two cephalopod groups are probably the reason why many researchers focused on ammonoids with their high potential for stratigraphical purposes, while nautiloids played only a subordinate role in research projects. Another reason for fewer studies using nautiloids may be the fact that, in most of the Late Permian cephalopod occurrences, nautiloid specimens occur in much smaller numbers than ammonoids.

In contrast to nautiloids, morphospace or disparity, analyses of ammonoids have been achieved rather frequently in the last decades, both for Palaeozoic (e.g. Saunders & Swan 1984; Korn 2000; Korn & Klug 2003, 2012; Saunders *et al.* 2004, 2008; Villier & Korn 2004; Korn *et al.* 2015) and Mesozoic groups (e.g. Dommergues *et al.* 1996, 2001; Klug *et al.* 2005; Moyne & Neige 2007; Gerber *et al.* 2008; Dera *et al.* 2010; Smith *et al.* 2014). However, it is rather obvious that the methods developed for disparity analyses of ammonoids can also be applied for coiled nautiloids, at least when their conchs are planispirally coiled. New methods for the study of nautiloid conchs by using 3-D scanning techniques are promising for future studies of recent and fossil forms (Lemanis *et al.* 2016; Tajika *et al.* 2018).

In the following, we present the first disparity analyses of the Late Permian coiled nautiloids with respect to their conch geometry. We focus on similarities and differences in time (Wuchiapingian and Changhsingian) and space (occurrences in the Dolomites of Italy, Transcaucasia and NW Iran, the Salt Range of Pakistan and South China).

Material and methods

Late Permian nautiloids are known from a number of regions worldwide, but only some of them can be listed which yielded assemblages with more than eight species. These are the Transcaucasus-NW Iran region, the Salt Range of Pakistan, South China and

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the Dolomites of Italy (Fig. 1). Currently, there are about 45 genera of coiled nautiloids known from these regions, of which, however, only 17 genera are known from more than one region (Fig. 2). A total of 28 out of the 45 genera are possibly endemic; most of them belong to the Changhsingian occurrences of South China.

Transcaucasus, NW Iran

The fossil content of the exposures in the Araxes (Aras) Valley was first investigated by Abich (1878) and Arthaber (1900), including descriptions of several nautiloid species. Later, studies (Shimansky 1962, 1965, 1979; Rostovtsev & Azaryan 1973; Kotlyar *et al.* 1983) had been extended to other localities in the region (e.g. Vedi and Ogbin in Armenia, Karabaglyar in Azerbaijan) and led to the result that more than 40 coiled nautiloids were named, although many of them in open nomenclature. On the Iranian side of the Araxes Valley, Stepanov *et al.* (1969) and Teichert *et al.* (1973) described Permian-Triassic boundary sections in the Ali Bashi Mountains. The nautiloids from this site were monographically described by Teichert & Kummel (1973), but many species were also held in open nomenclature. New collections by the authors between 2010 and 2018 revealed many rather well-preserved nautiloid specimens, which are currently being studied including a revision of the earlier articles. At current state, at least 38 Wuchiapingian and 11 Changhsingian nautiloid species can be separated.

The Salt Range

Nautiloids were described in three principal monographs. The first of them was the pioneering study by Waagen (1879) with a first overview on the nautiloid diversity in the lower and upper *Productus* limestones. According to conodonts, these formations belong to the Wuchiapingian and Changhsingian, respectively (Shen *et al.* 2006). Based on the study by Waagen, Reed (1931, 1944) added more nautiloid species to the list. Unfortunately, a modern revision of these assemblages does not exist; according to current knowledge, at least 24 Wuchiapingian and 12 Changhsingian nautiloid species can be separated.

South China

In contrast to the two other regions, the study of Late Permian nautiloids began rather late in South China.

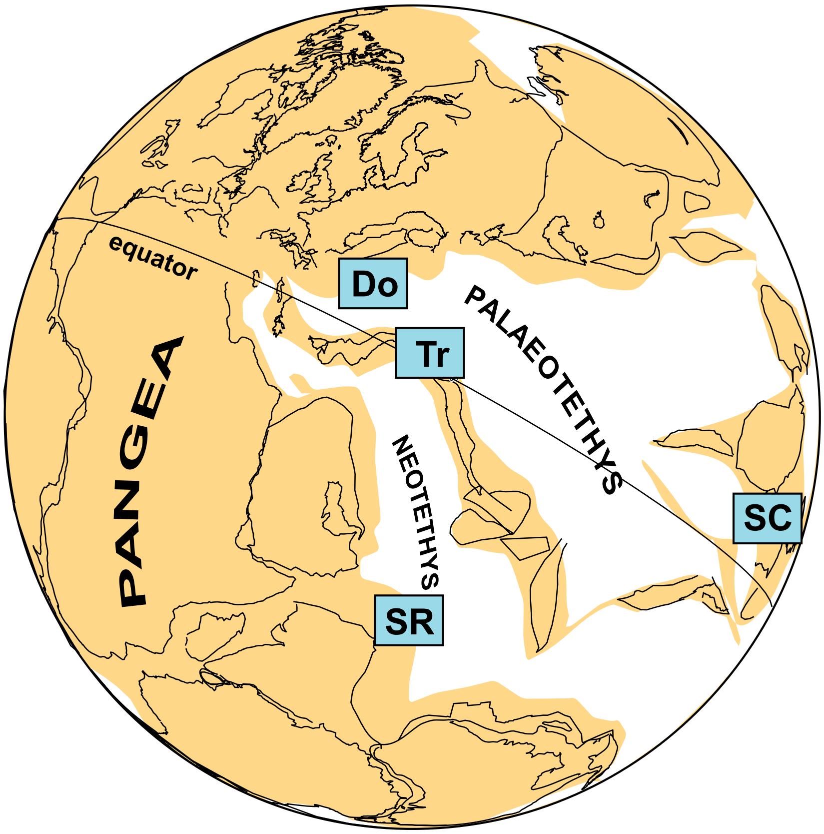


Fig. 1. Palaeogeographical position of the Late Permian nautiloid occurrences analysed here; after Stampfli & Borel (2002). Do = Dolomites, Tr = Transcaucasus, SR = Salt Range, SC = South China. [Colour figure can be viewed at wileyonlinelibrary.com]

It was mainly the voluminous monograph on the Late Permian cephalopods, predominantly ammonoids, by Zhao *et al.* (1978), which formed solid ground for the subsequent descriptions of nautiloids (Liang 1984; Zheng 1984; Qin 1986; Yang *et al.* 1987; Wu & Kuang 1992). At current state, at least 13 Wuchiapingian and 32 Changhsingian nautiloid species can be separated.

The Alps

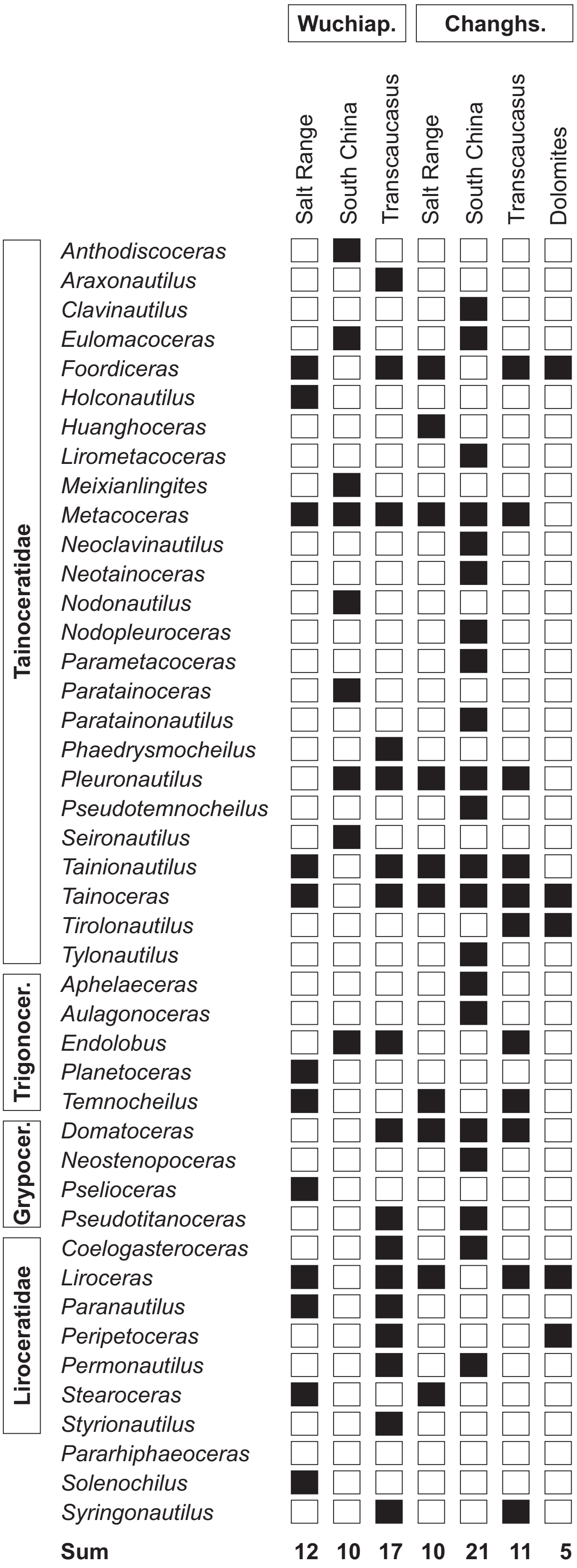
In the Dolomites, Late Permian nautiloids are known for a rather long time (Stache 1877; Merla 1930); a revision of the assemblage was provided in the large monograph by Prinoth & Posenato (2007). According to this study, eight species of nautiloids occur in the Changhsingian *Bellerophon* Formation.

Other regions

There are some other regions from which Late Permian nautiloids are known, but the assemblages are too small for a quantitative analysis. An assemblage with a rather similar composition like the *Bellerophon* Formation was described by Schréter (1974) from the Bükk Mountains of Hungary; however, this material is poorly preserved and can only tentatively be assigned to distinct species. A small nautiloid assemblage, probably of Late Permian age, from western Serbia was described by Simić (1933). Two specimens belonging to *Tirolonautilus* were described by Chirat *et al.* (2006) from Central Saudi Arabia; they closely resemble the material of that genus from the Dolomites. From Central Iran, a number of nautiloid taxa were listed (Bando 1979; Taraz *et al.* 1981) but not yet described. Diener (1903) described a species of *Domatoceras* from the Central Himalayas. Material of *Stearoceras* was listed by Miller & Cline (1934) from the Phosphoria Formation of Wyoming. One species of *Permonautilus* was described by Tichy (1975) from Greenland. Finally, a few nautiloid occurrences from the Zechstein Formation of Central Europe and the British Isles need to be mentioned; these occurrences yielded only two liroceratid species (e.g. Geinitz 1841; King 1850).

Disparity analysis

Our disparity analysis follows the development of the method as outlined by various authors (e.g. Foote 1993a,b; Wills *et al.* 1994; Roy & Foote 1997; Ciampaglio *et al.* 2001; Wills 2001; Gerber 2017; Walton & Korn 2018). For the morphometric analyses, we



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		Salt Range	South China	Transcaucasus	Salt Range	South China	Transcaucasus	Dolomites
Tainoceratidae	*Anthodiscoceras*	□	■	□	□	□	□	□
	Araxonautilus	□	□	■	□	□	□	□
	Clavinautilus	□	□	□	□	■	□	□
	Eulomacoceras	□	■	□	□	■	□	□
	Foordiceras	■	□	■	■	□	■	■
	Holconautilus	■	□	□	□	□	□	□
	Huanghoceras	□	□	□	■	□	□	□
	Lirometacoceras	□	□	□	□	■	□	□
	Meixianlingites	□	■	□	□	□	□	□
	Metacoceras	■	■	■	■	■	■	□
	Neoclavinautilus	□	□	□	□	■	□	□
	Neotainoceras	□	□	□	□	■	□	□
	Nodonautilus	□	■	□	□	□	□	□
	Nodopleuroceras	□	□	□	□	■	□	□
	Parametacoceras	□	□	□	□	■	□	□
	Paratainoceras	□	■	□	□	□	□	□
	Paratainonautilus	□	□	□	□	■	□	□
	Phaedrysmocheilus	□	□	■	□	□	□	□
	Pleuronautilus	□	■	■	■	■	■	□
	Pseudotemnocheilus	□	□	□	□	■	□	□
	Seironautilus	□	■	□	□	□	□	□
	Tainionautilus	■	□	■	■	■	■	□
	Tainoceras	■	□	■	■	■	■	■
	Tirolonautilus	□	□	□	□	□	■	■
	Tylonautilus	□	□	□	□	■	□	□
Trigonocer.	*Aphelaeceras*	□	□	□	□	■	□	□
	Aulagonoceras	□	□	□	□	■	□	□
	Endolobus	□	■	■	□	□	■	□
	Planetoceras	■	□	□	□	□	□	□
	Temnocheilus	■	□	□	■	□	■	□
Grypocer.	*Domatoceras*	□	□	■	■	■	■	□
	Neostenopoceras	□	□	□	□	■	□	□
	Pselioceras	■	□	□	□	□	□	□
	Pseudotitanoceras	□	□	■	□	■	□	□
Liroceratidae	*Coelogasteroceras*	□	□	■	□	■	□	□
	Liroceras	■	□	■	■	□	■	■
	Paranautilus	■	□	■	□	□	□	□
	Peripetoceras	□	□	■	□	□	□	■
	Permonautilus	□	□	■	□	■	□	□
	Stearoceras	■	□	□	■	□	□	□
	Styrionautilus	□	□	■	□	□	□	□
	Pararhiphaeoceras	□	□	□	□	□	□	□
	Solenochilus	■	□	□	□	□	□	□
	Syringonautilus	□	□	■	□	□	■	□
	Sum	**12**	**10**	**17**	**10**	**21**	**11**	**5**

Fig. 2. The stratigraphical and geographical occurrence of Late Permian nautiloid genera in the regions analysed here.

measured representative specimens of 89 Wuchiapingian and 69 Changhsingian coiled nautiloid species with respect to their cardinal conch parameters (Raup 1966, 1967; Korn 2010; Klug *et al.* 2015): conch width index (CWI = whorl width/conch diameter), umbilical width index (UWI = umbilical width/conch diameter) and whorl expansion rate (WER = expansion rate of the conch diameter per volution) (Fig. 3). In cases of incomplete preservation, missing characters were interpolated from the most closely related species.

These three parameters were processed using two methods:

1 A principal components analysis (PCA; using the correlation procedure) was carried out, and results were plotted in a morphospace diagram (Fig. 4). The first axis of this explains 61.7% of the total variance; the second axis explains 24.4% and the third 13.9%. This means that the bivariate plots shown here explain about 86% of the variance; displaying the third axis was thus omitted. All three characters are responsible for the position of the respective species on the first axis (higher WWI and higher WER but lower UWI towards higher PCA scores). On the second axis, higher WWI and higher WER lead to higher PCA scores.
2 A non-metric multidimensional scaling analysis (NMDS; using the Bray–Curtis similarity algorithm) was carried out and also plotted in a morphospace diagram (Fig. 5). The diagrammatic representation very closely resembles the PCA plot, just being rotated by 180 degrees, with very similar positions of the analysed species in the scatter plots. A set of diagrams with details regarding differences of morphospace occupation in time and space can be found in the supplementary online material (Figs S1–S5).

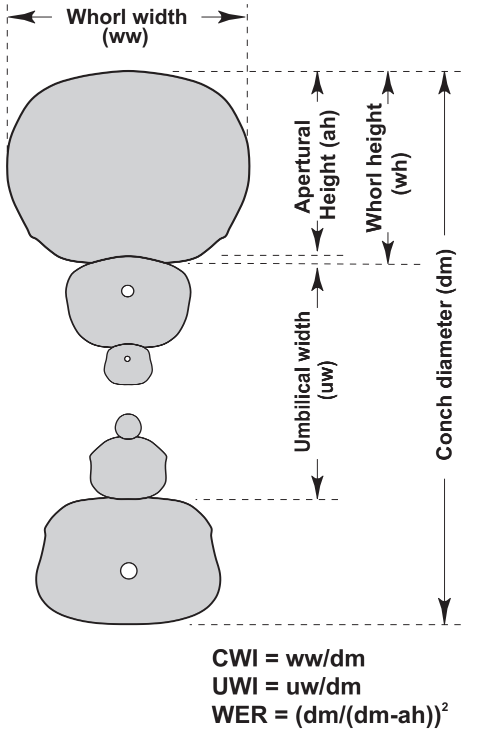

Fig. 3. The cardinal conch parameters used for the morphospace analysis of Late Permian nautiloids.

For the evaluation of the width morphospace occupation, we computed the sum of range (SOR) and the sum of variance (SOV) of the PCA plots. In a first step, the total values of each assemblage and, in a second step, subsampling (100 iterations) based on the smallest assemblage were applied.

Results

The results of the morphospace analysis can be grouped in the light of taxonomic, stratigraphical and palaeogeographical patterns. The total morphospace expressed on the first two axes of the PCA diagram has a triangular shape with the most evolute, thinly discoidal species in the left corner and the more involute and globular forms on the right side. These results can be discussed when paying attention to several aspects, discussed below.

Taxonomy

Four families are most dominant to constitute the Late Permian nautiloid assemblages: Tainoceratidae, Trigonoceratidae, Grypoceratidae and Liroceratidae (classification following Dzik 1984). All four are long-ranging families that occur from the Early Carboniferous to the Late Permian or even into the Triassic (e.g. Kummel 1964; Shimansky 1967; Dzik 1984). These groups are mainly defined by their conch shape characteristics and, secondarily, by their sculptures and ornaments. Low within-family plasticity and characteristic conch shapes over long time intervals allow a rather clear separation of three of the four families, when their position in the conch shape morphospace of the Late Permian nautiloids is regarded (Fig. 6). The Trigonoceratidae, Grypoceratidae and Liroceratidae occupy areas in the morphospace with only small overlap, both in the PCA and NMDS scatter plots. In both plots, the Tainoceratidae superimposes the morphospace of the Trigonoceratidae (which differ mainly in their sculpture from the other three families) and the Grypoceratidae but only touches that of the Liroceratidae.

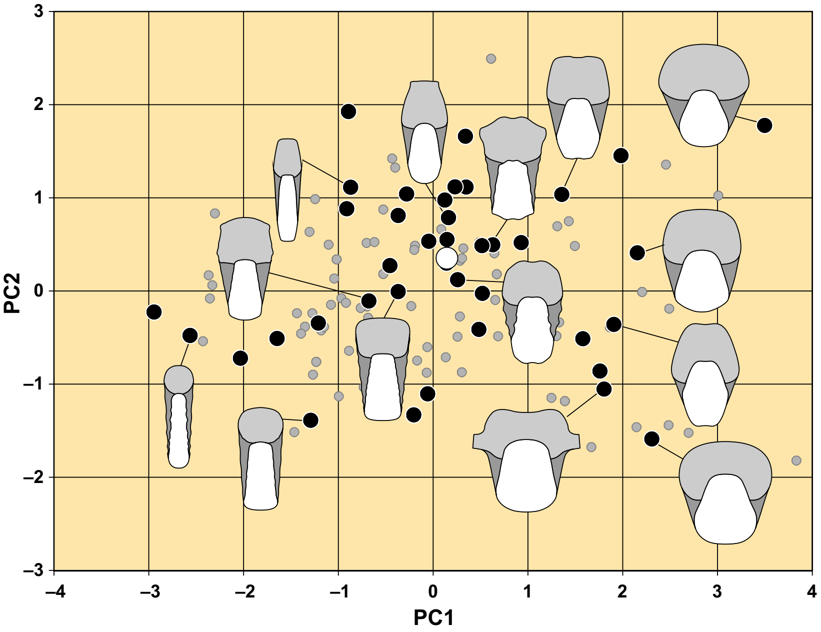

Fig. 4. First two axes of the empirical morphospace of the Late Permian nautiloids; the three cardinal conch parameters CWI, UWI and WER are analysed with the principal components analysis (correlation mode). Highlighted are the Wuchiapingian nautiloids, representative apertural views are from specimens of NW Iran. [Colour figure can be viewed at wileyonlinelibrary.com]

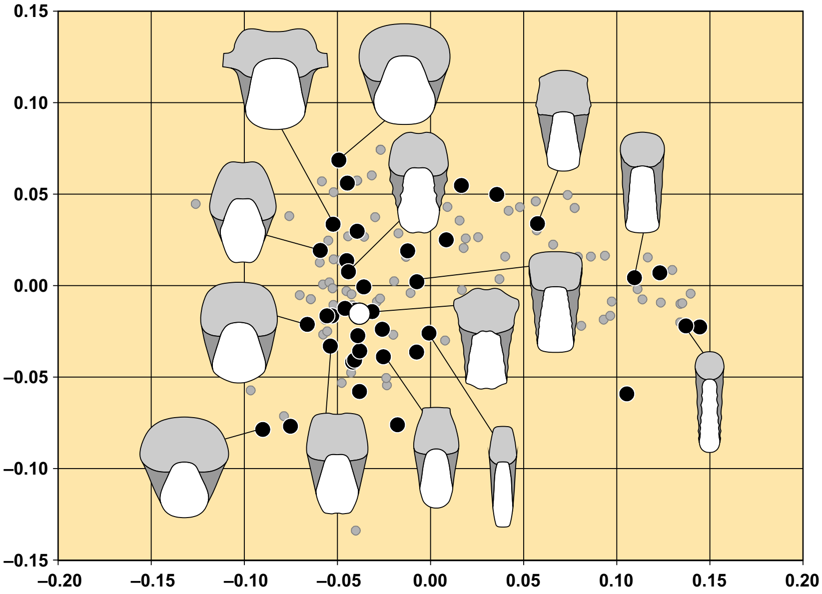

Fig. 5. First two axes of the empirical morphospace of the Late Permian nautiloids; the three cardinal conch parameters CWI, UWI and WER are analysed with the NMDS method (Bray–Curtis similarity index). Highlighted are the Wuchiapingian nautiloids, representative apertural views are from specimens of NW Iran. [Colour figure can be viewed at wileyonlinelibrary.com]

Stratigraphy

Both methods, PCA and NMDS, show very similar distributions of the Wuchiapingian and Changhsingian in the morphospace (Fig. 7), demonstrating that major evolutionary steps did not occur between during the Late Permian nautiloids. Furthermore, the disparity analysis shows that both Late Permian stages are very similar with respect to sum of range and sum of variance (Fig. 8). However, the three regions with both Wuchiapingian and Changhsingian assemblages show an inconsistent pattern: while the disparity measures between the Wuchiapingian and the Changhsingian increases in the Salt Range

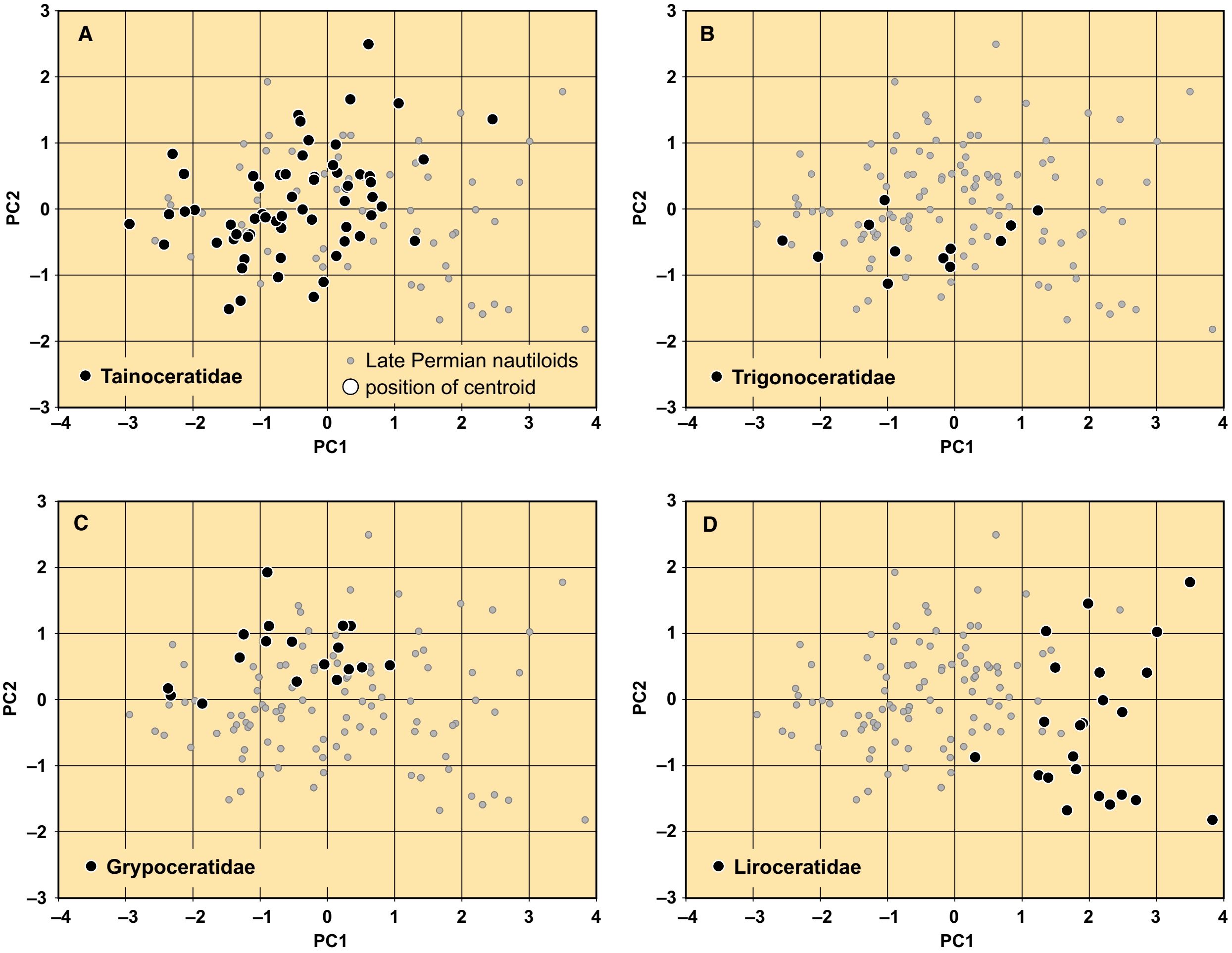

Fig. 6. Morphospace occupation of Late Permian nautiloids of the four most important families, analysed by using the PCA method. [Colour figure can be viewed at wileyonlinelibrary.com]

and South China, it decreases in the Transcaucasus. However, it has to be kept in mind that the Transcaucasian sections show a facies shift during the two stages (Stepanov *et al.* 1969; Leda *et al.* 2014) towards a deeper environment, paralleled by a significant decrease in numbers of species of nautiloids.

Palaeogeography

Differences in morphospace occupation and disparity between the four analysed regions are surprisingly small (Figs 9, 10), when compared to the time equivalent ammonoids (e.g. Zhao *et al.* 1978; Leonova 2002; Korn & Klug 2012; Korn *et al.* 2016). Several of the nautiloid genera occur in all four regions, and it is mainly the proportion between them that causes some differences. It appears that the South Chinese assemblages contain a number of endemic genera, but this is not as distinct as in the ammonoids, where differences between regions are expressed on the family level (Korn *et al.* 2016).

Environment

Changes in the generic composition can be observed in the sections of NW Iran, where nautiloids of the shallower environment in the early Wuchiapingian lower Julfa Beds (Stepanov *et al.* 1969; Ghaderi *et al.* 2014) are dominated by grypoceratids (*Domatoceras*) and liroceratids (*Liroceras*, *Permonautilus*) with additional tainoceratids (*Metacoceras*). They are replaced, in the deeper facies of the late Wuchiapingian upper Julfa beds by other liroceratid genera (*Peripetoceras*, *Coelogasteroceras*) and finally in the Ali Bashi Formation of the Changhsingian, by predominant tainoceratids (*Pleuronautilus*, *Tainionautilus*, *Tirolonautilus*).

The plots for the Wuchiapingian show that the Transcaucasian region nearly occupies the entire morphospace of the Late Permian nautiloids, while the margins are somewhat trimmed in the Salt Range assemblage; the South Chinese morphospace is restricted to the central area (Fig. 9). The plot

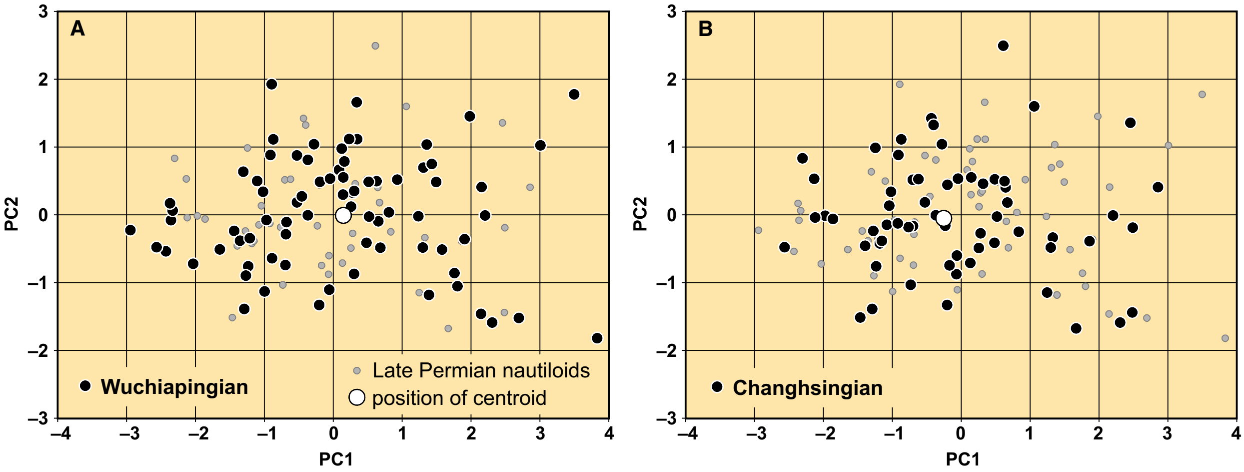

Fig. 7. Morphospace occupation of Late Permian nautiloids in the Wuchiapingian and Changhsingian stages, analysed by using the PCA method. [Colour figure can be viewed at wileyonlinelibrary.com]

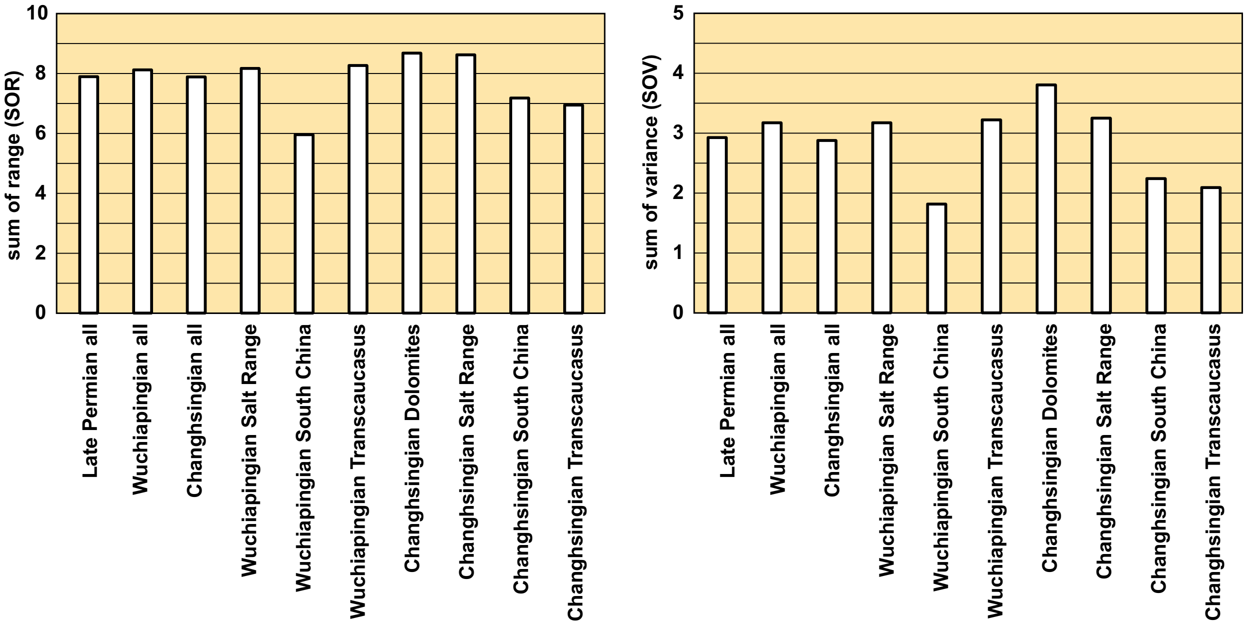

Fig. 8. Disparity of Late Permian nautiloids with respect the Wuchiapingian and Changhsingian stages and the occurrences in selected regions, analysed by using the PCA method. [Colour figure can be viewed at wileyonlinelibrary.com]

including the northern regions (Zechstein of Central Europe and the British Isles and Greenland) shows a very restricted picture with only liroceratids occurring in these areas (Fig. 9D).

The Changhsingian plots show then a relatively uniform occupation of morphospace of the samples from the Transcaucasus, the Salt Range and South China; they differ mainly in the density of dots (Fig. 10). The assemblage from the Dolomites differs from the others as the species occupy rather marginal areas in the morphospace, caused by the dominance of liroceratids and the lack of grypoceratids and trigonoceratids. However, despite of this taxonomic restriction it is remarkable that the assemblage contains very different nautiloid morphologies by the liroceratids and tainoceratids.

Discussion

The nautiloid evolution in the Late Permian shows remarkable differences to the time equivalent ammonoids. For the ammonoids, the time from the Capitanian to the Early Triassic was an interval with two major crises, one at the end of the Capitanian (end-Guadalupian crisis) and one at the end of the Changhsingian (end-Permian mass extinction) and one minor crisis at the end of the Wuchiapingian.

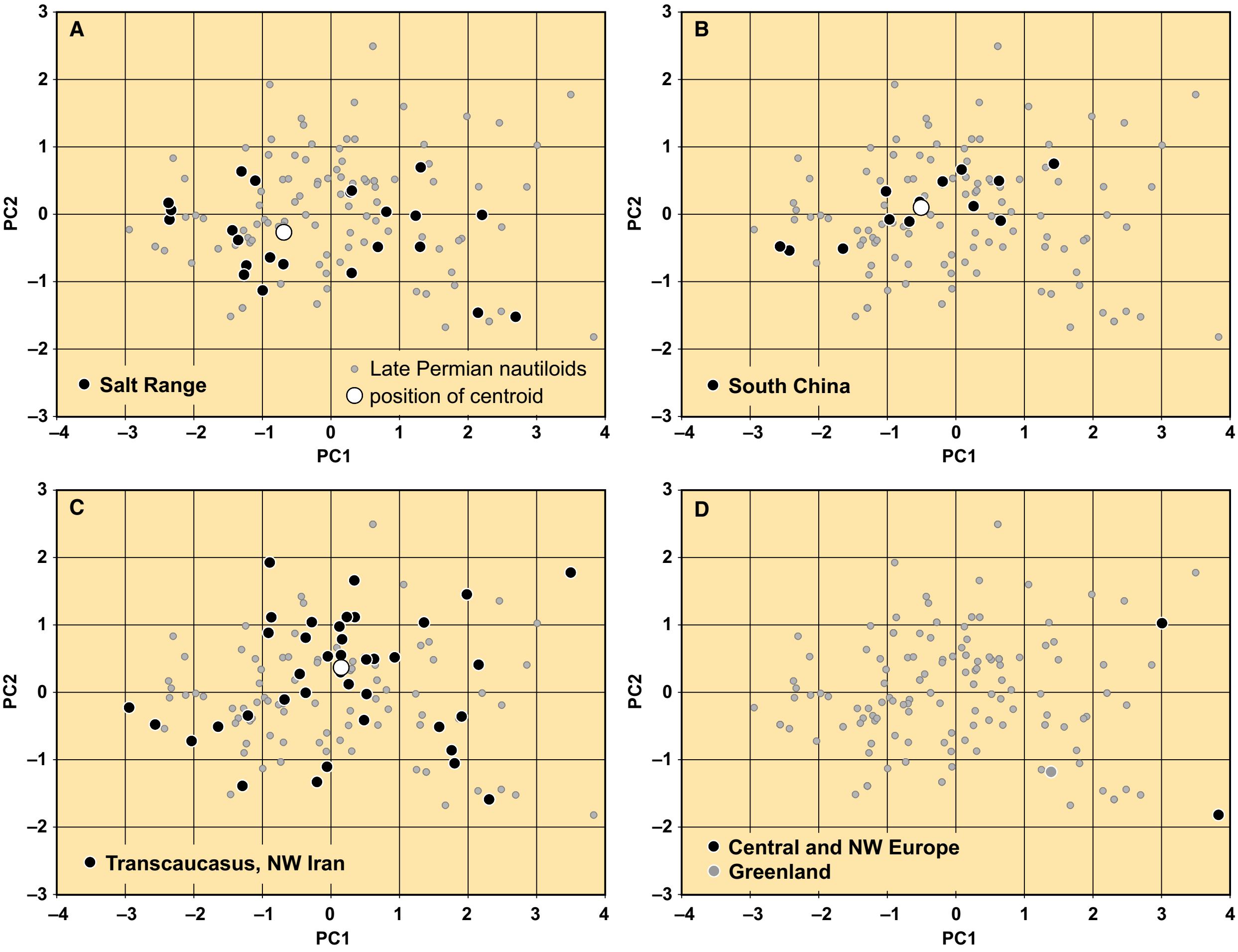

Fig. 9. Morphospace occupation of Wuchiapingian nautiloids in selected regions, analysed by using the PCA method. [Colour figure can be viewed at wileyonlinelibrary.com]

The evolutionary history of the Late Permian ammonoids was outlined for three cardinal regions, the Transcaucaus-NW Iran region (Ruzhencev 1962; Ruzhencev & Shevyrev 1965; Shevyrev 1965; Zakharov 1992; Ghaderi *et al.* 2014; Korn *et al.* 2016), Central Iran (Bando 1979) and South China (Zhao *et al.* 1978; Liang 1984; Zheng 1984; Qin 1986; Yang *et al.* 1987).

The two ammonoid orders Goniatitida and Prolecanitida show a drastic decline at the end of the Capitanian, but the third order Ceratitida appeared to profit from this event and became diverse in the Wuchiapingian with the predominant superfamily Otoceratoidea (Ruzhencev 1962, 1963; Spinosa *et al.* 1975; Zhao *et al.* 1978). However, a major turnover at the Wuchiapingian-Changhsingian transition shows a decline of the Otoceratoidea and a Changhsingian bloom of the Xenodiscoidea with the family Dzulfitidae in the Transcaucasus-NW Iran and Central Iran regions (Ruzhencev 1962; Shevyrev 1965; Bando 1979; Korn *et al.* 2016) and the Pseudotirolitidae in South China (Zhao *et al.* 1978).

When the coiled nautiloids are regarded, differences and also similarities in the composition between the assemblages, either temporal or spatial, may be explained by (1) evolutionary aspects; (2) environmental aspects; (3) different sampling; and (4) different taxonomic practices.

Evolutionary aspects

Evolutionary processes may play only a minor role, as many of the genera occur in both the Wuchiapingian and the Changhsingian stages (many of them are even known as the Middle Permian and the Early Triassic assemblages). According to the current state of knowledge, the evolutionary pattern seen in the ammonoids is not known from the nautiloids. With respect to the present data, there is no turnover in nautiloids between the Wuchiapingian and the Changhsingian. The lack of faunal turnover can be seen as the main reason for the stability of the nautiloid morphospace during the Late Permian.

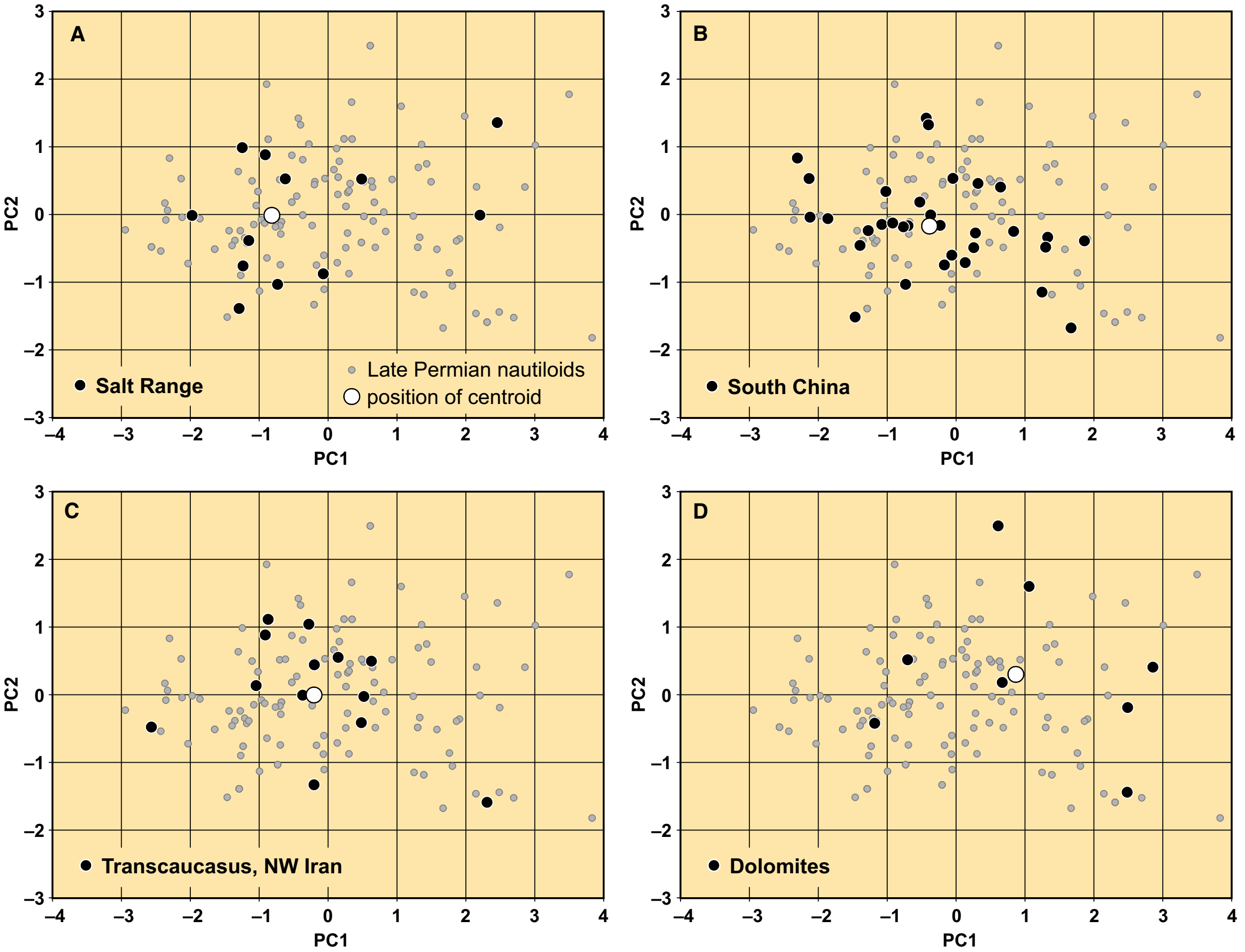

Fig. 10. Morphospace occupation of Changhsingian nautiloids in selected regions, analysed by using the PCA method. [Colour figure can be viewed at wileyonlinelibrary.com]

Environmental aspects

Environmental aspects may play a more important role. Generally, Permian nautiloids occur in four different facies: (1) reefs, although in such an environment, only few nautiloids occurred (Wu & Kuang 1992); (2) moderately shallow-water settings, which are usually very rich in brachiopods and other benthos, but without or with very rare ammonoids (e.g. *Bellerophon* Formation of the Alps, *Productus* Limestone of the Salt Range), are usually dominated by the liroceratids and other nautiloids with stout and involute conch (Prinoth & Posenato 2007); (3) intermediate settings, in which nautiloids co-occur with ammonoids in almost equal numbers (e.g. Julfa Formation of the Transcaucasus and NW Iran), liroceratids are still present but an increasing number of tainoceratids and grypoceratids can be recognized (Shimansky 1965); and (4) deeper water settings on the outer shelf, where ammonoids are commonest and nautiloids are very rare (e.g. *Paratirolites* Limestone of the Transcaucasus) show only few liroceratids but increasing numbers of tainoceratids (Shimansky 1965).

Sampling biases

Sampling biases may occur particularly in the case of nautiloids because often material of this group can only be regarded as by-catch during sampling of other fossils such as ammonoids, which are obviously more important for stratigraphical purposes. Our own sampling in the NW Iranian sections led to the result that many of the identified species are represented by only one specimen, which may be an indicator of increasing species-richness in the case of larger material.

Taxonomic practice

Taxonomic practice may play an important role in the knowledge of Late Permian nautiloids. One has to keep in mind that the various regions differ significantly in the state of revision. From only one region, the Dolomites, a modern revision of the material, are existing (Prinoth & Posenato 2007). The nautiloids from the Transcaucasus-NW Iran region had been figured and partly described in several articles (Shimansky 1965, 1979; Stepanov *et al.* 1969; Teichert & Kummel 1973), but none of them provides a complete overview on all the taxa known from this region. For the assemblages from the *Productus* Limestone of the Salt Range, after the pioneering study of Waagen (1879), revisions had been made only in the 1930 and 1940 (Reed 1931, 1944); the material urgently requires revision. The studies of the South Chinese material date back from 1970s to 1980s. Newly collected material from NW Iran and Central Iran is currently being revised by the authors; the taxonomic attributions are already used here. These differences in the status of description may particularly be a source of error when taxonomic diversity is analysed.

Conclusions

Late Permian nautiloids are known from a number of occurrences worldwide, but they have never been analysed in terms of spatial and temporal disparity changes. We quantitatively analysed the morphospace occupation and its variation in time and space using the cardinal conch parameters introduced by Raup (1967) for coiled cephalopods: conch width index, umbilical width index and whorl expansion rate. Based on these data, we subsequently analysed the data by using principal components analysis and non-metric multidimensional scaling, which allowed for the construction of a Late Permian nautiloid morphospace.

The analyses show that there is a stable occupation within the morphospace and stable disparity of the coiled nautiloids from the Wuchiapingian to the Changhsingian. Obvious turnovers do not exist. Differences between the three major Late Permian nautiloid occurrences (Salt Range, South China, Transcaucasus-NW Iran) are considerably small. The most important variation in morphospace occupation is caused by environmental differences such as water depth.

To summarize, several aspects are important to explain differences and also similarities in the composition between the analysed assemblages:

1. Evolutionary processes play only a minor role, as there appears, at least on the genus level, no significant turnover from the Wuchiapingian to the Changhsingian;
2. Environmental aspects play a more important role. Shallow-water settings are usually dominated by the liroceratids and other nautiloids with stout and involute conch. In intermediate settings, liroceratids are still present but there is an increasing number of tainoceratids and grypoceratids. Deeper water settings on the outer shelf show only few liroceratids but increasing numbers of tainoceratids;
3. Sampling biases may occur because nautiloids have usually not been as well-sampled as other fossil groups with higher potential for stratigraphical purposes; and
4. The taxonomic practice may play an important role as the knowledge of the Late Permian nautiloids differs significantly between the various regions.

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Supporting Information

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

Fig. S1. Morphospace occupation of Late Permian nautiloids of the four most important families; analysed by using the NMDS method.

Fig. S2. Morphospace occupation of Late Permian nautiloids in the Wuchiapingian and Changhsingian stages; analysed by using the NMDS method.

Fig. S3. Disparity of Late Permian nautiloids with respect the Wuchiapingian and Changhsingian stages and the occurrences in selected regions; analysed by using the NMDS method.

Fig. S4. Morphospace occupation of Wuchiapingian nautiloids in selected regions; analysed by using the NMDS method.

Fig. S5. Morphospace occupation of Changhsingian nautiloids in selected regions; analysed by using the NMDS method.

Table S1. List of analysed nautiloid species with their conch parameters.