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Original article

Smithian (Early Triassic) ammonoids from Tulong, South Tibet☆

Ammonoïdes du Smithien (Trias inférieur) de Tulong, Tibet du Sud

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Abstract

Intensive sampling of the Tulong Formation in South Tibet has facilitated the construction of a highly-resolved middle and late Smithian ammonoid succession. The new biostratigraphical sequence comprises the middle Smithian *Brayardites compressus* beds, *Nammalites pilatoides* beds, and the *Nyalamites angustecostatus* beds followed by the late Smithian *Wasatchites distractus* beds and *Glyptophiceras sinuatum* beds. This faunal succession correlates very well with that of other Tethyan sequences such as the Salt Range (Pakistan), Spiti (India), Oman and South China. The Smithian faunal sequence from Tulong contains several taxa with broad geographic distribution (e.g., *Owenites*, *Paranannites spathi*, *Shigetaceras*, *Wasatchites*), thus enabling correlation with faunal successions from areas outside the Tethys (e.g., USA, British Columbia, Arctic Canada, South Primorye, Siberia). Early Smithian ammonoid faunas are almost absent in Tulong because of a preservation bias (absence of carbonate rocks). Five new ammonoid genera (*Brayardites*, *Nammalites*, *Nyalamites*, *Shigetaceras*, *Tulongites*) and six new species (*Brayardites crassus*, *Brayardites compressus*, *Prionites involutus*, ?*Subflemingites compressus*, *Tulongites xiaoqiaoi*, *Urdyceras tulongensis*) are described.

Keywords: Ammonoidea; Early Triassic; South Tibet; Smithian; Biostratigraphy

Résumé

Un échantillonnage intensif de la Formation Tulong du sud-Tibet permet l'établissement d'une séquence très détaillée des faunes d'ammonites du Smithien moyen et supérieur. Cette nouvelle séquence comprend les faunes d'assemblage du Smithien moyen à *Brayardites compressus*, à *Nammalites pilatoides*, et à *Nyalamites angustecostatus*, suivies par les faunes du Smithien supérieur à *Wasatchites distractus* et à *Glyptophiceras sinuatum*. Cette succession faunique se corrèle très bien avec celles d'autres localités téthysiennes telles que les Salt Ranges (Pakistan), le Spiti (Inde), l'Oman et le Sud de la Chine. Les faunes smithiennes de Tulong contiennent également plusieurs taxons ayant une large distribution géographique (p. ex., *Owenites*, *Paranannites spathi*, *Shigetaceras*, *Wasatchites*) permettant ainsi des corrélations avec d'autres successions en dehors de la Téthys (p. ex. USA, Colombie britannique, Arctique canadien, sud du Primorye, Sibérie). Les faunes du Smithien inférieur sont par contre quasiment absentes de Tulong en raison d'un biais de préservation (absence de roches carbonatées). Cinq genres (*Brayardites*, *Nammalites*, *Nyalamites*, *Shigetaceras*, *Tulongites*) et six espèces (*Brayardites crassus*, *Brayardites compressus*, *Prionites involutus*, ?*Subflemingites compressus*, *Tulongites xiaoqiaoi*, *Urdyceras tulongensis*) sont nouvellement décrits.

Mots clés : Ammonoidea ; Trias inférieur ; Sud-Tibet ; Smithien ; Biostratigraphie

1. Introduction

In the aftermath of the end-Permian mass extinction that wiped out more than 90% of all marine species (e.g., Raup and Sepkoski, 1982), ammonoids recovered very fast in comparison with other marine clades (Brayard et al., 2006, 2009c). Following low values in the Griesbachian, diversity increased slowly during the Dienerian and first peaked in the Smithian. This first major evolutionary radiation was followed by a severe extinction event in the end Smithian, after which a second major and explosive radiation took place during the Spathian.

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For more than a century, Smithian ammonoids have been known from various localities in the Tethyan realm, such as the Salt Range in Pakistan (Waagen, 1895; Noetling, 1905; Guex, 1978), Afghanistan (Kummel and Erben, 1968), Spiti in Northern India (Diener, 1897; Krafft and Diener, 1909; Krystyn et al., 2007a, b), Kashmir (Diener, 1913), Madagascar (Collignon, 1933-1934), Guangxi in South China (Chao, 1959; Brayard and Bucher, 2008), Vietnam (Khuc, 1984) and Timor (Welter, 1922). However, the number of studies based on bed-by-bed sampling is very limited (Guex, 1978; Krystyn et al., 2007a, b; Brayard and Bucher, 2008). Therefore, additional high-resolution ammonoid successions from various localities are crucial for establishing a precise and laterally reproducible biochronological subdivision of the Smithian within the Tethys and within the Early Triassic tropics.

Recently, we provided the first complete and detailed description of the Lower Triassic sedimentary and carbon isotope records from the Tulong area in South Tibet (Brühwiler et al., 2009). Extensive sampling enabled us to precisely date the section by means of detailed ammonoid and conodont biostratigraphy. Our investigations have yielded abundant, diverse and reasonably well preserved Smithian ammonoid faunas including several new taxa. Here, we focus on the description of these faunas. They add significantly to our knowledge of Smithian ammonoid taxonomy and biostratigraphy and provide valuable data for biogeographical, phylogenetic and chemostratigraphic studies.

2. General palaeogeographical and geological setting

During Early Triassic times, the Tulong area was located in a distal position of the northern Gondwanian margin, on the southern side of the Tethys Ocean (Ogg and von Rad, 1994; Fig. 1). As shown by different authors (Marcoux and Baud, 1996; Ricou, 1996; Garzanti and Sciunnach, 1997) at least two rifting processes affected the North Indian plate. The first event is linked to the break-off of the Quiantang block from Gondwana during the Early Carboniferous. A second rifting phase during the Early Permian detached the Lhasa block from the Gondwanian margin, thus giving birth to the Neotethys. In this process the southern Neotethyan Indian margin was acting as the upper plate, thereby inducing basalt flows (Panjal Traps) and volcanism (Stampfli et al., 1991; Baud et al., 1996; Garzanti et al., 1996). During the expansion of the Neotethys in the Early Triassic, the Indian margin underwent thermal subsidence and was characterized by large tilted blocks. This may at least partly explain the differences in lithological successions between closely spaced localities such as Tulong and Selong (35 km apart) in South Tibet (Garzanti et al., 1998; Brühwiler et al., 2009).

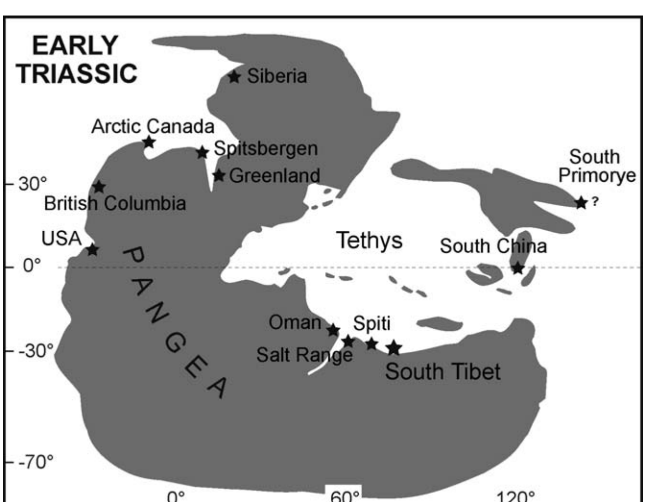

Fig. 1. Simplified Early Triassic palaeogeography (modified after Brayard et al., 2006, 2009b; Shigeta et al., 2009a) with the position of South Tibet and other localities mentioned in the text.

3. The Tulong succession

For the Tulong area (Fig. 2), previously published reports of the Lower Triassic sedimentary succession (Liu, 1992; Liu and Einsele, 1994; Garzanti et al., 1998; Shen et al., 2006) are incomplete and/or poorly or incorrectly dated. Only recently has the complete Lower Triassic sedimentary record from this area been described and dated by means of detailed ammonoid and conodont biostratigraphy (Brühwiler et al., 2009). In that work we subdivided the Lower Triassic succession of Tulong into six lithostratigraphic units as follows (Fig. 3; Supplementary data, Fig. S1).

The basal Triassic sequence consists of three meters of carbonates (Unit I) that are subdivided into two meters of Griesbachian yellow dolomite (Subunit Ia), and one meter of Dienerian light grey, thin-bedded limestone (Subunit Ib). These are followed by about 50-100 m of Dienerian-early Smithian aged, dark green, silty shales (Unit II) devoid of macrofossils. This interval is overlain by nine meters of thin-bedded, light grey fossil-rich limestone of middle to late Smithian age (Unit III; subdivided into four Subunits IIIa-d). These are followed by four meters of early Spathian shales containing a few limestone beds

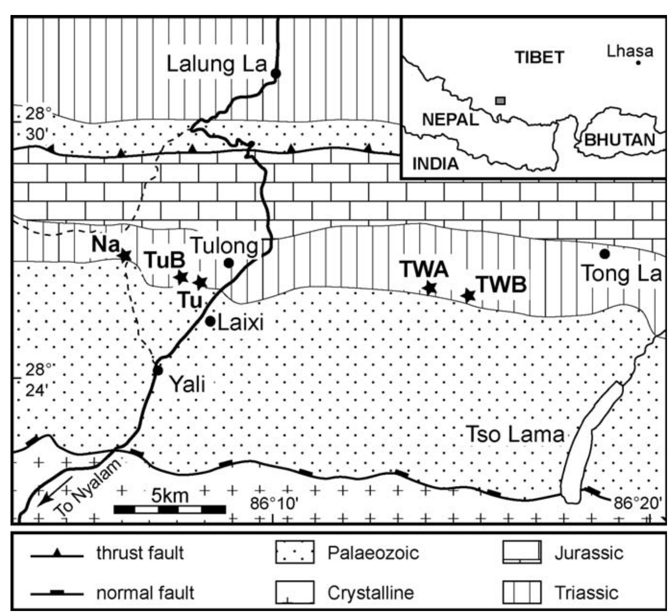

Fig. 2. Geological sketch map of the study area (modified after Burg, 1983) and location of studied sections.

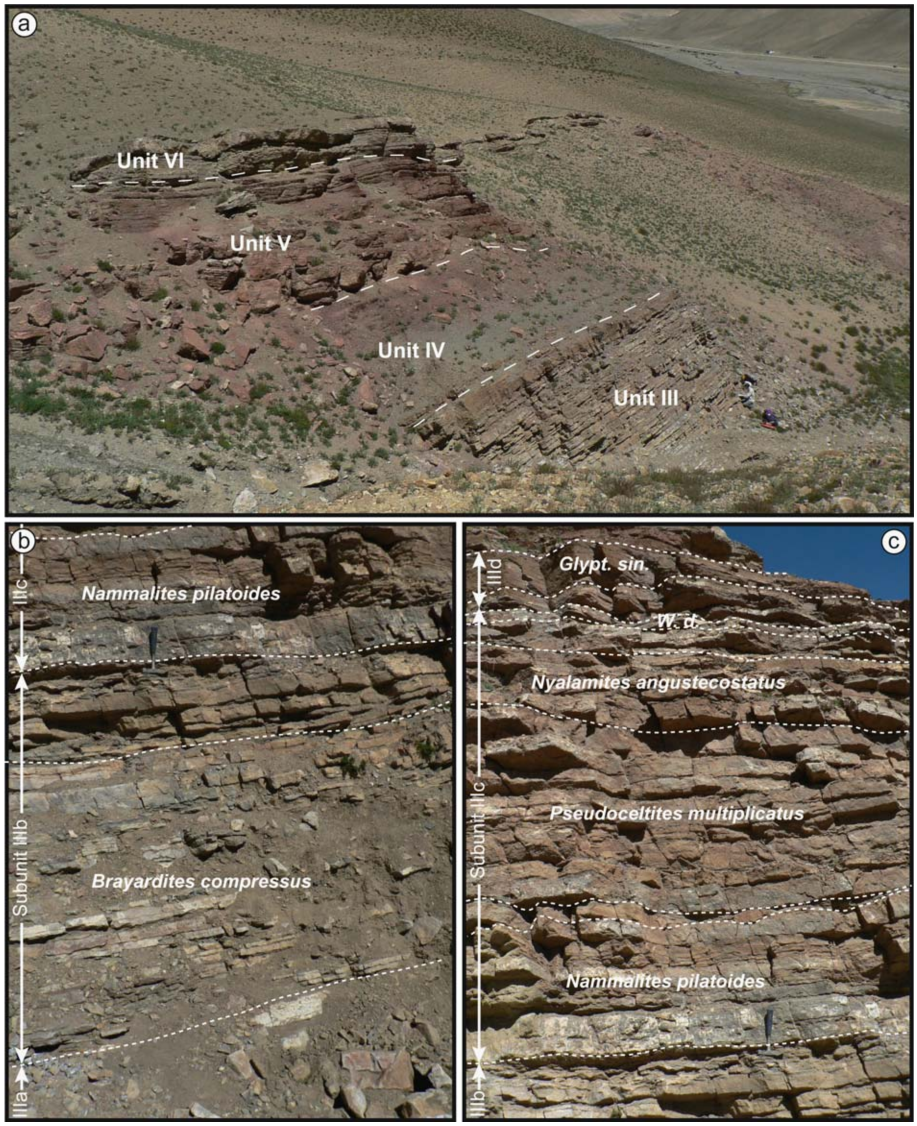

Fig. 3. (**a**) Classical section (Tu) near the village of Tulong, with lithologic units (Brühwiler et al., 2009). (**b**) Subunits IIIb and IIIc, with stratigraphic positions of ammonoid faunas. (**c**) Subunits IIIc and IIId, with stratigraphic positions of ammonoid faunas. Abbreviations: *W. d. Wasatchites distractus; Glypt. sin. Glyptophiceras sinuatum.* Hammer (28 cm in length) for scale.

and nodules (Unit IV). The shales are typically green in the lower part (Subunit IVa) and red in the upper part (Subunit IVb). The late early and middle Spathian consists of six meters of red, bioclastic nodular limestone ("Ammonitico Rosso" type facies; Unit V). The late Spathian-Anisian part of the succession is strongly condensed and is characterized by two meters of grey, thin-bedded limestone with phosphatized ammonoids (Unit VI).

In addition to the classic section located near the village of Tulong (Garzanti et al., 1998; Shen et al., 2006), several new and complementary sections were discovered both west and east of Tulong (Figs. 2 and 3). These new localities were essential for establishing the entire Lower Triassic succession since exposures in the classic Tulong section only include the middle Smithian-Anisian interval (Brühwiler et al., 2009). All outcrops of Lower Triassic rocks can be correlated on a bed-by-bed basis across a minimal distance of ca. 15 km along the W-E tectonic strike, thus revealing remarkable lateral depositional continuity within the same thrusted sheet.

The studied sections were sampled bed-by-bed in order to obtain a precise, detailed ammonoid record (Supplementary data, Fig. S1). The dark green shales of Unit II are essentially barren and only one incomplete floated specimen (*Kashmirites* sp. indet.) was found in the upper part of the unit. On the contrary ammonoids are very abundant in almost all beds of Unit III, except for Subunit IIIa, where they are rare and too poorly preserved for identification. Preservation is highly variable throughout Unit III, and in some levels an intensive sampling effort was necessary to obtain reasonably well preserved material.

4. Biostratigraphical discussion

4.1. General subdivisions of the Early Triassic

Subdivision of the Early Triassic into stages is still controversial. It is commonly subdivided into two (Induan

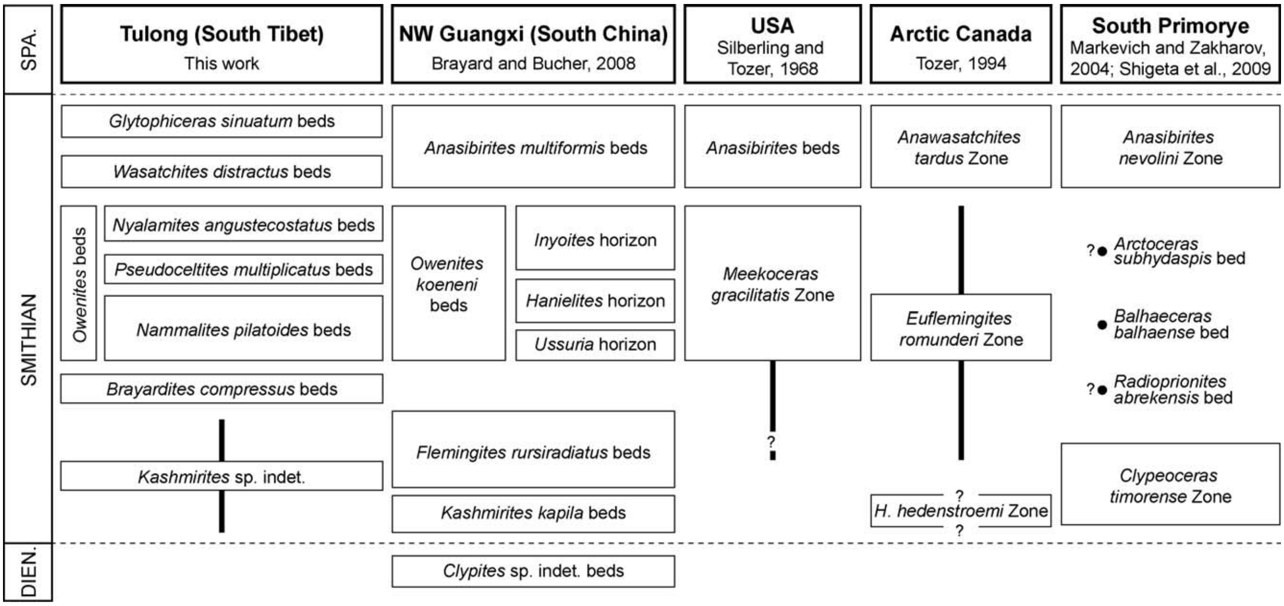

Fig. 4. Biostratigraphical subdivisions of the Smithian of South Tibet and correlation with zonations of other regions. See text for discussion. Three middle Smithian ammonoid faunas (*Nammalites pilatoides*, *Pseudoceltites multiplicatus* and *Nyalamites angustecostatus* beds) from Tulong are grouped together as equivalent of *Owenites* beds.

and Olenkian; Kiparisova and Popov, 1956), three (Griesbachian, Nammalian and Spathian; Guex, 1978) or four stages (Griesbachian, Dienerian, Smithian and Spathian; Tozer, 1965, 1967). In this paper we use the four-stage subdivision, whose boundaries are well defined in terms of ammonoid evolution. The Griesbachian/Dienerian boundary is defined by the first occurrence of Meekoceratidae, which is a bio-event that can be traced worldwide (e.g., Shevyrev, 2001). The early Smithian is characterized by the first major ammonoid diversification phase during the Early Triassic recovery. Therefore, the Dienerian/Smithian (or Induan/Olenekian) boundary is easily recognizable with the appearance of several new ammonoid families such as the Flemingitidae, the Paranannitidae and the Xenoceltitidae (e.g., Brayard and Bucher, 2008). Interest in this boundary is relatively recent, and a section near Mud in the Indian Himalayas has been proposed as GSSP (Krystyn et al., 2007a, b). The Smithian/Spathian boundary is marked by a profound faunal turnover and it is only crossed by very few ammonoid lineages such as the Xenoceltitidae, the Proptychitidae and the Hedenstroemiidae (Brayard et al., 2006). Several new families such as the Tirolitidae and the Columbitidae appear in the early Spathian. The main weakness of the two-stage scheme (Induan-Olenekian) is that it completely ignores the largest intra-Triassic extinction event (i.e., the end-Smithian extinction) that profoundly affected both ammonoids and conodonts (Brayard et al., 2006; Orchard, 2007).

4.2. The Smithian of South Tibet and correlation with other Tethyan localities

Until now, the only illustrations of Smithian ammonoids from South Tibet were provided by Wang and He (1976) from the Mount Everest region, but these authors did not publish a stratigraphical succession, which seriously hampers the interpretation of their data. Moreover, the preservation of their material is rather poor. Our study, based on bed-by-bed sampling, provides for the first time the distribution of Smithian ammonoids in the Tulong succession (Supplementary data, Fig. S1 and Fig. 4). A total of six well differentiated ammonoid faunas of middle to latest Smithian age occurs throughout Unit III. This Smithian ammonoid succession of South Tibet is entirely new except for a preliminary version presented in a conference abstract (Brühwiler et al., 2007). A description of the faunas as well as discussion of their correlation with ammonoid zonations from other areas is provided hereafter. No formal zone names are introduced here since we prefer to use the term "beds" for the time being to describe the local faunal sequence. Such usage would imply a well-established lateral reproducibility of the faunal sequence between various basins, which is still a subject of ongoing work.

4.2.1. Early Smithian

Equivalent faunas of the early Smithian *Kashmirites kapila* beds and the *Flemingites rursiradiatus* beds of South China (Brayard and Bucher, 2008) have not been found in the Tulong area because of the lack of carbonate sediments for this time interval. The single specimen of *Kashmirites* sp. indet. found as float in the upper part of Unit II may possibly have been derived from one of these faunas. It is notable that in other localities on the Northern Indian Margin such as Spiti, the Salt Range and Oman, equivalents of the *Flemingites rursiradiatus* beds are present (Waagen, 1895; Bhargava et al., 2004; Brühwiler et al., 2007, ongoing work; Krystyn et al., 2007a, b).

4.2.2. Brayardites compressus *beds*

These beds in Subunit IIIb are characterized by the association of *Aspenites acutus*, *Brayardites compressus* nov. gen., nov. sp., *B. crassus* nov. gen., nov. sp., *Jinyaceras* *hindostanum*, *Pseudaspidites* sp. indet., *Tulongites xiaoqiaoi* nov. gen., nov. sp., *Urdyceras tulongensis* nov. sp. and Genus indet. A. Recently, this association was also discovered in the Salt Range (Pakistan) and in Spiti (India) (Brühwiler et al., 2007, ongoing work; provisionally labeled ‘‘new prionitid A beds’’), but a faunal equivalent is not known from South China. It probably correlates with an interval between the *Flemingites rursiratiatus* beds and the *Owenites koeneni* beds in the South China succession (Fig. 4).

4.2.3. Nammalites pilatoides *beds*

These beds at the base of Subunit IIIc are characterized by the association of abundant *Nammalites pilatoides* nov. comb., *Owenites simplex*, *Paranannites spathi* and *Shigetaceras dunajensis* nov. comb. Rare specimens of ?*Leyeceras* sp. indet., Flemingitidae gen. indet. A and B, Prionitidae gen. indet. A and *‘‘Anasibirites’’* cf. *pluriformis* also co-occur. This association was also recently discovered in the Salt Range, in Spiti, and in an exotic block of Hallstatt facies from Oman (i.e., ‘‘new prionitid B beds’’ in Brühwiler et al., 2007, ongoing work). Note that *‘‘Anasibirites’’ pluriformis* Guex, 1978 is herein not regarded as a true *Anasibirites*, which is a genus of late Smithian age (see systematic section). The *Nammalites pilatoides* beds correlate with the lower part of the middle Smithian *Owenites koeneni* beds of South China (i.e., *Ussuria* and *Hanielites* horizons; Brayard and Bucher, 2008), with which they share the occurrences of *Owenites simplex* and *Paranannites spathi*.

4.2.4. Pseudoceltites multiplicatus *beds*

These beds in Subunit IIIc are characterized by the association of *Anaxenaspis* sp. indet. A and B, *Owenites koeneni* and *Pseudoceltites multiplicaus*. This fauna occurs also in the Salt Range and in Spiti (Brühwiler et al., 2007, ongoing work; preliminarily termed Flemingitid A beds). An exact correlative is not known from South China.

4.2.5. Nyalamites angustecostatus *beds*

These beds in Subunit IIIc contain a diverse fauna that is characterized by the association of *Nyalamites angustecostatus* nov. comb., *Owenites carpentieri*, *O. koeneni*, *Prionites involutus* nov. sp., *Stephanites superbus*, ?*Subflemingites compressus* nov. sp., *Subvishnuites* sp. indet., and Xenoceltitidae gen. indet. A. This fauna is also known from Spiti, the Salt Range and Oman (Brühwiler et al., 2007, ongoing work), and it correlates with the *Inyoites* horizon in the upper part of the *Owenites koeneni* beds of South China, with which it shares *Owenites carpentieri*.

4.2.6. Wasatchites distractus *beds*

These beds at the top of Subunit IIIc include the occurrence of *Wasatchites distractus*, associated with Genus indet. B. Correlatives of this late Smithian fauna, which contain *Anasibirites* and/or *Wasatchites*, are known from many Tethyan localities such as Oman, Salt Range, Spiti (Bhargava, 2004; Brühwiler et al., 2007, ongoing work) and South China (Brayard and Bucher, 2008) as well as worldwide localities (see below).

4.2.7. Glyptophiceras sinuatum *beds*

These beds in Subunit IIId are characterized by the association of *Glyptophiceras sinuatum*, *Pseudosageceras augustum* and *Xenoceltites* cf. *variocostatus*. This latest Smithian fauna also occurs in Spiti and in the Salt Range (Brühwiler et al., 2007; ongoing work). In South China the *Xenoceltites variocostatus* fauna also occurs above the horizons with *Anasibirites*, but was included in the *Anasibirites multiformis* beds by Brayard and Bucher (2008). Note that the genus *Glyptophiceras* was originally considered to be of Griesbachian age, but is now known to be restricted to the latest Smithian (see systematic section for discussion).

4.2.8. Early Spathian

The lowermost limestone beds in the shales of Subunit IVa yielded only the ammonoid ?*Pseudaspidites* sp., which is not age diagnostic. However, conodonts *Borinella*? nov. sp. C (Orchard, unpublished), transitional forms to *Gladigondolella*, as well as early forms of *Icriospathodus* from this level indicate an early Spathian age (Brühwiler et al., 2009). The limestone nodules in the middle part of Subunit IVa have yielded two different early Spathian ammonoid faunas, i.e. a *Nordophiceras* fauna and a *Columbites* fauna. The Spathian ammonoid faunas from the Tulong area will be discussed in more detail in a separate paper.

4.3. Biostratigraphical correlations with other regions

As shown above, Smithian ammonoid successions are very uniform on the Northern Indian Margin and they correlate well with the South China record. However, correlations with records from outside the Tethys are less precise. Since most early-middle Smithian ammonoids have latitudinally restricted geographic distributions (Brayard et al., 2007, 2009a, 2009b), correlations of early-middle Smithian successions across palaeolatitudes are difficult. In contrast, the extinction phase during the late Smithian is marked by a low latitudinal gradient of diversity and a high degree of cosmopolitanism (Brayard et al., 2006, 2007). A few genera such as *Anasibirites*, *Wasatchites* and *Xenoceltites* occur world-wide (e.g., Tozer, 1994; Brühwiler et al., 2007; Brayard and Bucher, 2008), thus facilitating the correlation of late Smithian ammonoid faunas across palaeolatitudes.

4.3.1. Western USA (low-palaeolatitudes)

The Smithian of the USA is subdivided into two ammonoid zones, i.e. the *Meekoceras gracilitatis* Zone and the *Anasibirites* beds (Silberling and Tozer, 1968; Jenks, 2007). Several genera such as *Guodunites*, *Inyoites*, *Lanceolites*, *Metussuria* and *Owenites* from the *Meekoceras gracilitatis* Zone are known also from the middle Smithian *Owenites* beds of the Tethys (Brühwiler et al., 2007, ongoing work; Brayard and Bucher, 2008; Brayard et al., 2009a). On the other hand, the *Meekoceras gracilitatis* Zone also contains early Smithian ammonoids such as *Euflemingites*. Thus, the *Meekoceras gracilitatis* Zone probably corresponds to the Tethyan early and middle Smithian, but a better resolved documentation of this interval in the USA is still needed for more precise correlations. Correlation of the late Smithian *Anasibirites* beds between the Tethys and the USA is straight forward, but no equivalent of the latest Smithian *Glyptophiceras sinuatum* beds is known from USA.

4.3.2. South Primorye (Russia)

While a recent quantitative biogeographical analysis has emphasized the low-palaeolatitude affinities of Early Triassic ammonoids from South Primorye (Brayard et al., 2009b), monazite age patterns in the sandstones favor a middle palaeolatitude origin for this terrane (Yokoyama et al., 2009a, b). Early-middle Smithian ammonoid faunas from South Primorye have recently been described by Shigeta et al. (2009b), but according to these authors our knowledge of these faunas is still insufficient. The early Smithian *Clypeoceras timorense* Zone is followed by three successive beds containing three different faunas, i.e. the *Radioprionites abrekensis* bed, the *Balhaeceras balhaense* bed and the *Arctoceras subhydaspis* bed. An early Smithian age for the *Clypeoceras timorense* Zone is indicated by the occurrence of *Rohillites* in this zone (Krystyn et al., 2007a, b; Brayard and Bucher, 2008). The *Balhaeceras balhaense* bed contains *Shigetaceras* (termed *Hemiprionites* sp. in Shigeta et al., 2009b) and therefore, correlates with the *Nammalites pilatoides* beds from Tulong. The late Smithian in Primorye is characterized by the *Anasibirites nevolini* Zone (Markevich and Zakharov, 2004), which correlates with beds containing *Anasibirites* and/or *Wasatchites* in the Tethys.

4.3.3. British Columbia (mid-palaeolatitudes)

In this realm, the Smithian is subdivided into the *Euflemingites romunderi* Zone and the *Wasatchites tardus* Zone (Silberling and Tozer, 1968; Tozer, 1994). The former is more or less correlative with the *Meekoceras gracilitatis* Zone (Tozer, 1967), and thus also with the *Owenites* beds of the Tethys. However, some taxa from the *Euflemingites romunderi* Zone such as *Euflemingites* are known also from the early Smithian in the Tethys (Krystyn et al., 2007a). Correlation of the late Smithian *Wasatchites tardus* Zone from British Columbia with the beds containing *Anasibirites* and/or *Wasatchites* in the Tethys is clear-cut. Moreover, in British Columbia beds with *Xenoceltites subevolutus* occur above the beds with *Wasatchites tardus* (Tozer, 1994), similar to the *Glyptophiceras sinuatum* beds in the Tethys.

4.3.4. Arctic Canada, Spitsbergen, Siberia (high-palaeolatitudes)

In the palaeoartic realm the Smithian is subdivided into three ammonoid zones: the *Hedenstroemia hedenstroemi* Zone, the *Euflemingites romunderi* Zone (equivalent to the *Lepiskites kolymensis* Zone in Siberia) and the *Wasatchites tardus* Zone (Silberling and Tozer, 1968; Dagys and Ermakova, 1990; Tozer, 1994; Ermakova, 2002). Correlation of the *Hedenstroemia hedenstroemi* Zone with the Tethys is difficult since this zone is characterized by very few taxa. A few taxa from the next younger *Euflemingites romunderi* Zone such as *Anaxenaspis* and *Parananites spathi* from Canada (Tozer, 1994) are known also from the Tethys, thus indicating that at least part of this zone correlates with the middle Smithian *Owenites* beds from the Tethys. However, as mentioned earlier some taxa from this zone such as *Euflemingites* are known also from the early Smithian in the Tethys (Krystyn et al., 2007a). Again, correlation of the late Smithian *Wasatchites tardus* Zone of the palaeoartic realm with beds containing *Anasibirites* and/or *Wasatchites* in the middle-/low-palaeolatitudes is beyond question. However, in Spitsbergen *Xenoceltites* co-occurs with *Anasibirites* and *Wasatchites* (Weitschat and Lehmann, 1978). Therefore, the subdivision of the late Smithian as observed in low- and middle-palaeolatitudes (i.e., *Anasibirites* beds followed by *Glyptophiceras/Xenoceltites* beds) cannot be extended to the high-palaeolatitudes.

5. Conclusions

Intensive bed-by-bed sampling of the Smithian series in the area around the village of Tulong in South Tibet has resulted in the first detailed description of Smithian ammonoids from this area. A total of six differents middle to latest Smithian ammonoid associations have been found. In ascending order the new local biostratigraphical sequence comprises the *Brayardites compressus* beds, the *Nammalites pilatoides* beds, the *Pseudoceltites multiplicatus* beds, the *Nyalamites angustecostatus* beds, the *Wasatchites distractus* beds and the *Glyptophiceras sinuatum* beds. Early Smithian ammonoid faunas are almost lacking in the studied area because of the absence of carbonate sediments in this time interval. Comparison of the new faunal sequence from Tulong with Oman, the Salt Range and Spiti reveals that the Smithian ammonoid successions are very uniform on the Northern Indian Margin (Brühwiler et al., 2007, ongoing work). Moreover, a detailed correlation with the well-studied record from Guangxi, South China (Brayard and Bucher, 2008) is facilitated by many common taxa. However, detailed correlations with sections from outside the Tethys are hampered by the still somewhat inadequate knowledge of Smithian ammonoid faunas from these areas on the one hand, and by the latitudinally restricted distribution of most early-middle Smithian ammonoids on the other hand.

6. Systematic paleontology

Systematic descriptions mainly follow the classification established by Tozer (1981, 1994) and refined by Brayard and Bucher (2008). Provided that measurements were available for at least four specimens, the quantitative morphological range of each species is expressed utilizing the four classic geometrical parameters of the ammonoid shell: diameter (D), whorl height (H), whorl width (W) and umbilical diameter (U). The three parameters (H, W and U) are plotted in absolute values as well as in relation to diameter (H/D, W/D, and U/D). Occurrence of taxa described herein includes the number of specimens obtained from each sample. For example, Tu50 (2) means that two specimens were identified from sample Tu50. Sample numbers are reported in the composite section (Supplementary data, Fig. S1).

Abbreviations: *non*: material not forming part of the current species; *p: pars*; *v.*: *video* or *vidimus*; ?: questionable; PIMUZ: Paläontologisches Institut und Museum der Universität Zürich, Switzerland. Photographs of ammonoids and corresponding plots of measurements are shown in Figs. 5–16 and in Supplementary data, Fig. S2–S7 respectively.

Class CEPHALOPODA Cuvier, 1797
Subclass AMMONOIDEA Zittel, 1884
Order CERATITIDA Hyatt, 1884
Superfamily XENODISCACEAE Frech, 1902
Family XENOCELTITIDAE Spath, 1930
Genus ***Pseudoceltites*** Hyatt, 1900
Type species: *Celtites multiplicatus* Waagen, 1895.

Pseudoceltites multiplicatus (Waagen, 1895)
Fig. 5(1–7)

1895. *Celtites multiplicatus* nov. sp. - Waagen, p. 78, pl. 7, fig. 2a–c.

1895. *Celtites dimorphus* nov. sp. - Waagen, p. 80, pl. 7, fig. 5a–c.

1976. *Pseudoceltites multiplicatus* (Waagen) - Wang and He, p. 289, pl. 6, figs. 7–11.

? 1976. *Eukashmirites* cf. *blaschkei* (Diener) - Wang and He, p. 290, pl. 6, fig. 12.

? 1976. *Eukashmirites* cf. *subarmatus* (Diener) - Wang and He, p. 291, pl. 6, figs. 13, 14.

Occurrence: Samples Tu47 (1), Tu48 (1?), Tu50 (2), TuB1 (30), Tu52 (6), Tu53 (1), Tu54 (1), Tu55 (1?) (*Pseudoceltites multiplicatus* beds).

Measurements: See Supplementary data, Fig. S2.

Description: Evolute shell with a subrectangular whorl section. Flanks flattened, converging very weakly. Venter broad and subtabulate, arched, with rounded shoulders. Umbilicus with a high vertical wall and marked, slightly rounded shoulders. Ornamentation varies from strong, distant radial ribs to fine, dense and slightly sinuous ribs. Ribs usually fade out on ventral shoulders, but occasionally cross the venter as faint ridges. Suture line ceratitic with broad saddles.

Remarks: *Celtites dimorphus* Waagen, 1895 comes from the same horizon as *Celtites multiplicatus* and is here regarded as a synonym of this species, representing a variant with distant ribs on inner whorls. The older (early Smithian) species *Kashmirites armatus* (Waagen, 1985) from the Ceratite Sandstone of the Salt Range differs from *P. multiplicatus* by a more depressed whorl section, a more rounded umbilical edge and a suture with slightly phylloid saddles (Waagen, 1895; Brühwiler et al., ongoing work). The specimens from Kashmir described as *Kashmirites blaschkei*, *K. subarmatus* and *K.* aff. *subarmatus* by Diener (1913) differ from *P. multiplicatus* by their flatter venter and more pronounced ribs on the venter. The specimens from South Tibet described as *Eukashmirites* cf. *blaschkei* and *E.* cf. *subarmatus* by Wang and He (1976) are similar in shape and ornamentation but too poorly preserved for a definitive assignment.

Genus ***Kashmirites*** Diener, 1913
Type species: *Celtites armatus* Waagen, 1895.

Kashmirites sp. indet.
Fig. 5(9)

Occurrence: Near section Na, a single incomplete specimen was found as float in the upper part of the shales of Unit II, about ten meters below Unit III. The exact stratigraphic position cannot be inferred due to faulting.

Description: Evolute shell with flat, parallel flanks. Venter subtabulate, low arched with rounded shoulders. Umbilicus wide with a vertical wall and rounded but narrow shoulders. Ornamentation consists of fine, rursiradiate ribs fading out on the ventral shoulders. Suture line not preserved.

Remarks: The evolute coiling and the subrectangular whorl section of this specimen favour assignment to *Kashmirites*. However, the specimen differs from typical *Kashmirites* by its rursiradiate ribbing and its relatively large size. It may represent a new species, but its poor preservation prevents the erection of a new taxon.

Genus ***Glyptophiceras*** Spath, 1930
Type species: *Xenodiscus aequicostatus* Diener, 1913 (=*Dinarites sinuatus* Waagen, 1895).

Remarks: The genus *Glyptophiceras* was erected by Spath (1930) for the species *"Xenodiscus" aequicostatus* Diener, 1913, which is herein considered as a synonym of *"Dinarites" sinuatus* Waagen, 1895. As already suspected by Tozer (1969), *Glyptophiceras* is now known to be of latest Smithian age and not Griesbachian. The so-called "*Glyptophiceras*" from the Griesbachian of the high latitudes (Spath, 1930; Trümpy, 1969) belongs to the genus *Hypophiceras* Trümpy, 1969 (see also Guex, 1978). *Glyptophiceras* is close to *Xenoceltites*, with which it has been synonymized (Guex, 1978). However, its very distinct stout ribbing clearly separates it from this genus.

Glyptophiceras sinuatum (Waagen, 1895)
Fig. 6(1–7)

1895. *Dinarites sinuatus* nov. sp. - Waagen, p. 33, pl. 10, fig. 4.

? 1913. *Xenodiscus* cf. *lissarensis* Diener - Diener, p. 5, pl. 1, fig. 11.

1913. *Xenodiscus aequicostatus* nov. sp. - Diener, p. 6, pl. 2, fig. 10.

1913. *Xenodiscus salomonii* nov. sp. - Diener, p. 7, pl. 2, fig. 5.

1913. *Xenodiscus althothae* nov. sp. - Diener, p. 8, pl. 2, figs. 6, 11.

1913. *Xenodiscus* cf. *ellipticus* Diener - Diener, p. 9, pl. 3, fig. 1.

1913. *Xenodiscus comptoni* - Diener, p. 10, pl. 2, fig. 7.

? 1913. *Xenodiscus* cf. *rotula* Waagen - Diener, p. 11, pl. 3, fig. 2.

1913. *Xenodiscus* cf. *ophioneus* Waagen - Diener, p. 12, pl. 2, figs. 8, 9.

? 1913. *Xenodiscus* cf. *sitala* Diener - Diener, p. 14, pl. 3, fig. 3.

v. 1978. *Xenoceltites pulcher* nov. sp. - Guex, p. 112, pl. 7, fig. 8.

Occurrence: Samples Tu73a (1), Tu73b (6), TWA4 (13) (*Glyptophiceras sinuatum* beds).

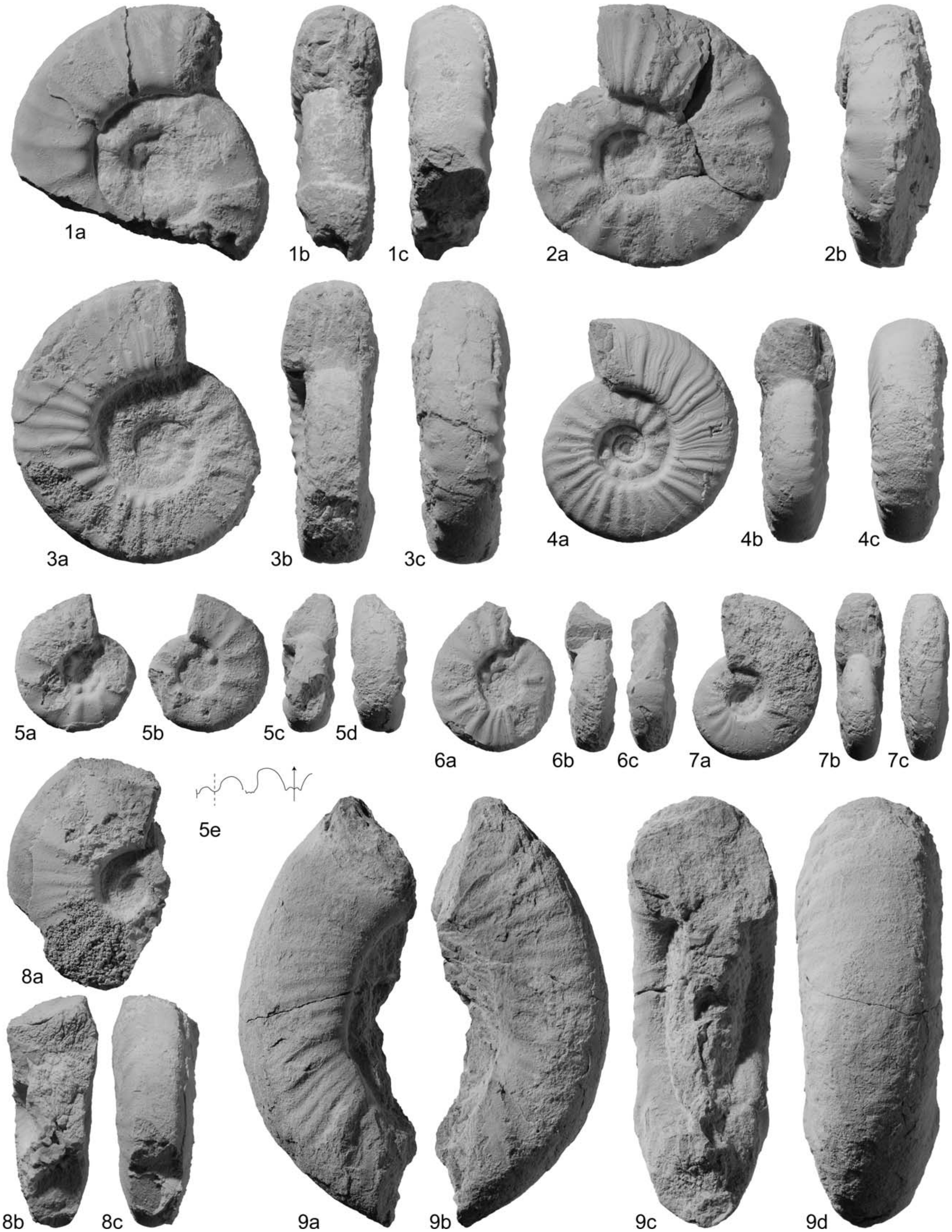

Fig. 5. **1–7**. *Pseudoceltites multiplicatus* (Waagen, 1895); 1a–c, PIMUZ 27595, sample TuB1; 2a, b, PIMUZ 27596, sample TuB1; 3a–c, PIMUZ 27597, sample TuB1; 4a–c, PIMUZ 27598, sample TuB1; 5a–e, PIMUZ 27599, sample Tu50, 5e × 1.5; 6a–c, PIMUZ 27600, sample TuB1; 7a–c, PIMUZ 27601, sample TuB1. **8a–c**. *"Anasibirites"* cf. *pluriformis* Guex, 1978; PIMUZ 27602, sample Tu44. **9a–d**. *Kashmirites* sp. indet, PIMUZ 27603 found as float in Unit II. All natural size unless otherwise indicated.

Description: Evolute, platycone shell with convex and convergent flanks. Venter narrowly rounded with rounded shoulders. Umbilicus wide and shallow with low vertical wall and rounded shoulders. Ornamentation highly variable from low, dense and sinuous to very strong, distant and concave ribs. Ribs may occasionally cross the venter, depending on their overall strength. Suture line ceratitic with slightly tapered saddles, but poorly preserved.

Remarks: A comprehensive study of this species based on newly collected, abundant and well preserved material from the Salt Range (Pakistan) and from Spiti (India) is currently under progress by our group. That new material shows the same high intraspecific variation that can also be seen on Diener's (1913) numerous specimens from a single layer in Kashmir that he described as various species of *Xenodiscus*. Thus, *Glyptophiceras sinuatum* is here understood as a species exhibiting a high intraspecific variation. Although rather poorly preserved, specimens from Tulong reported here clearly fall within this variation. The three specimens illustrated on Fig. 6(5–7) are rather poorly preserved and are only tentatively included within this species.

Genus ***Xenoceltites*** Spath, 1930

Type species: *Xenoceltites subevolutus* Spath, 1930.

Xenoceltites cf. *variocostatus* Brayard and Bucher, 2008
Fig. 7(1, 2)

Occurrence: Samples TWA4 (2), Tu75 (1), TWA2 (3) (*Glyptophiceras sinuatum* beds).

Description: Moderately evolute, platycone shell with flat, only slightly convex flanks. Venter narrowly rounded with indistinct shoulders. Umbilicus shallow with rounded shoulders. Inner whorls ornamented with low, slightly prorsiradiate ribs, outer whorls smooth or with very faint ribs on mid-flanks. Suture line simple, but poorly preserved.

Remarks: This species resembles *Xenoceltites variocostatus* from South China, but the relatively poor preservation of our material precludes a definitive specific assignment.

Genus ***Nyalamites*** nov. gen.

Etymology: Named after the small town of Nyalam, south of Tulong.

Type species: *Xenodiscus angustecostatus* Welter, 1922.

Composition of the genus: Type species only.

Diagnosis: Small-sized, evolute Xenoceltitidae with ornamentation consisting of evenly distributed, sharp ribs that do not cross the venter.

Discussion: *Preflorianites* differs from *Nyalamites* nov. gen. by its rounded ribs. *Nyalamites* nov. gen. also differs from other Xenoceltitidae such as *Kashmirites*, *Pseudoceltites*, *Xenoceltites* and *Glyptophiceras* by its evenly distributed ribs. The type species was assigned to *Anakashmirites* (genotype: *K. nivalis* Diener, 1897) by Kummel and Steele (1962), which is herein considered as a synonym of *Kashmirites*. Guex (1978) assigned this species to *Eukashmirites* (genotype: *E. acutangularis* Welter, 1922) which differs however by its distinct rectangular whorl section.

Nyalamites angustecostatus nov. comb. (Welter, 1922)
Fig. 7(3–5)

? 1895. *Celtites acuteplicatus* nov. sp. - Waagen, p. 82, pl. 7a, figs. 5, 5c, 6, 7.

1922. *Xenodiscus angustecostatus* nov. sp. - Welter, p. 110, pl. 4, figs. 14–17.

? 1922. *Xenodiscus oyensi* nov. sp. - Welter, p. 111, pl. 5, figs. 1, 2, 17.

1968. *Anakashmirites angustecostatus* (Welter) - Kummel and Erben, p. 128, pl. 19, figs. 1–8.

1973. *Anakashmirites angustecostatus* (Welter) - Collignon, p. 144, pl. 5, figs. 7, 8.

? 1973. *Anakashmirites oyensi* (Welter) - Collignon, p. 146, pl. 5, figs. 9, 10.

1976. *Pseudoceltites angustecostatus* (Welter) - Wang and He, p. 289, pl. 6, figs. 3–6.

v. 1978. *Eukashmirites angustecostatus* (Welter) - Guex, pl. 7, figs. 4, 9.

v. non 2008. *Pseudoceltites? angustecostatus* (Welter) - Brayard and Bucher, p. 18; pl. 3, figs. 1–7; fig. 19 (= *Preflorianites radians*).

Occurrence: Samples Tu56 (8), Tu59 (1), Tu60 (1) (*Nyalamites angustecostatus* beds).

Description: Small, very evolute shell with slightly convex, subparallel flanks. Venter subtabulate with rounded shoulders. Umbilicus shallow and wide with inclined wall and rounded shoulders. Ornamentation consists of regularly spaced, strong, radial, sharp ribs that fade out on ventral shoulders. Suture line ceratitic with broad saddles.

Remarks: This species is very common in the late middle Smithian of the Tethys. *"Celtites" acuteplicatus* Waagen, 1895 is probably conspecific but is too poorly preserved for definitive identification. *"Xenodiscus" oyensi* Welter, 1922 is very similar too, but differs mainly by its larger size. *"Celtites" trapezoidalis* Waagen, 1895 from the Salt Range is older and differs by its divergent flanks.

Xenoceltitidae gen. indet. A
Fig. 6(8, 9)

Occurrence: Sample Tu58 (2) (*Nyalamites angustecostatus* beds).

Description: Moderately involute shell with a subrectangular whorl section. Flanks slightly convex. Venter broad and subtabulate with rounded shoulders. Umbilicus with a high, steep wall and rounded shoulders. Ornamentation consists of slightly sinuous ribs. Most ribs fade out on ventral shoulders, but some may cross the venter as faint ridges. Suture line simple with rather broad first lateral saddle.

Remarks: This species is close to *Pseudoceltites multiplicatus*, but it is more involute.

Superfamily MEEKOCERATACEAE Waagen, 1895
Family PROPTYCHITIDAE Waagen, 1895
Genus ***Leyeceras*** Brayard and Bucher, 2008
Type species: *Leyeceras rothi* Brayard and Bucher, 2008.

?*Leyeceras* sp. indet.
Fig. 7(8)

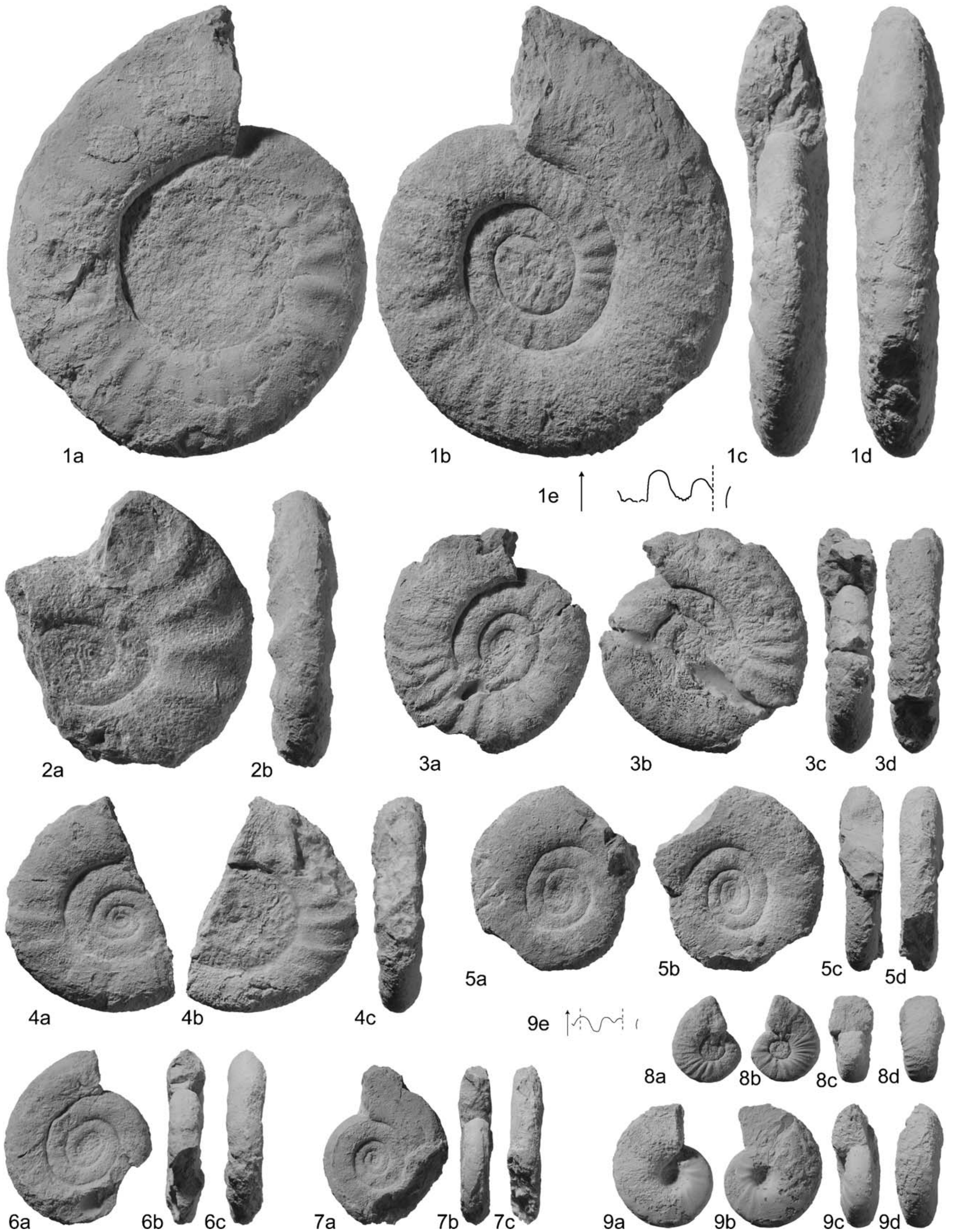

Fig. 6. **1–7**. *Glyptophiceras sinuatum* (Waagen, 1895); 1a–e, PIMUZ 27604, sample TWA4, 1e × 1.5; 2a, b, PIMUZ 27605, sample Tu73a; 3a–d, PIMUZ 27606, sample TWA4; 4a–c, PIMUZ 27607, sample TWA4; 5a–d, PIMUZ 27608, sample Tu75; 6a–c, PIMUZ 27609, sample Tu73b; 7a–c, PIMUZ 27610, sample TWA4. **8, 9**. Xenoceltitidae gen. indet. A; 8a–d, PIMUZ 27611, sample Tu58; 9a–e, PIMUZ 27612, sample Tu58, 9e × 1.5. All natural size unless otherwise indicated.

Occurrence: A single specimen from sample TuB3 (*Nammalites pilatoides* beds).

Description: Large, moderately evolute shell with convex flanks and an elliptical whorl section. Venter rounded with rounded shoulders. Umbilical wall moderately high, umbilical shoulders rounded. Surface with weak, distant plications near umbilicus. Suture line not preserved on our specimen.

Remarks: The elliptical whorl section and the amount of involution of our specimen is similar to that of *Leyeceras rothi* Brayard and Bucher, 2008, but its rather poor preservation precludes a definitive generic assignment. *Anaflemingites* is also similar in shape but is more evolute. *Arctoceras* and *Submeekoceras* differ by their subangular umbilical shoulders.

Genus ***Tulongites*** nov. gen.

Etymology: Named after the type locality of the type species near the village of Tulong, South Tibet.

Type species: *Tulongites xiaoqiaoi* nov. gen., nov. sp.

Composition of the genus: Type species only.

Diagnosis: Compressed Proptychitidae with weak, prorsiradiate and biconcave folds, umbilicus with steeply inclined wall and rounded shoulders.

Remarks: This genus differs from other Proptychitidae by its prorsiradiate folds. However, its shape and suture line favor assignment to this family. *Lingyunites* Chao, 1959 differs by its more involute coiling and its umbilicus with a vertical umbilical wall and narrowly rounded shoulders.

Tulongites xiaoqiaoi nov. gen., nov. sp.
Fig. 7(9, 10)

Etymology: Named after Wan Xiaoqiao (China University of Geosciences, Beijing).

Holotype: Specimen PIMUZ 27621, Fig. 7(9).

Type locality: Section TuB, Tulong, Nyalam County, South Tibet.

Type horizon: Sample TuB5; Early Triassic, Smithian, *Brayardites compressus* beds.

Occurrence: Sample TuB5 (2) (*Brayardites compressus* beds).

Diagnosis: As for the genus.

Remarks: Involute, platycone shell with slightly convex flanks. Maximum whorl width near mid flank. Venter narrow and rounded with rounded shoulders. Umbilicus small with steeply inclined wall and rounded shoulders. Shell ornamented with weak, biconcave and prorsiradiate folds. Suture line ceratitic; first and second lateral saddles tapered; second lateral saddle slightly asymmetrical; third lateral saddle small.

Genus ***Pseudaspidites*** Spath, 1934

Type species: *Aspidites muthianus* Krafft and Diener, 1909.

Pseudaspidites sp. indet.
Fig. 7(11)

Occurrence: Samples Na23 (1), TuB5 (1) (*Brayardites compressus* beds).

Description: Involute, compressed shell with slightly convex, convergent flanks. Maximum whorl width near umbilicus. Venter subtabulate with rounded shoulders. Umbilicus small and deep with high, vertical wall and marked, slightly rounded shoulders. Surface smooth. Suture line ceratitic with deep lobes; first lateral saddle narrow, second lateral saddle slightly phylloid and slightly curved towards umbilicus; auxiliary series with a small fourth saddle.

Remarks: Typical *Pseudaspidites* differ from this species by a more complex suture line with phylloid and more distinctly curved saddles.

Family FLEMINGITIDAE Hyatt, 1900

Genus ***Subflemingites*** Spath, 1934

Type species: *Subflemingites involutus* Spath, 1934 (= *Aspidites meridianus involutus* Welter, 1922).

?*Subflemingites compressus* nov. sp.
Fig. 8(1–6)

Etymology: Refers to the compressed whorl section of the species.

Holotype: Specimen PIMUZ 27625, Fig. 8(2).

Type locality: Section Tu, Tulong, Nyalam County, South Tibet.

Type horizon: Sample Tu58; Early Triassic, Smithian, *Nyalamites angustecostatus* beds.

Occurrence: Samples Tu56 (2?), Tu58 (6), Tu63 (2), Tu64 (2), Tu65 (1?) (*Nyalamites angustecostatus* beds).

Measurements: See Supplementary data, Fig. S3.

Diagnosis: *Subflemingites* with a compressed whorl section.

Description: Moderately involute, compressed shell with flat, slightly convex flanks. Venter rounded without distinct shoulder. Umbilicus with low, inclined wall and rounded shoulders. Surface smooth or with weak radial folds on inner flanks. Suture line ceratitic with slightly phylloid saddles.

Remarks: This species differs from the type species by its more compressed whorl section, but it is otherwise very similar. Unfortunately, the suture line of the type species has never been illustrated. Based on the descriptions by Welter (1922) and Spath (1934), it has possibly a longer auxiliary series than our species. Therefore, the generic assignment to *Subflemingites* of this new species is only tentative. *Flemingites* Waagen, 1895 differs by its strigation and radial ribs; *Galfettites* Brayard and Bucher, 2008 differs by its convergent flanks and its tabulate venter; *Anaflemingites* Kummel and Steele, 1962 is more evolute.

Genus ***Anaxenaspis*** Kiparisova, 1956

Type species: *Xenaspis orientale* Diener, 1895.

?*Anaxenaspis* sp. indet. A
Fig. 9(1)

Occurrence: A single specimen from Sample TuB1 (*Pseudoceltites multiplicatus* beds).

Description: Compressed and moderately evolute shell with convex flanks. Venter rounded with rounded shoulders. Umbilicus with low rounded wall without distinct shoulders. Surface smooth except for weak folds on outer flanks. Suture line not preserved.

Remarks: Our single specimen is very similar to the type species *Anaxenaspis orientale*, but since the suture line is not preserved, no definitive specific assignment can be made.

?*Anaxenaspis* sp. indet. B
Fig. 9(3–7)

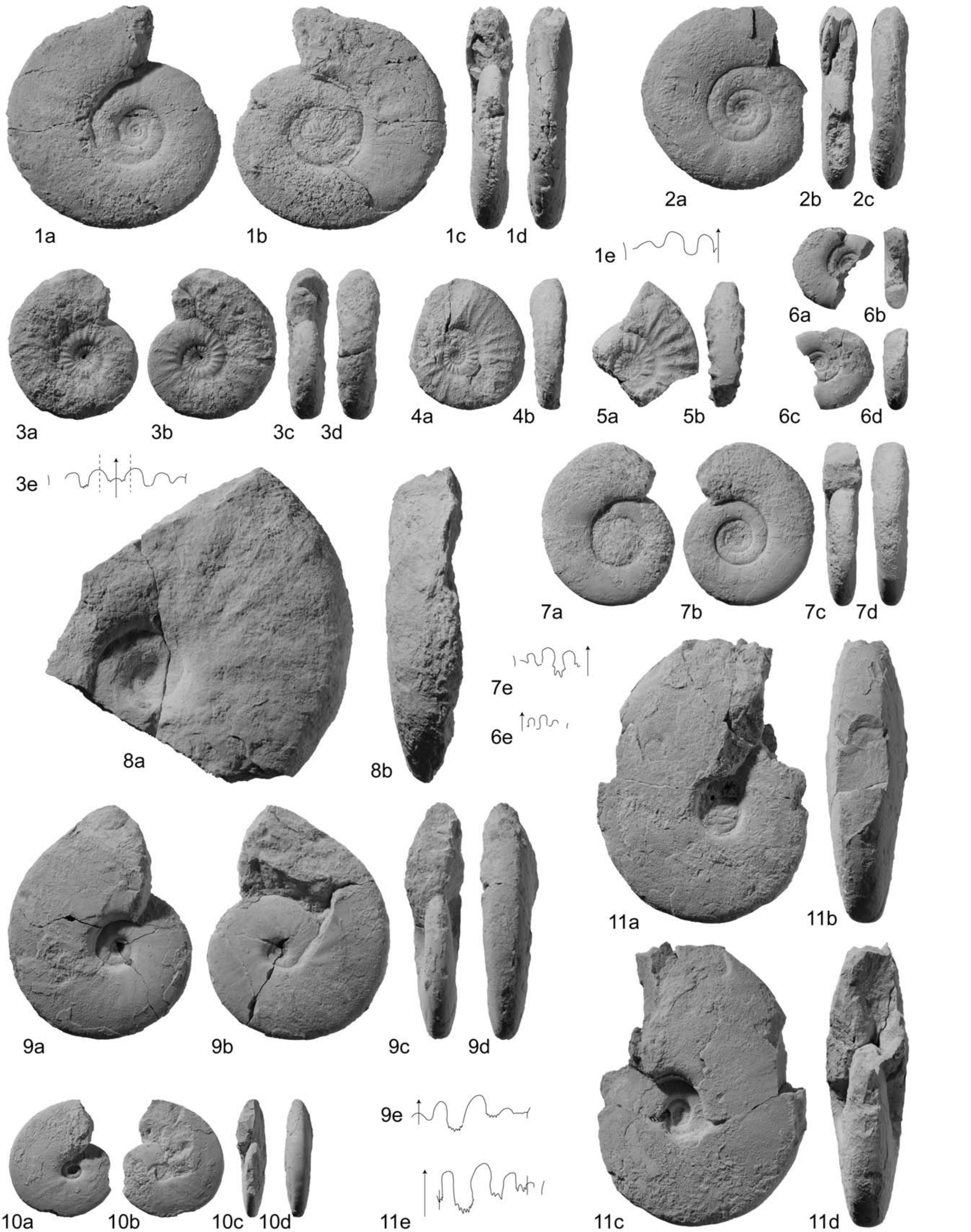

Fig. 7. **1, 2**. *Xenoceltites* cf. *variocostatus* Brayard and Bucher, 2008; 1a–e, PIMUZ 27613, sample TWA4, 1e × 1.5; 2a–c, PIMUZ 27614, sample Tu75. **3–5**. *Nyalamites angustecostatus* nov. comb. (Welter, 1922). 3a–e, PIMUZ 27615, sample Tu56, 3e × 1.5; 4a, b, PIMUZ 27616, sample Tu56; 5a, b, PIMUZ 27617, sample Tu56. **6, 7**. Genus indet. A; 6a–e, PIMUZ 27618, sample Na28, 6e × 2; 7a–e, PIMUZ 27619, sample Na28, 7e × 2. **8a, b**. ?*Leyeceras* sp. indet., PIMUZ 27620, sample TuB3, × 0.5. **9–10**. *Tulongites xiaoqiaoi* nov. gen., nov. sp.; 9a–e, PIMUZ 27621, sample TuB5, 9e × 1.5. 10a–d, PIMUZ 27622, sample TuB5. **11a–e**. *Pseudaspidites* sp. indet., PIMUZ 27623, sample TuB5. All natural size unless otherwise indicated.

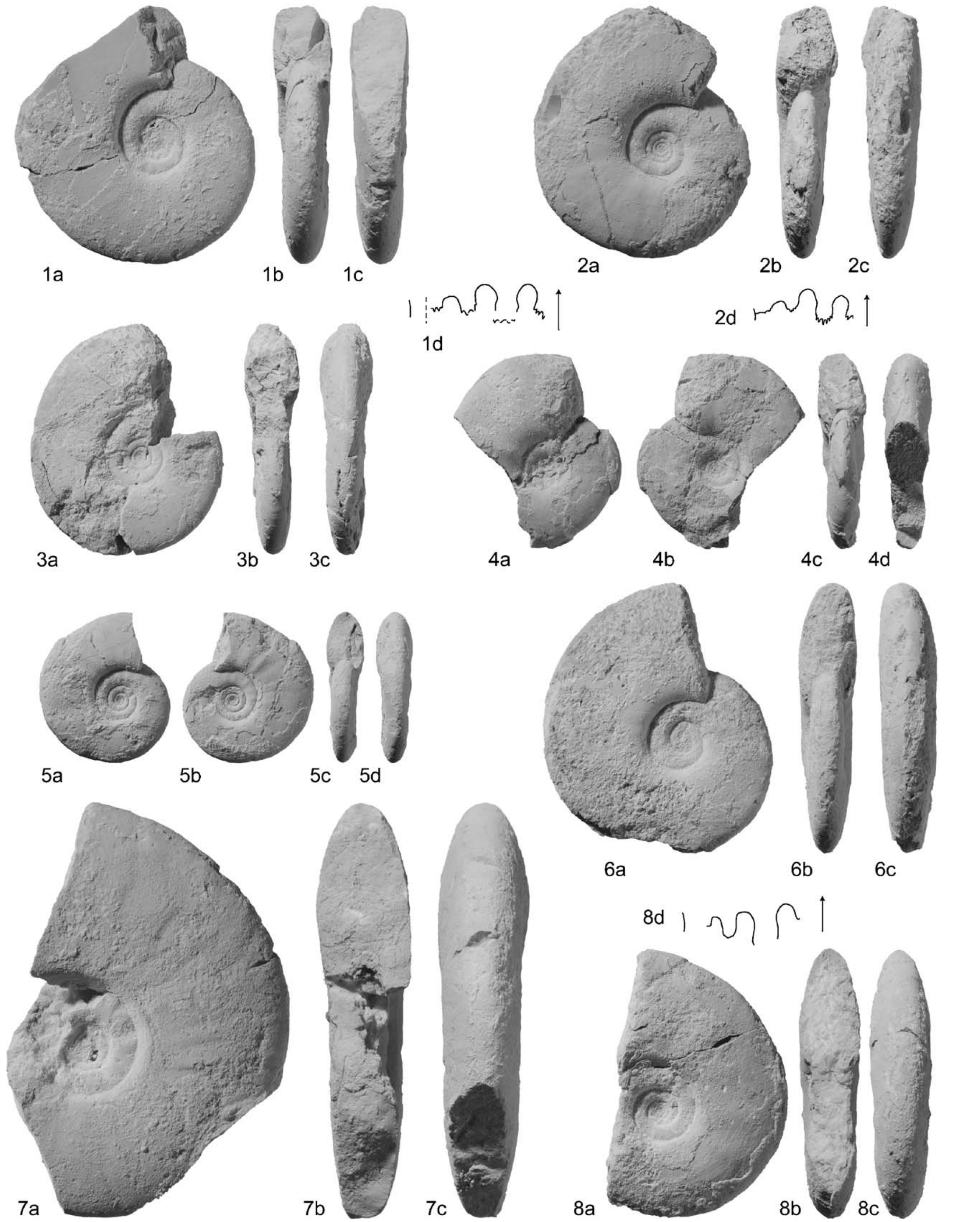

Fig. 8. **1–6**. ?*Subflemingites compressus* nov. sp.; 1a–d, PIMUZ 27624, sample Tu58, 1d × 1.5; 2a–d, PIMUZ 27625, sample Tu58, 2d × 1.5; 3a–c, PIMUZ 27628, sample Tu58; 4a–d, PIMUZ 27627, sample Tu58; 5a–d, PIMUZ 27626, sample Tu58; 6a–c, PIMUZ 27629, sample Tu63. **7, 8.** Flemingitidae gen. indet. A; 7a–c, PIMUZ 27630, sample TuB3; 8a–d, PIMUZ 27631, sample Tu44, 8d × 1.5. All natural size unless otherwise indicated.

Occurrence: Sample TuB1 (11) (*Pseudoceltites multiplicatus* beds).

Description: Evolute, compressed shell with convex flanks. Maximum whorl width slightly below mid-flank. Venter narrowly rounded without distinct shoulders. Umbilicus wide and shallow with inclined wall and rounded shoulders. Ornamented with slightly rursiradiate folds that fade out above mid-flank. Suture line not preserved.

Remarks: This species is common in the *Pseudoceltites multiplicatus* beds. It is similar in shape with the type species *Anaxenaspis orientale*, which does not exhibit rursiradiate folds. Since the suture line is not preserved, the assignment to *Anaxenaspis* is only provisional. Our single specimen described below as Flemingitidae gen. indet. B from the *Nammalites pilatoides* beds (Fig. 9(2)) differs by its thicker whorls.

Flemingitidae gen. indet. A
Fig. 8(7, 8)

Occurrence: Sample TuB3 (1), Tu44 (1) (*Nammalites pilatoides* beds).

Description: Compressed and moderately involute shell with convex and convergent flanks. Venter rounded with rounded shoulders. Umbilicus with steeply inclined wall and rounded shoulders. Ornamentation consists of blunt radial ribs that disappear on the external third of the flank. Ribs are strong on the inner whorls and become weaker on the outer whorls. Suture line with rather deep lobes and slightly phylloid saddles.

Remarks: This species differs from *Anaxenaspis* sp. indet. described above by its more involute coiling and different umbilical wall and shoulders.

Flemingitidae gen. indet. B
Fig. 9(2)

Occurrence: A single specimen from sample Tu44 (*Nammalites pilatoides* beds).

Description: Compressed and evolute shell with convex and convergent flanks. Venter rounded with indistinct shoulders. Umbilicus with steeply inclined wall and rounded shoulders. Ornamentation consists of blunt radial ribs that fade out on the external third of the flank. Strength of ribbing decreases throughout growth. Suture line not preserved.

Remarks: This species is close to Flemingitidae gen. indet. A described above, but differs by its more evolute coiling.

Genus ***Urdyceras*** Brayard and Bucher, 2008

Type species: *Urdyceras insolitus* Brayard and Bucher, 2008.

Remarks: This genus was originally assigned to Proptychitidae by Brayard and Bucher (2008). However, based on our new material from Tibet it is now clear that *Urdyceras,* with its relatively evolute coiling and tabulate venter with very angular shoulders, is not representative of Proptychitidae. The genus is herein provisionally included in Flemingitidae since these traits are found in certain other members of this family (e.g., *Rohillites*, *Galfettites*).

Urdyceras tulongensis nov. sp.
Fig. 10(5–11)

Etymology: Named after the type locality near the village of Tulong.

Holotype: Specimen PIMUZ 27644, Fig. 10(6).

Type locality: Section TuB, Tulong, Nyalam County, South Tibet.

Type horizon: Sample TuB5; Early Triassic, Smithian, *Brayardites compressus* beds.

Occurrence: Samples Na23 (1), TuB5 (8) (*Brayardites compressus* beds).

Measurements: See Supplementary data, Fig. S4.

Diagnosis: *Urdyceras* with a relatively narrow venter and flanks that have a tendency to become concave near the venter.

Description: Compressed and moderately evolute shell. Flanks convex and convergent, tending to become concave near the venter. Venter tabulate with very angular shoulders. Umbilicus with vertical wall and marked, but slightly rounded shoulders. Ornamentation on flanks consists of fine radial, slightly sinuous folds. One specimen (Fig. 10(8)) displays rather strong folds on inner flanks. Suture line ceratitic with deep lobes and slightly phylloid saddles. First lateral saddle narrow; second lateral saddle slightly curved towards umbilicus.

Remarks: The slightly older type species *Urdyceras insolitus* from the *Flemingites rursiradiatus* beds of South China differs by its thicker whorls and broader venter. The inner whorls of *Urdyceras tulongensis* are similar to *Anaflemingites hochulii* Brayard and Bucher, 2008, which differs by its rounded ventral shoulders.

Family ARCTOCERATIDAE Arthaber, 1911

Genus ***Nammalites*** nov. gen.

Etymology: Named after the type locality of the type species, Nammal Gorge in the Salt Range, Pakistan.

Type species: *Kazakhstanites pilatoides* Guex, 1978.

Composition of the genus: Type species only.

Diagnosis: Moderately evolute Arctoceratidae with convergent flanks and ribs that tend to develop umbilical tubercles.

Remarks: When describing the type species, Guex (1978) assigned it to the genus *Kazakhstanites* Shevyrev, 1968 of Spathian age (associated with *Columbites*), which indeed is very close in shape. However, *Kazakhstanites* clearly differs from *Nammalites* by having a simplified suture line with only two lateral saddles. The similarity of these two genera is herein interpreted as a case of convergence.

The assignment of *Nammalites* to the family Artoceratidae is based on its high vertical umbilical wall and the tendency of its ribs to form umbilical tubercles or bullae. Superficially, *Nammalites* resembles some members of the family Prionitidae, such as *Wasatchites*. However, all Prionitidae differ by their distinctly sloped umbilical wall, which forms a more or less funnel-shaped umbilicus, as well as by their suture line, which is characterized by low and broad saddles.

Nammalites pilatoides nov. comb. (Guex, 1978)
Fig. 15(6–8)

1909. *Meekoceras* sp. ind. aff. *pilato* - Krafft and Diener, p. 42, pl. 28, fig. 2a–c.

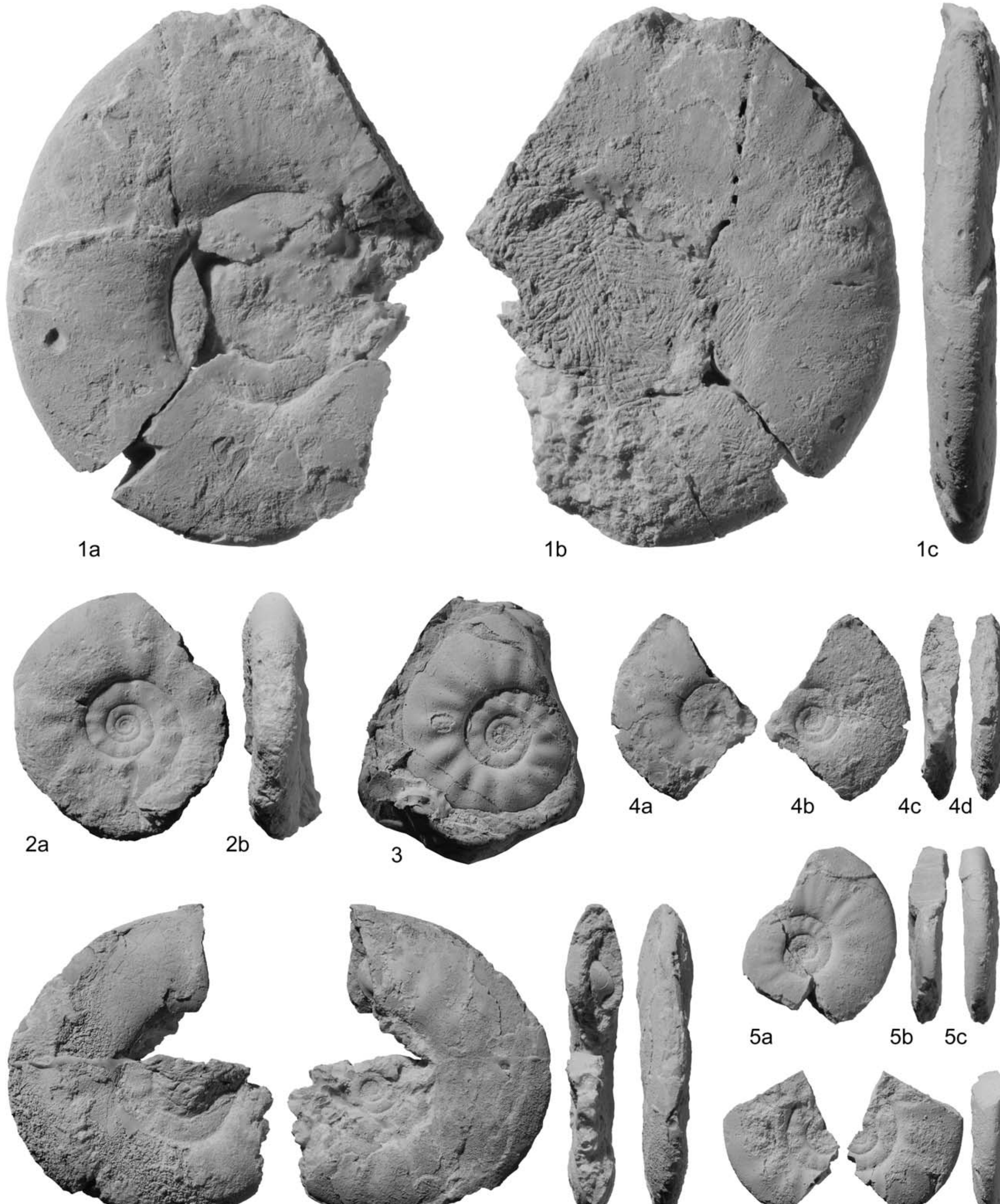

Fig. 9. **1a**–**c**. *?Anaxenaspis* sp. indet. A, PIMUZ 27632, sample TuB1, × 0.85. **2a, b**. Flemingitidae gen. indet. B, PIMUZ 27633, sample Tu44. **3**–**7**. *?Anaxenaspis* sp. indet. B; 3, PIMUZ 27634, sample TuB1; 4a–d, PIMUZ 27635, sample TuB1; 5a–c, PIMUZ 27636, sample TuB1; 6a–d, PIMUZ 27637, sample TuB1; 7a–c, PIMUZ 27638, sample TuB1. All natural size unless otherwise indicated.

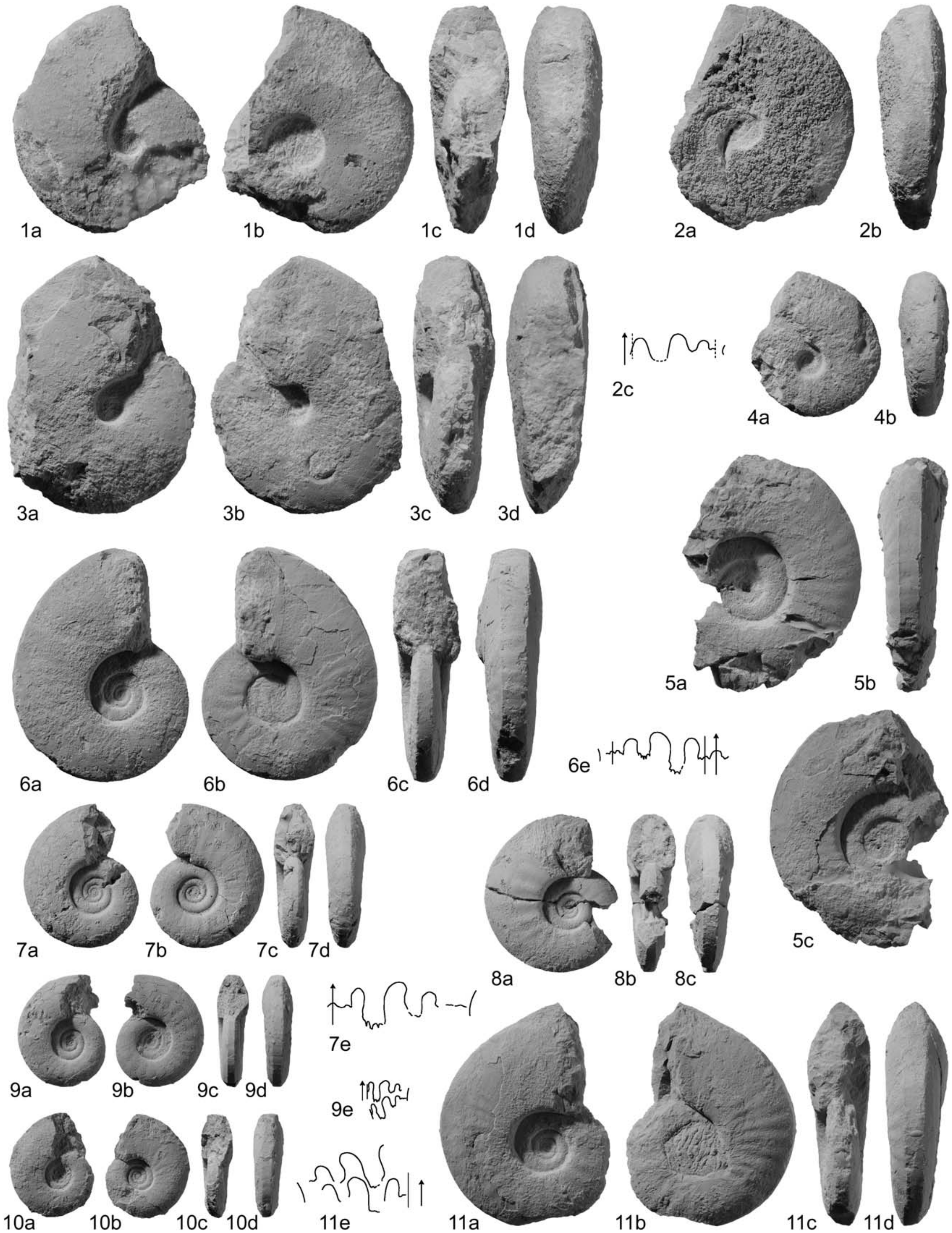

Fig. 10. **1**–**4**. *Shigetaceras dunajensis* nov. comb. (Zakharov, 1968); 1a–d, PIMUZ 27639, sample Tu44; 2a–c, PIMUZ 27640, sample Tu44; 3a–d, PIMUZ 27641, sample TuB3; 4a, b, PIMUZ 27642, sample Tu44. **5**–**11**. *Urdyceras tulongensis* nov. sp.; 5a, b, PIMUZ 27643, sample TuB5; 6a–e, PIMUZ 27644, sample TuB5, 6e × 2; 7a–e, PIMUZ 27645, sample TuB5, 7e × 2; 8a–c, PIMUZ 27646, sample TuB5; 9a–e, PIMUZ 27647, sample Na23, 9e × 2; 10a–d, PIMUZ 27648, sample TuB5. 11a–e, PIMUZ 27649, sample TuB5, 11e × 2. All natural size unless otherwise indicated.

1968a. *Wasatchites* sp. indet. - Kummel, p. 500, pl. 3, figs. 10, 11.

1968. *Eoptychites* sp. indet. - Kummel and Erben, p. 120, pl. 22, figs. 10, 11.

v. 1978. *Kazakhstanites pilatoides* nov. sp. - Guex, p. 109, pl. 6, figs. 5, 6, 16.

v. ? 1978. *Kazakhstanites pilatoides* nov. sp. - Guex, p. 109, pl. 8, fig. 6.

v. p. 1978. *Anasibirites pluriformis* nov. sp. - Guex, pl. 4, fig. 3 only.

Occurrence: Samples TuB2 (1?), Tu40 (2?), TuB3 (3), Tu44 (11), TuB4 (2) (*Nammalites pilatoides* beds).

Description: Moderately involute, compressed shell with convex, convergent flanks. Maximum whorl width at umbilical border. Venter subtabulate with rounded shoulders. Umbilicus with vertical wall and rounded shoulders. Ornamentation consists of rursiradiate to radiate ribs that tend to develop tubercles or elongated bullae near the umbilicus and then fade out towards the venter. Suture line ceratitic with tapered second lateral saddle on one specimen.

Genus ***Brayardites*** nov. gen.

Etymology: Named after Arnaud Brayard (Dijon, France).

Type species: *Brayardites crassus* nov. gen., nov. sp.

Composition of the genus: *Brayardites crassus* nov. gen., nov. sp. and *B. compressus* nov. gen., nov. sp.

Diagnosis: Moderately involute, compressed to subglobose Arctoceratidae with convergent flanks and prorsiradiate ribs that form strong tubercles near umbilical margin.

Remarks: *Brayardites* is slightly older than *Nammalites* and differs essentially by its prorsiradiate ribbing and stronger tubercles.

Brayardites crassus nov. gen., nov. sp.

Figs. 11(1–4) and 12(1–6)

Etymology: Refers to the thick whorls of this species.

Holotype: Specimen PIMUZ 27651, Fig. 11(2).

Type locality: Section TWB, Tulong, Nyalam County, South Tibet.

Type horizon: Sample TWB71; Early Triassic, Smithian, *Brayardites compressus* beds.

Occurrence: Samples TuB5 (14), TWB71 (2), TWB72 (2), Na22 (1), Na23 (1), Na25 (1), Na28 (1), Na41 (1?) (*Brayardites compressus* beds).

Measurements: See Supplementary data, Fig. S5.

Diagnosis: Evolute *Brayardites* with thick whorls and strongly convex flanks.

Description: Moderately evolute, shell with thick whorls and strongly convex flanks. Maximum whorl width below mid-flank. Venter broadly rounded with rounded shoulders. Umbilicus with steeply inclined wall and rounded shoulders. Ornamentation consists of prorsiradiate ribs that develop strong tubercles near umbilicus and fade out towards mid-flank. Suture line ceratitic, with broad, slightly tapered saddles.

Remarks: *Brayardites compressus* nov. gen., nov. sp. described below differs by its more compressed whorl section and more involute coiling.

Brayardites compressus nov. gen., nov. sp.

Fig. 13(1–6)

Etymology: Refers to the compressed shape of this species.

Holotype: Specimen PIMUZ 27660, Fig. 13(1).

Type locality: Section TWB, Tulong, Nyalam County, South Tibet.

Type horizon: Sample TWB71; Early Triassic, Smithian, *Brayardites compressus* beds.

Occurrence: Samples Tu16 (1), Tu18 (1), Tu33 (1), TuB5 (10), TuB6 (1), TWB72 (3), Na23 (2) (*Brayardites compressus* beds).

Measurements: See Supplementary data, Fig. S5.

Diagnosis: Involute *Brayardites* with compressed whorls and flat flanks.

Description: Moderately involute, compressed shell with flat, converging flanks. Maximum whorl width near umbilical border. Venter subtabulate with rounded shoulders. Umbilicus with high vertical wall and rounded shoulders. Ornamentation consists of prorsiradiate ribs that develop strong tubercles near umbilicus and fade out towards mid-flank. Growth lines biconcave. Suture line ceratitic with deep lobes and slightly tapered saddles.

Remarks: *Ceratites sagitta* Waagen, 1895 from the lower part of the Upper Ceratite Limestone of the Salt Range has similar ornamentation. Apparently, it differs by a rounded umbilical margin, but the preservation of Waagen's single specimen is rather poor. *B. crassus* nov. gen., nov. sp. and *B. compressus* nov. gen., nov. sp. co-occur in the Tulong succession. Whether or not these two species represent end-member variants of a single, highly variable species cannot be demonstrated on the basis of the limited number of available specimens, but a disparity of intermediate values of whorl width apparently does exist (Fig. 12).

Family PRIONITIDAE Hyatt, 1900

Genus ***Prionites*** Waagen, 1895

Type species: *Prionites tuberculatus* Waagen, 1895

Prionites involutus nov. sp.

Fig. 14(1–6)

Etymology: Refers to the involute coiling of this species in comparison with other *Prionites*.

Holotype: Specimen PIMUZ 27671, Fig. 14(3).

Type locality: Section Tu, Tulong, Nyalam County, South Tibet.

Type horizon: Sample Tu58; Early Triassic, Smithian, *Nyalamites angustecostatus* beds.

Occurrence: Samples Tu56 (1), Tu58 (9) (*Nyalamites angustecostatus* beds).

Measurements: See Supplementary data, Fig. S6.

Diagnosis: Involute and smooth *Prionites* with a persisting compressed whorl section at maturity.

Description: Involute, compressed shell with slightly convex flanks. Maximum whorl width below mid-flank. Venter broad and tabulate with slightly angular shoulders. Umbilicus small, deep and funnel-shaped. Umbilical wall inclined with rounded shoulders. Surface smooth. Suture line ceratitic with broad saddles; third lateral saddle very low.

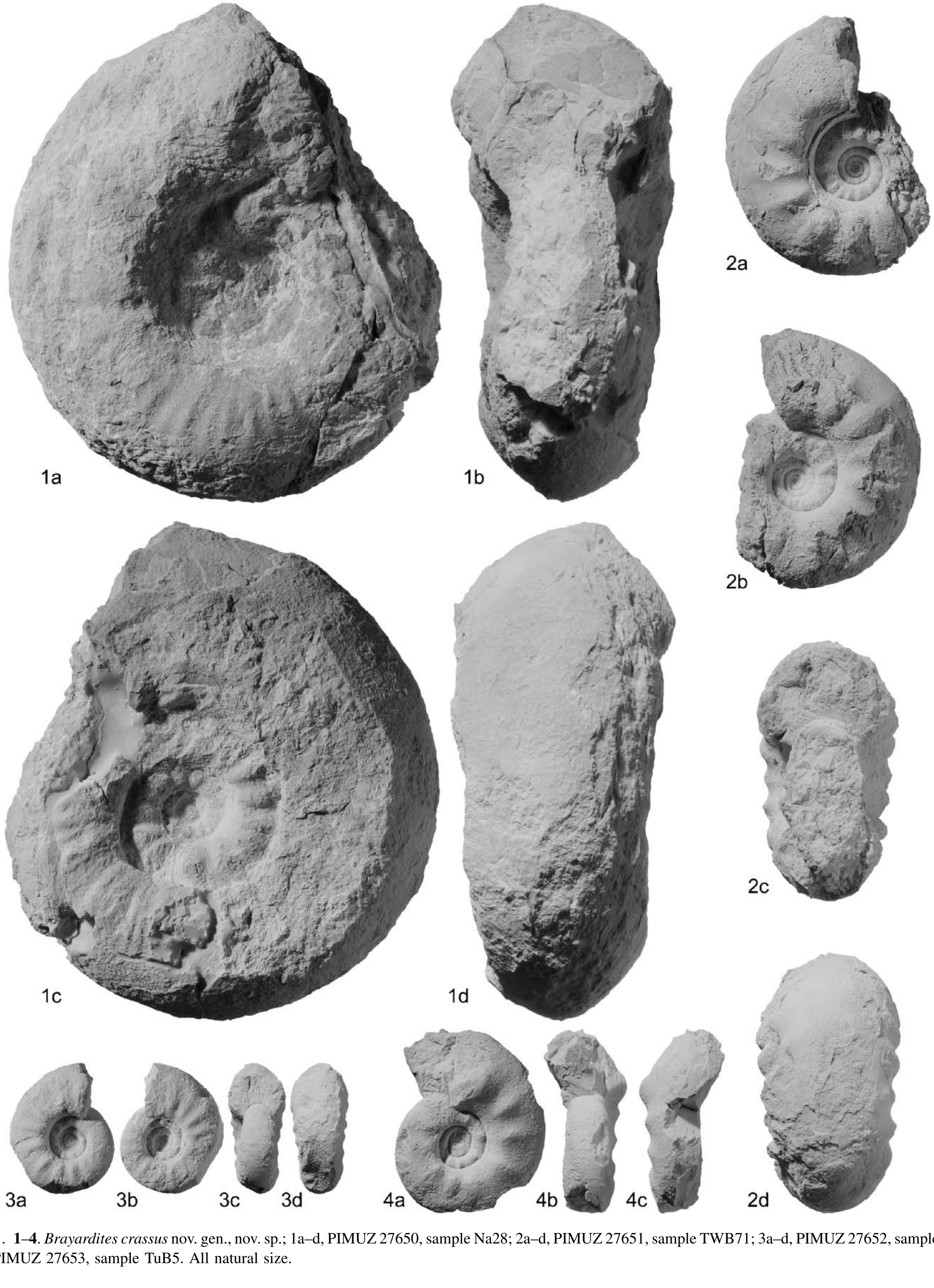

Fig. 11. **1**–**4**. *Brayardites crassus* nov. gen., nov. sp.; 1a–d, PIMUZ 27650, sample Na28; 2a–d, PIMUZ 27651, sample TWB71; 3a–d, PIMUZ 27652, sample TuB5; 4a–c, PIMUZ 27653, sample TuB5. All natural size.

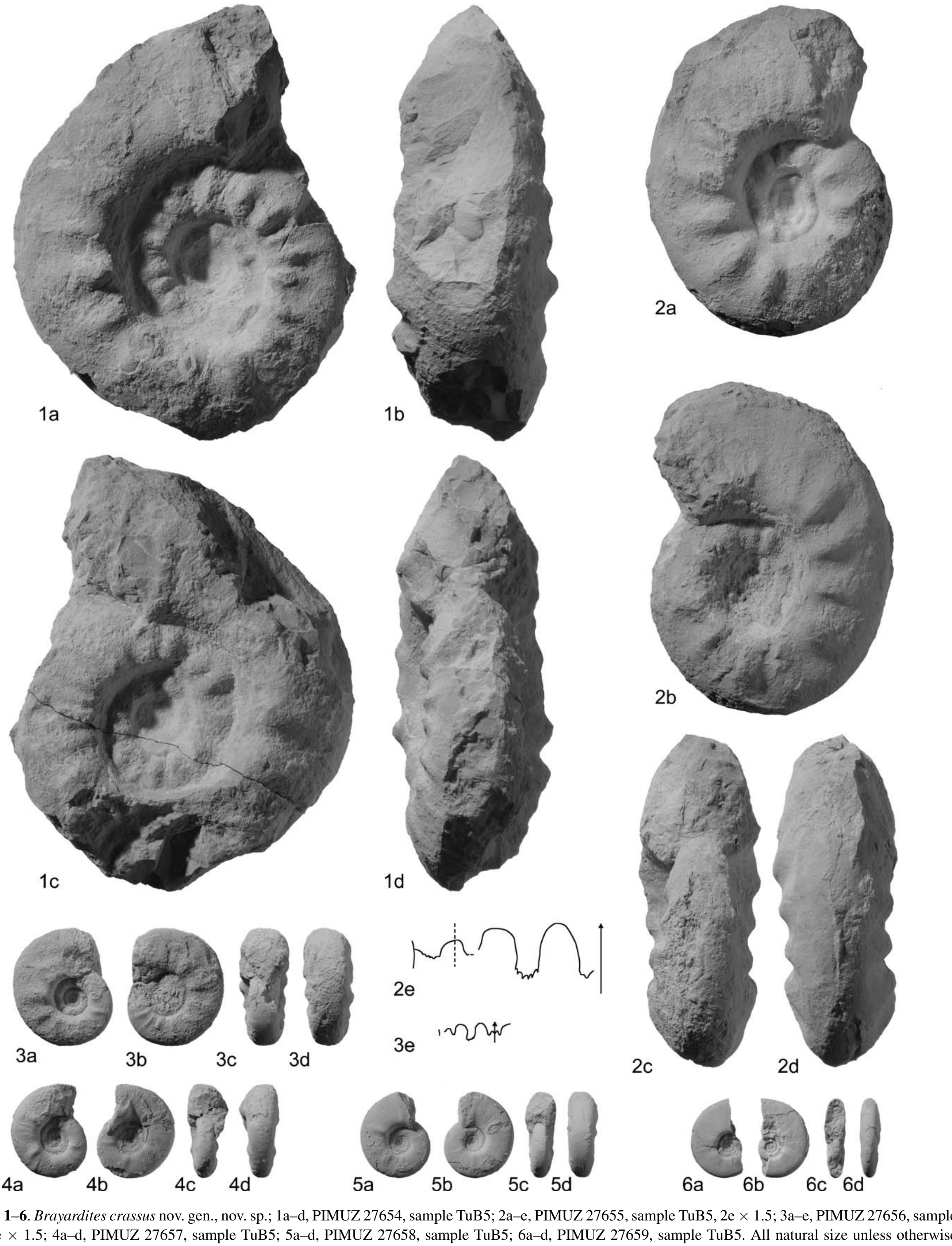

Fig. 12. **1–6**. *Brayardites crassus* nov. gen., nov. sp.; 1a–d, PIMUZ 27654, sample TuB5; 2a–e, PIMUZ 27655, sample TuB5, 2e × 1.5; 3a–e, PIMUZ 27656, sample Na23, 3e × 1.5; 4a–d, PIMUZ 27657, sample TuB5; 5a–d, PIMUZ 27658, sample TuB5; 6a–d, PIMUZ 27659, sample TuB5. All natural size unless otherwise indicated.

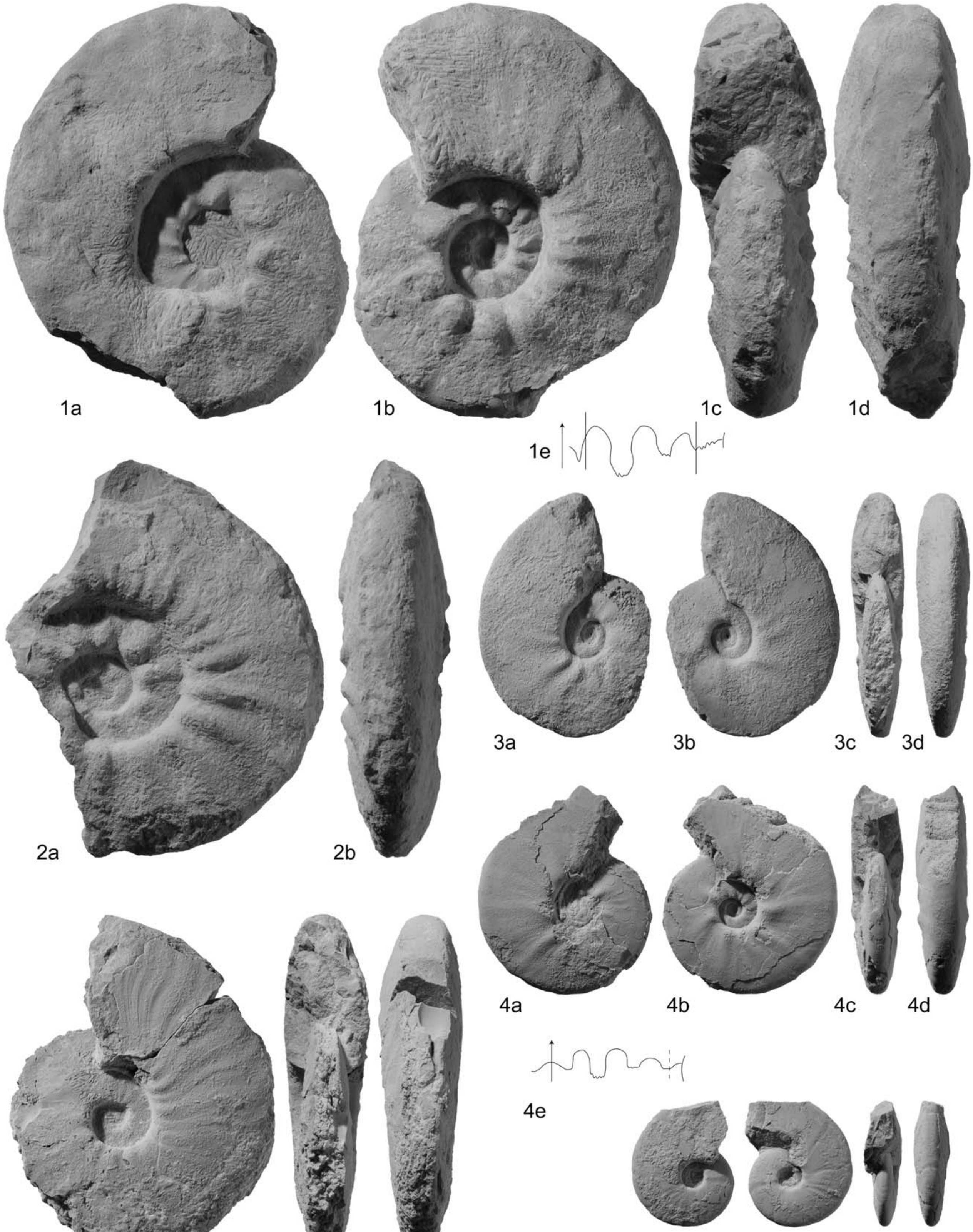

Fig. 13. **1–6**. *Brayardites compressus* nov. gen., nov. sp.; 1a–e, PIMUZ 27660, sample TuB5, 1e × 2; 2a, b, PIMUZ 27661, sample TuB5; 3a–d, PIMUZ 27662, sample Na23; 4a–e, PIMUZ 27663, sample TuB5, 1e × 2; 5a–c, PIMUZ 27664, sample TuB5. 6a-–d, PIMUZ 27667, sample Na23. All natural size unless otherwise indicated.

Remarks: The inner whorls of this species are similar to those of the type species and differ only by their more involute coiling (Waagen, 1895). The outer whorls of the type species differ by being more evolute and having a broader whorl section with broad swellings, whereas the new Tibetan species retains a compressed whorl section and involute coiling throughout ontogeny. *Hemiprionites klugi* Brayard and Bucher, 2008 is similar but differs by its smaller umbilicus with a steeper wall as well as by its suture line with characteristically tapered saddles.

Genus ***Stephanites*** Waagen, 1895

Type species: *Stephanites superbus* Waagen, 1895.

Remarks: *Stephanites* differs from the younger *Wasatchites* by the dorso-ventral elongation of its tubercles (especially on the inner whorls). Additionally, *Wasatchites* has more compressed and smoother inner whorls. Otherwise, these two genera are very similar, and thus, *Stephanites* is herein assigned to Prionitidae.

Stephanites superbus Waagen, 1895

Fig. 14(7–12)

1895. *Stephanites superbus* nov. sp. - Waagen, p. 101, pl. 2, fig. 2a–c.

1895. *Stephanites corona* nov. sp. - Waagen, p. 102, pl. 3, fig. 1a, b.

Occurrence: Samples Tu56 (1), Tu57 (1), Tu58 (3), Tu60 (2), Tu63 (4) (*Nyalamites angustecostatus* beds).

Description: Moderately involute shell with convex, convergent flanks. Maximum whorl width slightly below mid-flank. Venter broad and subtabulate with rounded shoulders. Umbilicus deep with well-rounded, inclined wall without distinct shoulders. Ornamentation consists of strong, distant tubercles on flanks, coinciding with maximum whorl width. Tubercles are elongated dorso-ventrally. Suture line with very broad first lateral saddle and very low third lateral saddle. Indentations of lobes not preserved.

Remarks: The minor differences between the type species and *Stephanites corona* Waagen, 1895 are here regarded as intraspecific variation.

Genus ***Wasatchites*** Mathews, 1929

Type species: *Wasatchites perrini* Mathews, 1929.

Wasatchites distractus (Waagen, 1895)

Fig. 15(1)

1895. *Acrochordiceras distractum* nov. sp. - Waagen, p. 94, pl. 3, fig. 4a–c.

1895. *Acrochordiceras coronatum* nov. sp. - Waagen, p. 96, pl. 3, fig. 5a–c.

1895. *Acrochordiceras* cf. *damesi* Noetling - Waagen, p. 97, pl. 4, fig. 5a–b.

1895. *Acrochordiceras compressum* nov. sp. - Waagen, p. 98, pl. 4, fig. 4a–c.

v. ? 1978. *Stephanites corona* Waagen - Guex, pl. 5, fig. 2.

Occurrence: Samples Tu67 (1), TWA3 (1) (*Wasatchites distractus* beds).

Description: Moderately involute shell with convex flanks. Maximum whorl width at mid-flank. Venter broad and subtabulate with rounded shoulders. Umbilicus deep with well-rounded, inclined wall without shoulders. Ornamentation very distinct, consisting of distant spiny tubercles on mid-flank. Venter poorly preserved and apparently smooth, but at some points there are faint indications of distant broad ribs. Suture line not preserved.

Remarks: The minor differences between the four species described by Waagen (1895) are here regarded as intraspecific variation of a single species, *W. distractus*. Note that a more comprehensive study of this species based on abundant and well preserved material from the Salt Range (Pakistan) and Spiti (India) is under progress by our group. The specimen described as *Stephanites corona* by Guex (1978) is probably conspecific but too poorly preserved for a definitive assignment. The boreal *Wasatchites* (i.e., *W. perrini* Spath, 1934) differs essentially by the lower position of spines on flanks.

Prionitidae gen. indet. A

Fig. 15(5)

Occurrence: A single specimen from sample TuB3 (*Nammalites pilatoides* beds).

Description: Involute shell with convex flanks. Maximum whorl width below mid-flank. Venter broad and tabulate with rounded shoulders, but poorly preserved. Umbilicus deep with well-rounded, inclined wall and rounded shoulders. Ornamented with distant ribs that are most prominent near umbilicus and fade out towards venter. Suture line ceratitic with broad first lateral saddle and low third lateral saddle.

Remarks: This specimen differs from *Nammalites pilatoides* by its inclined umbilical wall, which is indicative of Prionitidae. The poor preservation of this single specimen hinders a generic assignment.

"*Anasibirites*" cf. *pluriformis* (Guex, 1978)

Fig. 5(8)

Occurrence: A single specimen from sample Tu44 (*Nammalites pilatoides* beds).

Description: Moderately involute shell with flat, slightly converging flanks. Venter subtabulate, slightly arched, with rounded shoulders. Umbilicus with a high, vertical wall and marked, slightly rounded shoulders. Ornamentation consists of radial, slightly sinuous ribs with a faint thickening at ventral shoulders, not crossing the venter. Suture line not preserved.

Remarks: Our single specimen is very similar to weakly ornamented variants of *"Anasibirites" pluriformis*, but without additional material a definitive specific assignment would be speculative. This species was attributed to *Anasibirites* by Guex (1978). However, typical *Anasibirites* as well as all other Prionitidae differ greatly by having an umbilicus with an inclined wall and well-rounded shoulders. A revision of this species based on new material from the Salt Range is in progress by our group.

Family INYOITIDAE Spath, 1934

Genus ***Subvishnuites*** Spath, 1930

Type species: *Subvishnuites welteri* Spath, 1930 (= *Vishnuites* spec. Welter, 1922).

Subvishnuites sp. indet.

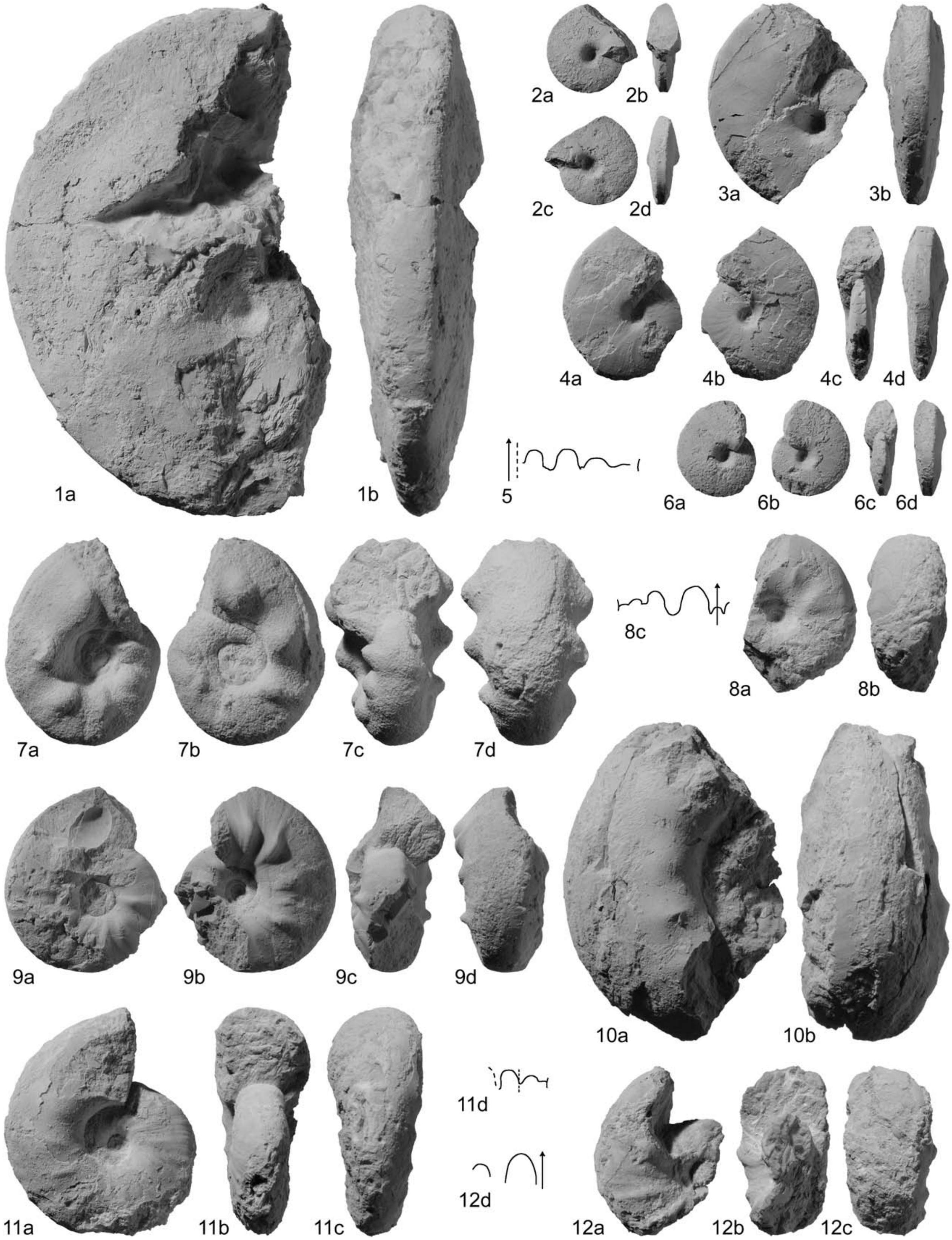

Fig. 14. **1–6**. *Prionites involutus* nov. sp.; 1a, b, PIMUZ 27669, sample Tu58; 2a–d, PIMUZ 27670, sample Tu58; 3a, b, PIMUZ 27671, sample Tu58; 4a–d, PIMUZ 27672, sample Tu58; 5, PIMUZ 27673, sample Tu58, × 2; 6a–d, PIMUZ 27674, sample Tu58. **7–12**. *Stephanites superbus* Waagen, 1895; 7a–d, PIMUZ 27675, sample Tu56; 8a–c, PIMUZ 27676, sample Tu63; 9a–d, PIMUZ 27677, sample Tu58; 10a, b, PIMUZ 27678, sample Tu63, × 0.5; 11a–d, PIMUZ 27679, sample Tu63; 12a–d, PIMUZ 27680, sample Tu63. All natural size unless otherwise indicated.

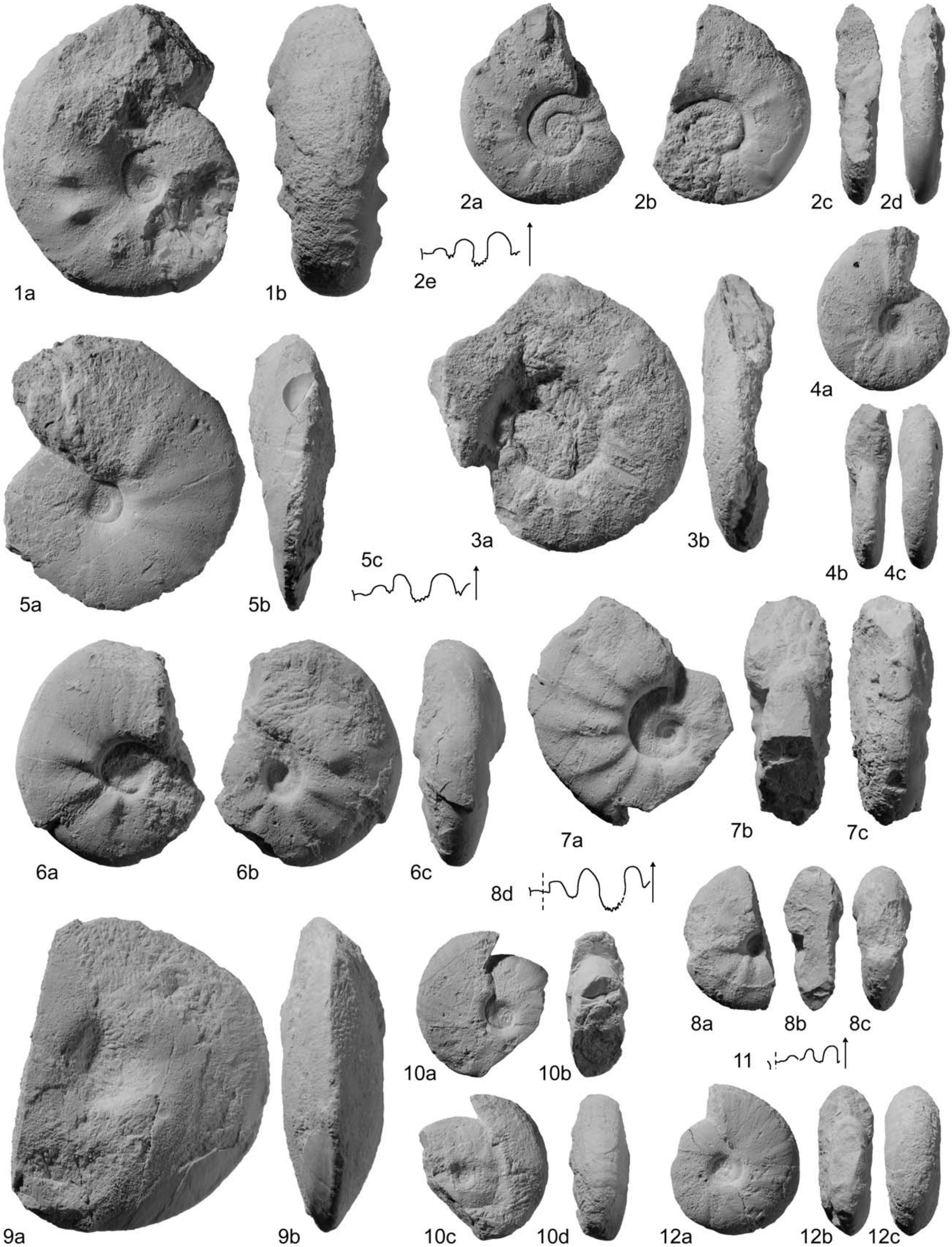

Fig. 15. **1a, b**, *Wasatchites distractus* (Waagen, 1895), PIMUZ 27681, sample Tu67. **2–4.** Genus indet. B; 2a–e, PIMUZ 27682, sample Tu67, 2e × 1.5; 3a, b, PIMUZ 27683, sample Tu66; 4a–c, PIMUZ 27684, sample Tu67. **5a–c**. Prionitidae gen. indet. A, PIMUZ 27685, sample TuB3, 5c × 1.5. **6–8**. *Nammalites pilatoides* nov. comb. (Guex, 1978); 6a–c, PIMUZ 27686, sample Tu44; 7a–c, PIMUZ 27687, sample Tu44; 8a–d, PIMUZ 27688, sample Tu44, 8d × 2. **9a, b**. *Owenites koeneni* Hyatt and Smith, 1905, PIMUZ 27689, sample Tu55. **10–12**. *Owenites simplex* Welter, 1922; 10a–d, PIMUZ 27690, sample Tu44; 11, PIMUZ 27691, sample Tu44, × 2; 12a–c, PIMUZ 27692, sample Tu44. All natural size unless otherwise indicated.

Fig. 16(9)

Occurrence: A single specimen from sample Tu58 (*Nyalamites angustecostatus* beds).

Description: Compressed, moderately evolute shell. Flanks convex, subparallel on inner half and converging strongly towards venter on outer half. Venter subacute. Umbilicus moderately deep with a vertical wall and rounded shoulders. Surface entirely smooth. Suture line not preserved.

Remarks: This species differs from the type species by its more involute coiling and thicker whorls. It is also more involute than *Subvishnuites stokesi*. It may represent a new species of *Subvishnuites*, but because of our sparse material we prefer to use an open nomenclature.

Family MELAGATHICERATIDAE Tozer, 1971

Genus ***Jinyaceras*** Brayard and Bucher, 2008

Type species: *Jinyaceras bellum* Brayard and Bucher, 2008.

Jinyaceras hindostanum (Diener, 1897)

Fig. 16(4–6)

1897. *Nannites hindostanus* nov. sp. - Diener, p. 68, pl. 7, figs. 3, 11, 12.

1897. *Nannites herberti* nov. sp. - Diener, p. 69, pl. 7, fig. 2.

Occurrence: Samples Na14 (3), Na23 (1), TuB5 (4), Tu16 (1) (*Brayardites compressus* beds).

Description: Small, moderately involute, laterally compressed shell with flat, subparallel flanks. Venter broadly arched, with rounded ventral shoulders. Umbilicus with vertical wall and subangular shoulders. Ornamentation consists of prorsiradiate constrictions that nearly disappear on venter. Suture line not preserved.

Remarks: This species is very similar to *Jinyaceras bellum* and differs only by its more involute coiling. *"Nannites" herberti* Diener, 1897 is slightly more involute than *Jinyaceras hindostanum*, but this minor difference is here regarded as intraspecific variation. The specimens described as *Paranannites aspenensis* by Kummel and Erben (1968) are very similar and may be conspecific, but differ by their larger size.

Family PARANANNITIDAE Tozer, 1971

Genus ***Paranannites*** Hyatt and Smith, 1905

Type species: *Paranannites aspenensis* Hyatt and Smith, 1905.

Paranannites spathi (Frebold, 1930)

Fig. 16(1, 2)

1930. *Prosphingites spathi* nov. sp. - Frebold, p. 20, pl. 4, figs. 2, 3, 3a.

1934. *Prosphingites spathi* Frebold - Spath, p. 195, pl. 13, figs. 1, 2.

p. ? 1959. *Prosphingites kwangsianus* nov. sp. - Chao, p. 296, pl. 28, figs. 17, 18.

p. ? 1959. *Prosphingites sinensis* nov. sp. - Chao, p. 297, pl. 27, figs. 14–17, fig. 40a.

? 1961. *Prosphingites spathi* Frebold - Tozer, p. 58, pl. 13, figs. 1, 2.

? 1982. *Prosphingites spathi* Frebold - Korchinskaya, pl. 5, fig. 2.

? 1994. *Paranannites spathi* Frebold - Tozer, p. 77, pl. 36, figs. 1, 2.

v. 2008. *Paranannites spathi* Frebold - Brayard and Bucher, p. 63, pl. 35, figs. 10–19.

Occurrence: Samples TuB3 (2), Tu44 (6) (*Nammalites pilatoides* beds).

Description: Moderately involute, globose shell with outer whorls characterized by a subtrigonal whorl section. Flanks convex, converging strongly to the venter from the umbilical margin. Umbilicus deep, with vertical wall and rounded shoulders. Ornamentation consists of prorsiradiate constrictions that cross the venter. Suture line not preserved.

Remarks: *Paranannites spathi* is very widely distributed in the middle Smithian (Brühwiler et al., 2007; Brayard and Bucher, 2008). It differs from other representatives of the genus by its subtrigonal outer whorls as well as by its stair-like umbilicus.

Paranannites sp. indet.

Fig. 16(3)

Occurrence: Sample Tu44 (3) (*Nammalites pilatoides* beds).

Description: Moderately involute, globose shell with a curved venter. Flanks flat, subparallel. Umbilicus deep with vertical wall and rounded shoulders. Ornamentation consists of faint prorsiradiate constrictions. Suture line with all three lateral saddles located on flanks. Indentations of lobes not preserved.

Remarks: This species differs from *Paranannites spathi* described above by its subparallel flanks and lower umbilical wall. Another perhaps more significant difference is that in the suture line of *P. spathi* the third lateral saddle is located on the umbilical wall (Brayard and Bucher, 2008), whereas for this species it is located on the flanks.

Genus ***Owenites*** Hyatt and Smith, 1905

Type species: *Owenites koeneni* Hyatt and Smith, 1905.

Owenites koeneni Hyatt and Smith, 1905

Fig. 15(9)

1905. *Owenites koeneni* nov. sp. - Hyatt and Smith, p. 83, pl. 10, figs. 1–22.

v. 2008. *Owenites koeneni* Hyatt and Smith - Brayard and Bucher, p. 67, pl. 36, figs. 1–8.

Occurrence: Samples Tu50 (1), Tu55 (1), Tu59 (1) (*Pseudoceltites multiplicatus* beds, *Nyalamites angustecostatus* beds).

Description: Involute, somewhat compressed shell with an inflated, lenticular whorl section. Umbilical wall inclined with a cone-shaped umbilicus, whose umbilical seam is hardly discernible. Venter narrowly rounded to acute. Surface generally smooth, weak concave folds may be present. Suture line not preserved.

Remarks: See Brayard and Bucher (2008) for a recent comprehensive study and a complete synonymy list for this species.

Owenites carpenteri Smith, 1932

Fig. 16(7, 8)

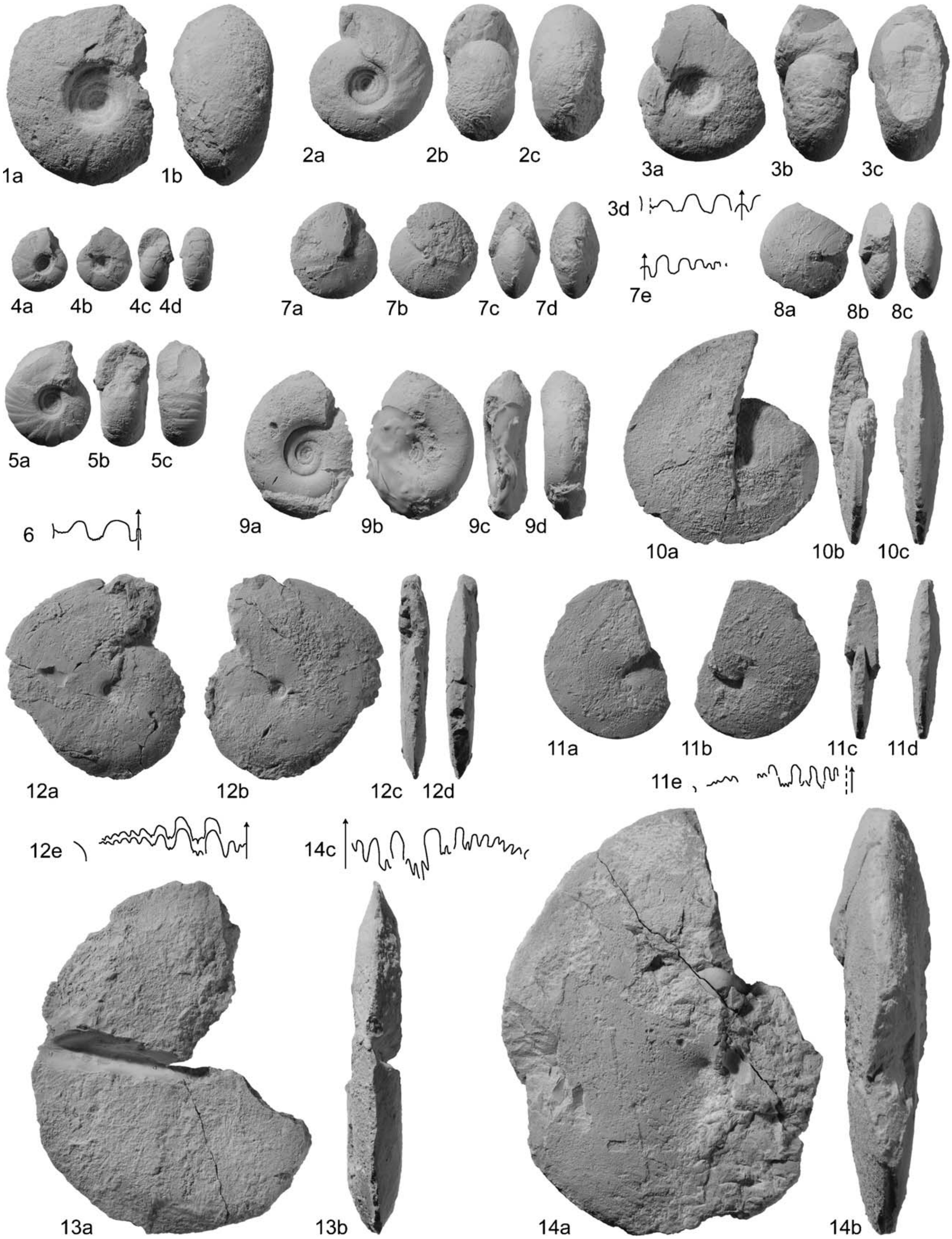

Fig. 16. **1, 2**. *Paranannites spathi* (Frebold, 1930); 1a, b, PIMUZ 27693, sample TuB3; 2a–c, PIMUZ 27694, sample Tu44. **3a–d**. *Paranannites* sp. indet., PIMUZ 27695, sample Tu44, × 1.5. **4–6**. *Jinyaceras hindostanum* (Diener, 1897); 4a–d, PIMUZ 27700, sample TuB5; 5a–c, PIMUZ 27698, sample TuB5; 6, PIMUZ 27699, sample TuB5, × 2. **7, 8**. *Owenites carpenteri* Smith, 1932; 7a–e, PIMUZ 27696, sample Tu58, 7e × 2; 8a–c, PIMUZ 27697, sample Tu58. **9a–d.** *Subvishnuites* sp. indet, PIMUZ 27668, sample Tu58. **10, 11**. *Pseudosageceras augustum* (Brayard and Bucher, 2008); 10a–c, PIMUZ 27702, sample Tu71; 11a–e, PIMUZ 27701, sample Tu71, 11e × 1.5. **12, 13.** *Aspenites acutus* Hyatt and Smith, 1905; 12a–e, PIMUZ 27703, sample TuB5; 13a, b, PIMUZ 27704, sample Tu16, 12e × 1.5. **14a–c**. *Pseudosageceras multilobatum* Noetling, 1905, PIMUZ 27705, sample Tu56. All natural size unless otherwise indicated.

1932. *Owenites carpenteri* nov. sp. - Smith, p. 100, pl. 54, figs. 31–34.

1966. *Owenites carpenteri* Smith - Hada, p. 112, pl. 4, fig. 1a–e.

1968. *Owenites carpenteri* Smith - Kummel and Erben, p. 122, fig. 12P.

1973. *Owenites carpenteri* Smith - Collignon, p. 139, pl. 4, figs. 5, 6.

v. 2008. *Owenites carpenteri* Smith - Brayard and Bucher, p. 70, pl. 43, figs. 15, 16.

Occurrence: Samples Tu 56 (1?), Tu58 (4), Tu59 (1?), Tu63 (1) (*Nyalamites angustecostatus* beds).

Description: Small, extremely involute to occluded shell with a subtriangular whorl section. Venter narrow and subangular. Umbilicus occluded. Maximum whorl width at umbilicus. Shell surface smooth except for very strong constrictions visible on internal mould only. Suture line with four lateral saddles; indentations of lobes poorly preserved.

Remarks: As shown by new material from Spiti (Brühwiler et al., ongoing work), constrictions may become closely spaced on outer whorls. If the shell is not preserved, this feature gives the false impression that the conch is ornamented with ''strong bundled radial ribs'' as described on the holotype by Smith (1932).

Owenites simplex Welter, 1922
Fig. 15(10–12)

1922. *Owenites simplex* nov. sp. - Welter, p. 153, pl. 15, figs. 1–8.

1934. *Parowenites simplex* Welter - Spath, p. 187, fig. 58.

1959. *Owenites kwangsiensis* nov. sp. - Chao, p. 250, pl. 22, figs. 1–6, fig. 26b.

1959. *Owenites plicatus* nov. sp. - Chao, p. 251, pl. 22, figs. 19–21, 24, 25, fig. 26e.

1968b. *Owenites simplex* Welter - Kummel, p. 2, pl. 1, figs. 1–9.

1968. *Owenites simplex* Welter - Kummel and Erben, p. 122, figs. 12k, n, o.

v. 2008. *Owenites simplex* Welter - Brayard and Bucher, p. 69, pl. 35, figs. 20–22; fig. 59.

Occurrence: Samples TuB3 (1?), Tu44 (4) (*Nammalites pilatoides* beds).

Description: Small, moderately involute, compressed shell with subparallel flanks. Venter narrowly rounded. Umbilicus deep with perpendicular wall and angular shoulder. Ornamentation consists of prosiradiate, slightly concave folds. Suture line not preserved.

Remarks: *Owenites simplex* is more evolute than *O. koeneni* and it has a more compressed shell.

Family INCERTAE SEDIS

Genus ***Shigetaceras*** nov. gen.

Etymology: Named after Yasunari Shigeta (National Museum of Nature and Science, Tokyo).

Type species: *Hemiprionites dunajensis* Zakharov, 1968.

Composition of the genus: Type species only.

Diagnosis: Compressed and involute Meekocerataceae. Venter broad and tabulate with angular shoulders. Umbilicus with vertical wall. Suture line with broad, tapered saddles.

Remarks: The type species was assigned to *Hemiprionites* by Zakharov (1968). However, true *Hemiprionites* as well as all other Prionitidae clearly differ from this species by having a funnel-shaped umbilicus with an inclined wall (Waagen, 1895; Brayard and Bucher, 2008). *Shigetaceras* is close to *Wailiceras* Brayard and Bucher, 2008 of earliest Smithian age (i.e., *Kashmirites kapila* beds), which differs by its narrower venter and a suture line with long, deep lobes and narrow saddles. Although more involute, the shape of *Shigetaceras* is also close to that of *Urdyceras tulongensis* described above, but its suture line is also notably different.

The familial affinity of *Shigetaceras* is unclear. Its shape and suture line are similar to Prionitidae, from which it differs by its umbilicus with a high, vertical wall and marked shoulders. Proptychitidae differ by having a rounded venter and a more complex suture line.

Shigetaceras dunajensis nov. comb. (Zakharov, 1968)
Fig. 10(1–4)

1968. *Hemiprionites dunajensis* nov. sp. - Zakharov, p. 125, pl. 23, figs. 6–8.

? 2009. *Hemiprionites* sp. indet. - Shigeta and Zakharov, p. 87, fig. 74.

Occurrence: Samples TuB3 (1), Tu44 (3) (*Nammalites pilatoides* beds).

Measurements: See Supplementary data, Fig. S7, which includes measurements of the type material from Primorye (Zakharov, 1968) for comparison.

Description: Compressed and involute shell with convex and convergent flanks. Venter tabulate with angular shoulders. Umbilicus small and deep with vertical wall and narrow, slightly rounded shoulders. Surface smooth. Suture line with broad, tapered saddles. Indentations of lobes not preserved.

Remarks: This species has recently been found in age-equivalent beds in Spiti (Brühwiler et al., in preparation).

Genus indet. A
Fig. 7(6, 7)

Occurrence: Sample Na28 (2) (*Brayardites compressus* beds).

Description: Evolute shell with convex flanks. Inner whorls with subquadratic whorl section, outer whorls becoming laterally compressed. Venter subtabulate with rounded shoulders. Umbilicus wide and shallow with rounded umbilical wall. Surface smooth except for very small nodes at umbilical shoulders. Suture line ceratitic with distinctly phylloid saddles and deeply indented lobes.

Genus indet. B
Fig. 15(2–4)

Occurrence: Samples Tu66 (1), TWA3 (2?), Tu67 (2) (*Wasatchites distractus* beds).

Description: Moderately evolute, compressed shell with slightly convex flanks. Maximum whorl width slightly below mid-flank. Venter narrow and rounded with rounded shoulders.

Umbilicus with inclined wall and rounded shoulders. Ornamented with distant radial ribs that fade out near mid-flank. Suture line ceratitic with large first lateral saddle and low third lateral saddle.

Remarks: The evolute coiling and the rather peculiar ornamentation suggest that this ammonoid represents a new genus, but our poorly preserved material precludes the erection of a new taxon. The familial affinity of this ammonoid is unclear. Its general shape is similar to that of some Flemingitidae, but its ornamentation is rather uncharacteristic of this family. On the other hand, some Xenoceltitidae such as *Xenoceltites* are relatively similar.

Superfamily SAGECERATACEAE Hyatt, 1884
Family HEDENSTROEMIIDAE Waagen, 1895
Genus ***Pseudosageceras*** Diener, 1895
Type species: *Pseudosageceras* sp. indet., Diener, 1895.

Pseudosageceras multilobatum Noetling, 1905
Fig. 16(14)

1895. *Pseudosageceras* sp. indet. - Diener, p. 28, pl. 1, fig. 8.

1905. *Pseudosageceras multilobatum* nov. sp. - Noetling, pl. 25, fig. 1a, b; pl. 26, fig. 3a, b.

v. 2008. *Pseudosageceras multilobatum* Noetling - Brayard and Bucher, p. 70, pl. 37, figs. 1–5, text-fig. 61.

2009. *Pseudosageceras multilobatum* Noetling - Shigeta and Zakharov, 2009, p. 140, figs. 129, 130.

Occurrence: A single specimen from sample Tu56 (*Nyalamites angustecostatus* beds).

Description: Oxycone, very involute shell (closed umbilicus) with narrow, bicarinate venter. Suture line complex with several adventitious lobes. Main lateral lobe trifid, others bifid.

Remarks: *Pseudosageceras multilobatum* is one of the most long-ranging and cosmopolitan ammonoid species of the Early Triassic. See Brayard and Bucher (2008) for a recent comprehensive study and a complete synonymy list for this species.

Pseudosageceras augustum (Brayard and Bucher, 2008)
Fig. 16(10, 11)

v. 2008. *Hedenstroemia augusta* nov. sp. - Brayard and Bucher, p. 72, pl. 39, figs. 1–11, text-fig. 63.

Occurrence: Samples Tu71 (2), TWA4 (1) (*Glyptophiceras sinuatum* beds); Tu82 (2) (*Procolumbites* beds [early Spathian]).

Description: Extremely involute, compressed oxyconic shell. Venter very narrow and weakly bicarinate. Umbilicus closed. Surface smooth. Suture line complex with several adventitious saddles and a long auxiliary series. Indentations of lobes poorly preserved.

Remarks: This species differs from true *Hedenstroemia* by its suture line with several adventitious saddles. Brayard and Bucher (2008) differentiated it from *Pseudosageceras multilobatum* on the basis of its apparently non-trifid main lateral lobe. However, an examination of the type material has revealed that the indentations of the lobes are rather poorly preserved and that the main lateral lobe could actually be trifid. Thus, this species is herein tentatively transferred to *Pseudosageceras*. The type species *P. multilobatum* differs by its different whorl section: its maximum width is located at the umbilicus, whereas on *P. augustum* it is located near mid-flanks. Moreover, juvenile specimens of *P. augustum* differ by their longitudinal line at mid-flank on, marking a very slight change in slope between umbilical and ventral portions of flanks (Brayard and Bucher, 2008). The Tulong section provides the first evidence that *P. augustum* crossed the Smithian-Spathian boundary.

Family ASPENITIDAE Spath, 1934
Type species: *Aspenites acutus* Hyatt and Smith, 1905.

Aspenites acutus Hyatt and Smith, 1905
Fig. 16(12, 13)

1905. *Aspenites acutus* nov. sp. - Hyatt and Smith, p. 96, pl. 2, figs. 9–13; pl. 3, figs. 1–5.

v. 2008. *Aspenites acutus* Hyatt and Smith - Brayard and Bucher, p. 77, pl. 42, figs. 1–9.

Occurrence: Samples TuB5 (1), Tu16 (2) (*Brayardites compressus* beds).

Description: Extremely involute, very compressed shell with slightly convex flanks. Maximum whorl width at mid-flank. Venter lanceolate with an acute keel. Umbilicus probably occluded, but outer shell is not preserved. Umbilical region slightly depressed. Surface nearly smooth except for fine radial folds and falcoid growth lines. Suture line not preserved.

Remarks: *Aspenites acutus* is a relatively long-ranging species and is known from the early to the middle Smithian (Brayard and Bucher, 2008, Brühwiler et al., ongoing work). See Brayard and Bucher (2008) for a recent comprehensive study and a complete synonymy list for this species.

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Appendix A. Supplementary data

Supplementary data (Figs. S1–S7) associated with this article can be found, in the online version, at doi:10.1016/j.geobios.2009.12.004.

References

Arthaber, G., 1911. Die Trias von Albanien. Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients 24, 169–277.

Baud, A., Atudorei, V., Sharp, Z., 1996. Late Permian and Early Triassic evolution of the Northern Indian margin: Carbon isotope and sequence stratigraphy. Geodinamica Acta 9, 57–77.

Bhargava, O.N., Krystyn, L., Balini, M., Lein, R., Nicora, A., 2004. Revised litho- and sequence stratigraphy of the Spiti Triassic. Albertiana 30, 21–39.

Brayard, A., Bucher, H., 2008. Smithian (Early Triassic) ammonoid faunas from northwestern Guangxi (South China): taxonomy and biochronology. Fossils and Strata 55, 1–179.

Brayard, A., Bucher, H., Escarguel, G., Fluteau, F., Bourquin, S., Galfetti, T., 2006. The Early Triassic ammonoid recovery: Paleoclimatic significance of diversity gradients. Palaeogeography, Palaeoclimatology, Palaeoecology 239, 374–395.

Brayard, A., Escarguel, G., Bucher, H., 2007. The biogeography of early Triassic ammonoid faunas: Clusters, gradients, and networks. Geobios 40, 749–765.

Brayard, A., Brühwiler, T., Bucher, H., Jenks, J., 2009a. *Guodunites*, a low-palaeolatitude and trans-panthalassic Smithian (Early Triassic) ammonoid genus. Palaeontology 52, 471–481.

Brayard, A., Escarguel, G., Bucher, H., Brühwiler, T., 2009b. Smithian and Spathian (Early Triassic) ammonoid assemblages from terranes: Paleoceanographic and paleogeographic implications. Journal of Asian Earth Sciences 36, 420–433.

Brayard, A., Escarguel, G., Bucher, H., Monnet, C., Brühwiler, T., Goudemand, N., Galfetti, T., Guex, J., 2009c. Good genes and good luck: ammonoid diversity and the end-Permian mass extinction. Science 325, 1118–1121.

Brühwiler, T., Bucher, H., Goudemand, N., Brayard, A., 2007. Smithian (Early Triassic) ammonoid faunas of the Tethys: new preliminary results from Tibet, India. Pakistan and Oman. New Mexico Museum of Natural History and Science Bulletin 41, 25–26.

Brühwiler, T., Goudemand, N., Galfetti, T., Bucher, H., Baud, A., Ware, D., Hermann, E., Hochuli, P.A., Martini, R., 2009. The Lower Triassic sedimentary and carbon isotope records from Tulong (South Tibet) and their significance for Tethyan palaeoceanography. Sedimentary Geology 222, 314–332.

Burg, J.P., 1983. Carte géologique du sud du Tibet /Ministère de la Géologie - Pékin (République Populaire de Chine) ; Contours synth. par J.P. Burg. China. Ministry of Geology and Mineral Resources, Paris.

Chao, K., 1959. Lower Triassic ammonoids from Western Kwangsi, China. Palaeontologia Sinica, NS B 9, 1-355.

Collignon, M., 1933-1934. Paléontologie de Madagascar XX. Les céphalopodes du Trias inférieur. Annales de Paléontologie 22, 151–162; 23, 1–43.

Collignon, M., 1973. Ammonites du Trias inférieur et moyen d'Afghanistan. Annales de Paléontologie 59, 127–163.

Cuvier, G., 1797. Tableau élémentaire de l'histoire naturelle des animaux. Éditions Baudouin, Paris.

Dagys, A.S., Ermakova, S.P., 1990. Early Olenekian Ammonoids of Siberia. Nauka, pp. 1–112.

Diener, C., 1895. Triadische Cephalopodenfaunen der ostsibirischen Küstenprovinz. Mémoires du Comité géologique de Saint Petersburg 14, 1–59.

Diener, C., 1897. The Cephalopoda of the Lower Trias. Himalayan Fossils. Palaeontologia Indica 15, 1–181.

Diener, C., 1913. Triassic faunae of Kashmir. Palaeontologia Indica 5, 1–133.

Ermakova, S.P., 2002. Zonal standard of the Boreal Lower Triassic. Nauka, pp. 1–109.

Frebold, H., 1930. Die Altersstellung des Fischhorizontes, des Grippianniveaus und des unteren Saurierhorizontes in Spitzbergen. Scrifter om Svalbard og Ishavet 28, 1–36.

Frech, F., 1902. Lethaea Geognostica, 1. Lethaea Palaeozoica 2 (4), Die Dyas (Schluss), pp. 579–788.

Garzanti, E., Sciunnach, D., 1997. Early Carboniferous onset of Gondwanian glaciation and Neo-Tethyan rifting in Southern Tibet. Earth Planetary Science Letters 148, 359–365.

Garzanti, E., Angiolini, L., Sciunnach, D., 1996. The Permian Kuling Group (Spiti. Lahaul and Zanskar; NW Himalaya): sedimentary evolution during rift/drift transition and initial opening of Neo-Tethys. Rivista Italiana di Paleontologia Stratigrafia 102, 175–200.

Garzanti, E., Nicora, A., Rettori, R., 1998. Permo-Triassic boundary and lower to middle Triassic in South Tibet. Journal of Asian Earth Sciences 16, 143–157.

Guex, J., 1978. Le Trias inférieur des Salt Ranges. Pakistan ; problèmes biochronologiques. Eclogae Geologicae Helvetiae 71, 105–141.

Hada, S., 1966. Discovery of Early Triassic ammonoids from Gua Musang, Kelantan, Malaya, Journal of Geosciences. Osaka University 9, 111–121.

Hyatt, A., 1884. Genera of fossil cephalopods. Proceedings of the Boston Society of Natural History 22, pp. 253–338.

Hyatt, A., 1900. Cephalopoda. In: Zittel, K.A.V. (Ed.), Textbook of palaeontology,, 1st English ed., vol.1. Eastman, C.R, London, pp. 502–604.

Hyatt, A., Smith, J.P., 1905. Triassic cephalopod genera of America. U. S. Geological Survey Professional Paper 40, 1–394.

Jenks, J., 2007. Smithian (Early Triassic) ammonoid biostratigraphy at Crittenden Springs, Elko County. Nevada and a new ammonoid from the Meekoceras gracilitatis zone. New Mexico Museum of Natural History and Science Bulletin 40, 81–90.

Khuc, V., 1984. Triassic ammonoids in Vietnam. Geoinform and Geodata Institute, Hanoi, pp. 1–134.

Kiparisova, L.D., Popov, Y.D., 1956. Subdivision of the lower series of the Triassic System into stages. Doklady Akademii Nauk SSSR 109, pp. 842–845.

Korchinskaya, M.V.,1982. Explanatory note on the biostratigraphic scheme of the Mesozoic (Trias) of Spitsbergen. USSR Ministry of Geology, PGO Sevmorgeologia, pp. 40–99.

Krafft, A.V., Diener, C., 1909. Lower Triassic cephalopoda from Spiti. Malla Johar, and Byans. Palaeontologia Indica 15, 1–186.

Krystyn, L., Bhargava, O.N., Richoz, S., 2007a. A candidate GSSP for the base of the Olenekian Stage: Mud at Pin Valley; district Lahul and Spiti, Himachal Pradesh (Western Himalaya). India. Albertiana 35, 5–29.

Krystyn, L., Richoz, S., Bhargava, O.N., 2007b. The Induan-Olenekian Boundary (IOB) in Mud - an update of the candidate GSSP section M04. Albertiana 36, 33–45.

Kummel, B., 1968a. Additional Scythian Ammonoids from Afghanistan. Bulletin of the Museum of Comparative Zoology. Harvard University 136, 483–509.

Kummel, B., 1968b. Scythian ammonoids from Timor. Breviora 283, 1–21.

Kummel, B., Erben, H.K., 1968. Lower and Middle Triassic cephalopods from Afghanistan. Palaeontographica Abt. A 129, 95–148.

Kummel, B., Steele, G., 1962. Ammonites from the *Meekoceras gracilitatus* Zone at Crittenden Spring, Elko County, Nevada. Journal of Paleontology 36, 638–703.

Liu, G., 1992. Permian to Eocene sediments and Indian passive margin evolution in the Tibetan Himalayas. Tübinger Geowissenschaftliche Arbeiten. Reihe A 13, 1–268.

Liu, G., Einsele, G., 1994. Sedimentary history of the Tethyan basin in the Tibetan Himalayas. Geologische Rundschau 83, 32–61.

Marcoux, J., Baud, A., 1996. Late Permian to Late Triassic Tethyan paleoenvironments. Three snapshots: Late Murgabian, Late Anisian, Late Norian. In: Nairn, X., Ricou, L.E., Vrielynck, B., Dercourt, J. (Eds.), The Tethys Ocean. The Ocean Basins and Margins. Plenum Press, New York, pp. 153–190.

Markevich, P.V., Zakharov, Y.,2004. Triassic and Jurassic of the Sikhote-Alin, 420 pp. Dalnauka, Vladivostok, Russia (in Russian with English summary).

Mathews, A.A.L., 1929. The Lower Triassic cephalopod fauna of the Fort Douglas area. Utah. Walker Museum Memoirs 1, 1–46.

Noetling, F., 1905. Die asiatische Trias. In: Frech, F. (Ed.), Lethaea geognostica: Handbuch der Erdgeschichte mit Abbildungen der für die Formationen bezeichnendsten Versteinerungen. Schweizerbart, Stuttgart, pp. 107–221.

Ogg, J.G., von Rad, U., 1994. The Triassic of the Thakkola (Nepal). II: Paleolatitudes and Comparison with other Eastern Tethyan Margins of Gondwana. Geologische Rundschau 83, 107–129.

Orchard, M.J., 2007. Conodont diversity and evolution through the latest Permian and Early Triassic upheavals. Palaeogeography, Palaeoclimatology, Palaeoecology 252, 93–117.

Raup, D.M., Sepkoski, J.J., 1982. Mass Extinctions in the Marine Fossil Record. Science 215, 1501–1503.

Ricou, L.E., 1996. The plate tectonic history of the past Tethys Ocean. In: Nairn, X., Ricou, L.E., Vrielynck, B., Dercourt, J. (Eds.), The Tethys Ocean. The Ocean Basins and Margins. Plenum Press, New York, pp. 3–70.

Shen, S.Z., Cao, C.Q., Henderson, C.M., Wang, X.D., Shi, G.R., Wang, Y., Wang, W., 2006. End-Permian mass extinction pattern in the northern peri-Gondwanan region. Palaeoworld 15, 3–30.

Shevyrev, A.A., 1968. Triassic ammonoidea from the southern part of the USSR. Transactions of the Palaeontological Institute 119. Nauka 1–272.

Shevyrev, A.A., 2001. Ammonite zonation and interregional correlation of the Induan stage. Stratigraphy and Geological Correlation 9, 473–482.

Shigeta, Y., Zakharov, Y., 2009.Systematic paleontology: cephalopods. In: Shigeta, Y., Zakharov, Y., Maeda, H., Popov, A.M. (Eds.), The Lower Triassic system in the Abrek Bay area, South Primorye, Russia. National Museum of Nature and Science Monographs 38, Tokyo, pp. 44–140.

Shigeta, Y., Maeda, H., Yokoyama, K., Zakharov, Y., 2009a. Paleogeographical and geological setting. In: Shigeta, Y., Zakharov, Y., Maeda, H., Popov, A.M. (Eds.), The Lower Triassic system in the Abrek Bay area, South Primorye, Russia. National Museum of Nature and Science Monographs 38, Tokyo, pp. 3–4.

Shigeta, Y., Maeda, H., Zakharov, Y., 2009b. Biostratigraphy: ammonoid succession. In: Shigeta, Y., Zakharov, Y., Maeda, H., Popov, A.M. (Eds.), The Lower Triassic system in the Abrek Bay area, South Primorye, Russia. National Museum of Nature and Science Monographs 38, Tokyo, pp. 24–27.

Silberling, N.J., Tozer, E.T., 1968. Biostratigraphic classification of the marine Triassic in North America. Special Paper. Geological Society of America 110, 1–63.

Smith, J.P., 1932. Lower Triassic ammonoids of North America. U. S. Geological Survey Professional Paper 167, 1–199.

Spath, L.F., 1930. The Eotriassic invertebrate fauna of East Greenland. Meddelelser om Grønland 83, 1–90.

Spath, L.F., 1934. Part 4: The ammonoidea of the Trias, Catalogue of the fossil cephalopoda in the British Museum (Natural History). The Trustees of the British Museum, London.

Stampfli, G., Marcoux, J., Baud, A., 1991. Tethyan Margins in Space and Time. Palaeogeography, Palaeoclimatology. Palaeoecology 87, 373–409.

Tozer, E.T., 1961. Triassic stratigraphy and faunas, Queen Elizabeth Islands, Arctic Archipelago. Geologic Survey of Canada. Memoir 316, 1–116.

Tozer, E.T., 1965. Lower Triassic stages and ammonoid zones of Arctic Canada. Geological Survey of Canada Paper 65, 1–14.

Tozer, E.T., 1967. A standard for Triassic time. Geologic Survey of Canada Bulletin 156, 1–141.

Tozer, E.T., 1969. Xenodiscaceaen ammonoids and their bearing on the discrimination of the Permo-Triassic boundary. Geological Magazine 106, 348–361.

Tozer, E.T., 1971. Triassic time and ammonoids. Canadian Journal of Earth Sciences 8, 989–1031.

Tozer, E.T., 1981. Triassic Ammonoidea; classification, evolution and relationship with Permian and Jurassic forms. In: House, M.R., Senior, J.R. (Eds.), The Ammonoidea; the evolution, classification, mode of life and geological usefulness of a major fossil group. Systematics Association Special Volume, vol.18. Academic Press, London, pp. 65–100.

Tozer, E.T., 1994. Canadian Triassic ammonoid faunas. Geological Survey of Canada, Bulletin 467, 1–663.

Trümpy, R., 1969. Lower Triassic ammonites from Jameson Land (East Greenland). Meddelelser om Grønland 168, 77–116.

Waagen, W., 1895. Salt-Range fossils. Vol. 2. Fossils from the Ceratite Formation. Palaeontologia Indica 13, 1–323.

Wang, Y.G., He, G.X., 1976. Triassic ammonoids from the Mount Jolmo Lungma region. A report of scientific expedition in the Mount Jolmo Lungma region (1966-1968). Palaeontology 3, 223–502 (in Chinese).

Weitschat, W., Lehmann, U., 1978. Biostratigraphy of the uppermost part of the Smithian Stage (Lower Triassic) at the Botneheia. W-Spitsbergen. Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg 54, 27–54.

Welter, O.A., 1922. Die Ammoniten der unteren Trias von Timor. Paläontologie von Timor 11, 83–154.

Yokoyama, K., Shigeta, Y., Tsutsumi, Y., 2009a. Age distribution of detrital monazites in the sandstone. In: Shigeta, Y., Zakharov, Y., Maeda, H., Popov, A.M. (Eds.), The Lower Triassic system in the Abrek Bay area, South Primorye, Russia. National Museum of Nature and Science Monographs 38, Tokyo, pp. 30–34.

Yokoyama, K., Shigeta, Y., Tsutsumi, Y., 2009b. Age data of monazites. In: Shigeta, Y., Zakharov, Y., Maeda, H., Popov, A.M. (Eds.), The Lower Triassic system in the Abrek Bay area, South Primorye, Russia. National Museum of Nature and Science Monographs 38, Tokyo, pp. 34–36.

Zakharov, Y.D., 1968. Biostratigraphiya i amonoidei nizhnego triasa Yuzhnogo Primorya. Lower Triassic biostratigraphy and ammonoids of South Primorye. Nauka, pp. 1–175.(in Russian).

Zittel, K.A., 1884. Handbuch der Paläontologie 2. Cephalopoda. Oldenbourg Druck und Verlag, Munich, pp. 239–522.

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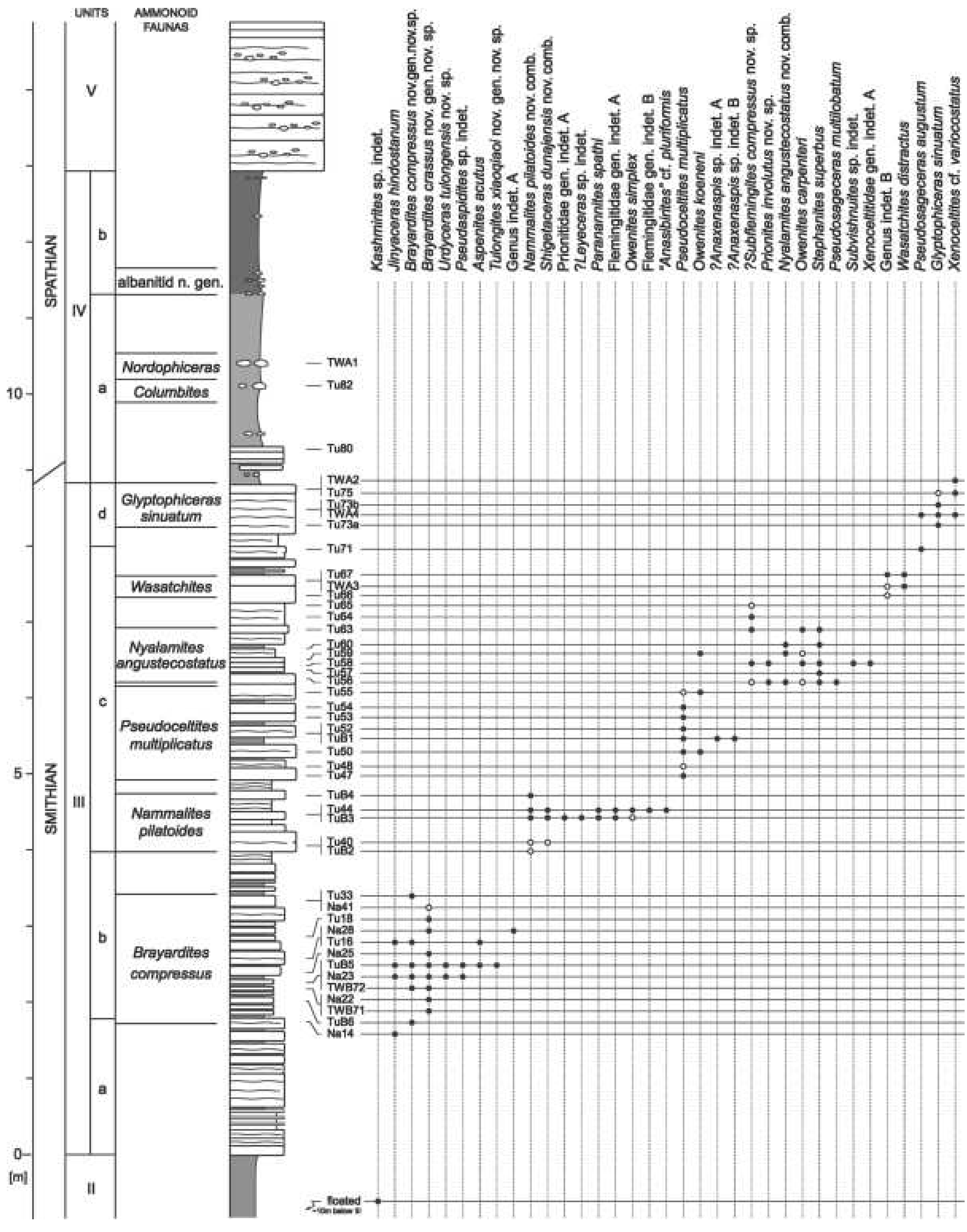
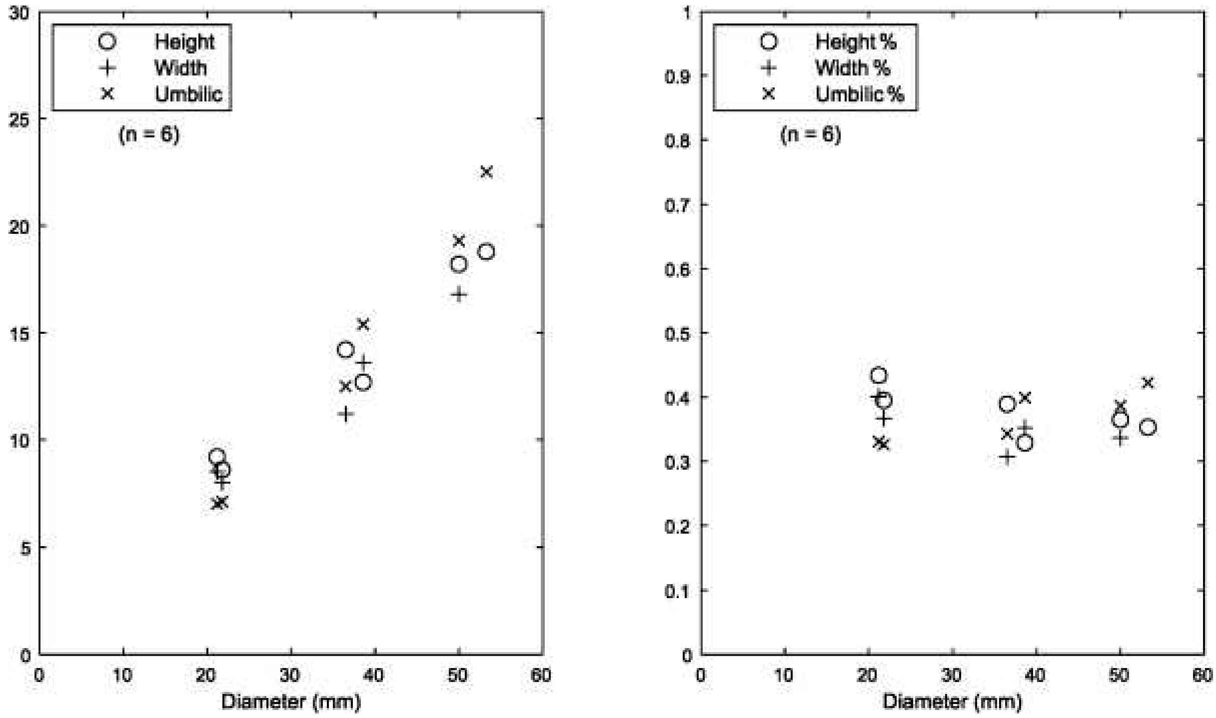
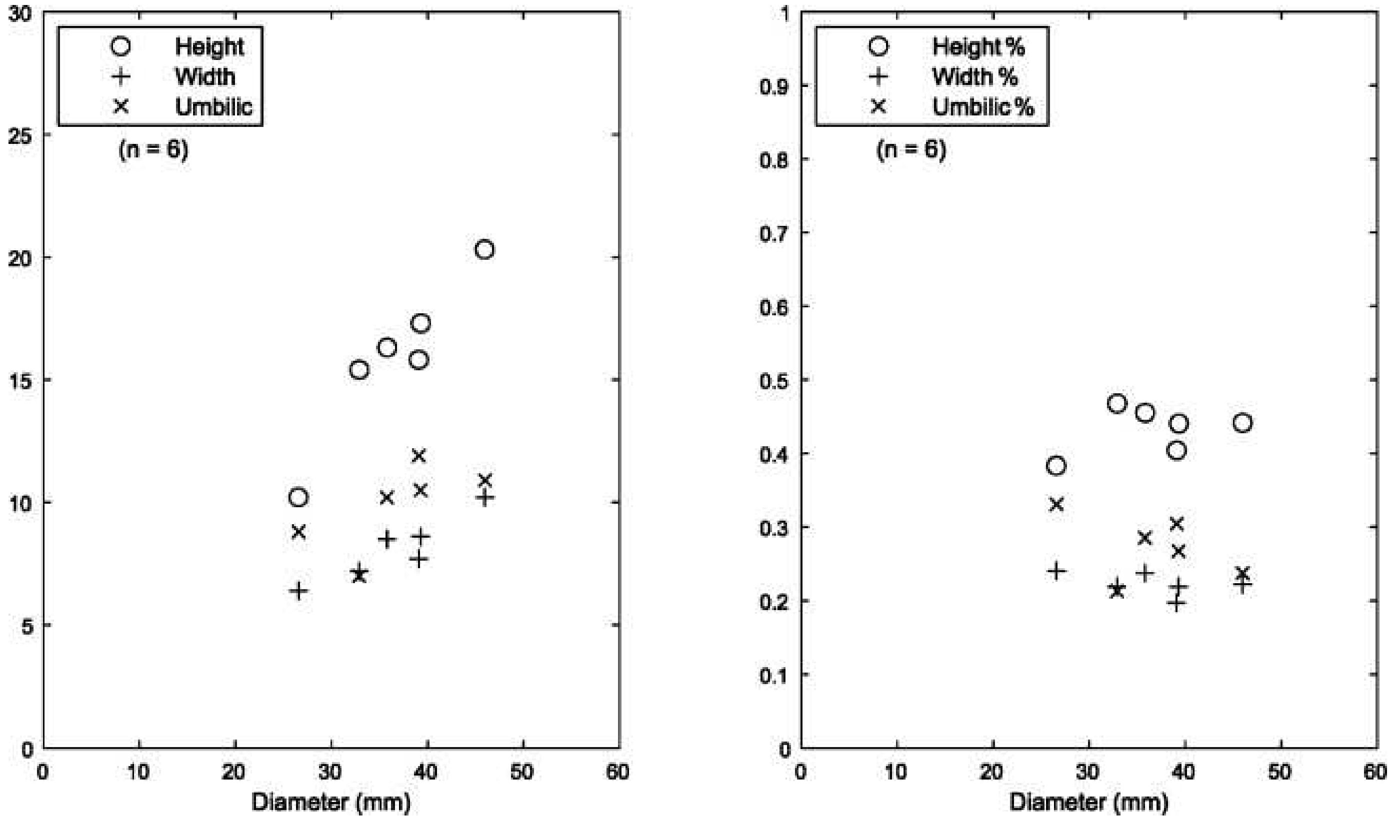


Supplementary Fig. S1. Composite section of the Smithian to Early Spathian of the Tulong area showing distribution of ammonoid faunas. Lithostratigraphic subdivisions after Brühwiler et al. (2009).



Supplementary Fig. S2. Scatter diagram of H, W, and U, and of H/D, W/D, and U/D for *Pseudoceltites multiplicatus* Waagen, 1895.



Supplementary Fig. S3. Scatter diagram of H, W, and U, and of H/D, W/D, and U/D for ?*Subflemingites compressus* nov. sp.

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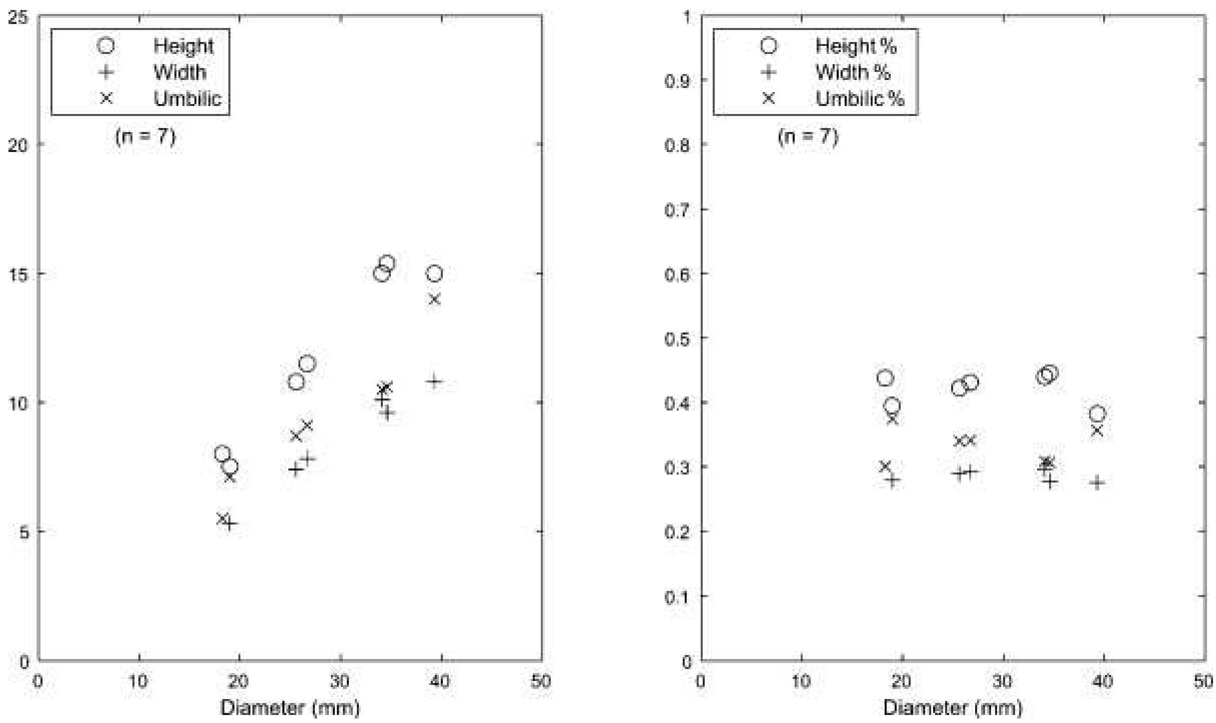

Supplementary Fig. S4. Scatter diagram of H, W, and U, and of H/D, W/D, and U/D for *Urdyceras tulongensis* nov. sp.

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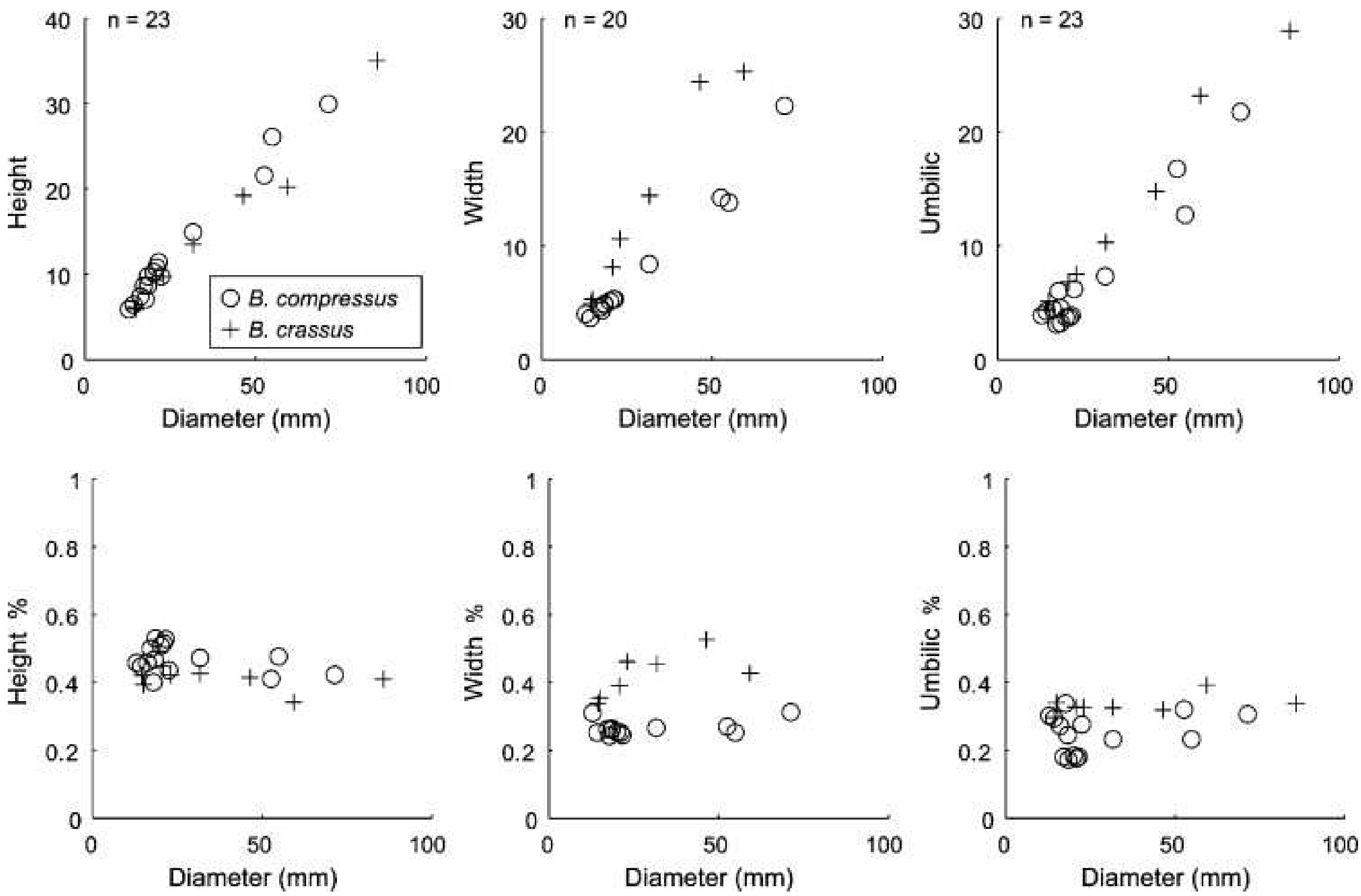
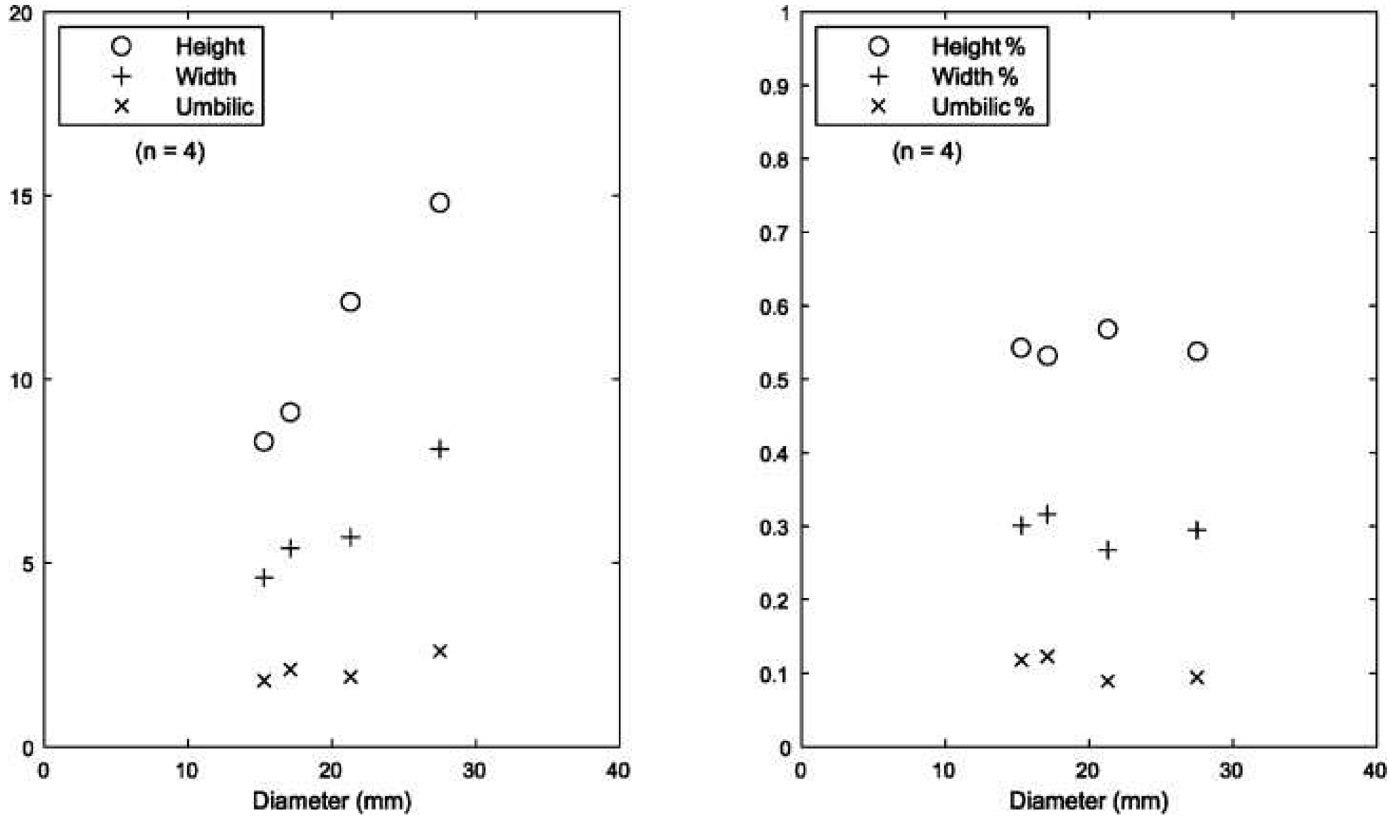


Supplementary Fig. S5. Scatter diagram of H, W, and U, and of H/D, W/D, and U/D for *Brayardites crassus* nov. gen., nov. sp. and for *B. compressus* nov. gen., nov. sp.



Supplementary Fig. S6. Scatter diagram of H, W, and U, and of H/D, W/D, and U/D for *Prionites involutus* nov. sp.

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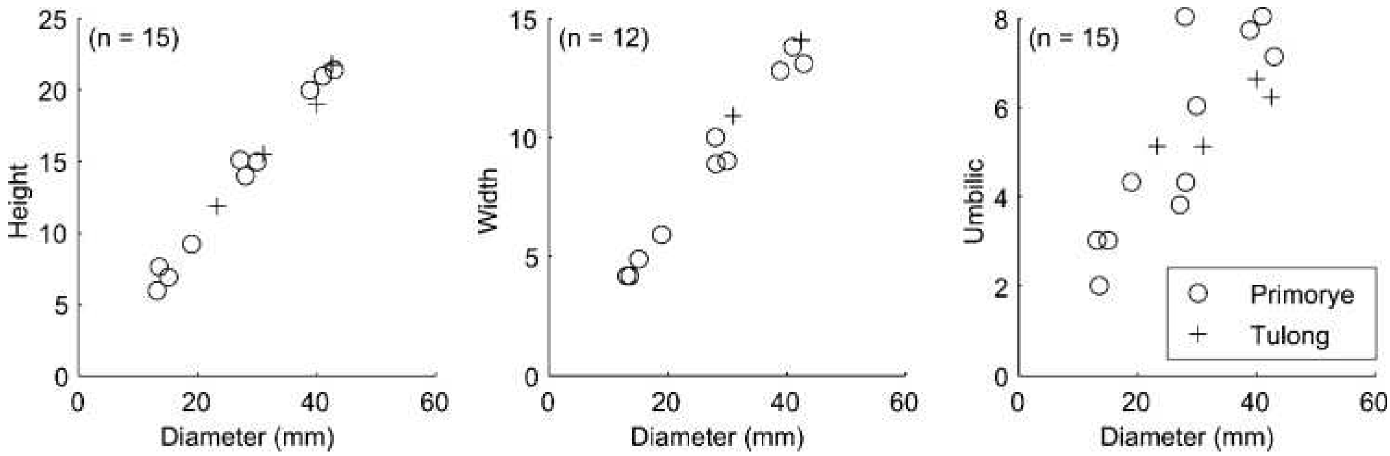

Supplementary Fig. S7. Scatter diagram of H, W, and U, and of H/D, W/D, and U/D for *Shigetaceras dunajensis* nov. gen. including the type material from Primorye illustrated by Zakharov (1968).