

AMMONOIDS AND THE TRIASSIC/JURASSIC BOUNDARY IN THE HIMALAYAS OF SOUTHERN TIBET

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Abstract: The sections of Germig in the Nyalam area, southern Tibet, provide a continuous exposure of ammonoid-bearing, uppermost Triassic and basal Jurassic strata. Eighteen species (three of them new) are described and illustrated: *Choristoceras marshi* Hauer, *C. aff. marshi*, *C. cf. nobile* Mojsisovics, *C. nyalamense* sp. nov., *Eopsiloceras germigense* sp. nov., *Pleuroacanthites aff. biformis* (Sowerby), *Rhacophyllites* sp., *Nevadaphyllites cf. psilomorphus* (Neumayr), *Neophyllites* sp. indet., *Neophyllites cf. biptychus* (Lange), *Psiloceras tibeticum* sp. nov., *P. calliphyllosum* (Neumayr), *Euphyllites cf. struckmanni* (Neumayr), *Discamphiceras pleuronotum* (Canavari), *Alsatites* spp., *Kammerkarites frigga*, and *K.* sp. The ammonoid fauna shows a strong affinity to that of the Northern Calcareous Alps, although diversity in the Calliphyllosum Zone is markedly lower. The ammonoid

succession across the Triassic/Jurassic boundary is subdivided into four zones: the Rhaetian Marshi, the basal Hettangian Tibeticum, the lower Hettangian Calliphyllosum, and the middle Hettangian Pleuronotum zones. It is the only known succession across the Triassic/Jurassic boundary in the Tethyan Realm that is not condensed. The Marshi and Calliphyllosum zones are correlated with the same zones in the Northern Calcareous Alps. The Tibeticum Zone, a new local zone, is transitional between the Marshi and the Calliphyllosum zones in that it yields both choristoceratids and psiloceratids. Its base is taken to mark the base of the Jurassic System in the eastern Tethys.

Key words: Triassic/Jurassic boundary, eastern Tethys Ocean, Tibetan Himalayas, ammonoids, biostratigraphy.

THE Triassic/Jurassic (T/J) boundary interval records one of the five largest extinctions in the Phanerozoic, which, in the case of the ammonoids, was followed by Early Jurassic recovery and spectacular success during the rest of the Mesozoic. However, because of eustatically low sea levels during the T/J interval, there are very few sites in the world where continuous stratigraphic sequences provide details of this event. It is also for this reason that a Global Stratotype Section and Point (GSSP) has not yet been agreed upon for the T/J boundary. In this context, much research effort is being devoted to documenting fully, and trying to correlate between, all the T/J sections that have been located so far (e.g. Golebiowski and Braunstein 1988; Hallam 1990; Hillebrandt 1994; Tipper *et al.* 1994; Warrington *et al.* 1994; Dagens 1996; Yin *et al.* 1999; Bloos and Page 2000; Pálfy and Dosztály 2000; Guex *et al.* 2004; Longridge *et al.* 2007).

The Germig site in the Nyalam area of the Himalayas of southern Tibet is the only locality in the eastern Tethys

Realm from which a T/J ammonoid succession has been reported. Previous work in this area has been summarized by Yin *et al.* (1999) and Yin and Enay (2000), and the lithological succession at Germig was discussed by Hallam *et al.* (2000). Here we present, for the first time, a detailed systematic treatment of the ammonoids from Germig. Previous collections have been re-examined and complemented with new samples, collected in 2003 and 2004, which permit a comprehensive biostratigraphic summary of the sections and their fauna.

GEOLOGICAL SETTING

The two stratigraphic sections at Germig (referred to as Sections A and B) are located adjacent to the China-Nepal Highway near the 5260 km road marker, at an altitude of 4400–4800 m above sea level (Text-fig. 1). Germig Section A is only 20–100 m east from the

highway, approximately 4400 m above sea level. Germig Section B is approximately 500 m east from Section A, at 4700–4800 m above sea level (Yin and Enay 2000; Text-fig. 1). Rhaetian and Hettangian sediments in the area reach a thickness of 30–40 m and comprise the Germig Formation, which is subdivided into eight informal units (Yin *et al.* 1999, with modifications by Hallam *et al.* 2000). The tectonic setting is complex and there are several faults in the study area. In Section B, where the beds are overturned, the Germig Formation is in fault contact with Upper Jurassic strata with angular unconformity. The slope between Germig Sections A and B, which is covered by abundant sandstone talus of the Norian Derirong Formation, is probably underlain by a fault because correlation indicates that the two sections are repeated (Yin 2005). The eight informal units of the Germig Formation present in Section A (Yin *et al.* 1999) are faulted at the top of the succession against the Norian Derirong Formation, as suggested by the recent discovery there of the Triassic ammonoid *Paratibetites* (Text-fig. 2). Lithostratigraphic correlation between Sections A and B is based on a conspicuous bivalve-rich bed (referred to as the ‘main bivalve bed’) from which 20 bivalve spe-

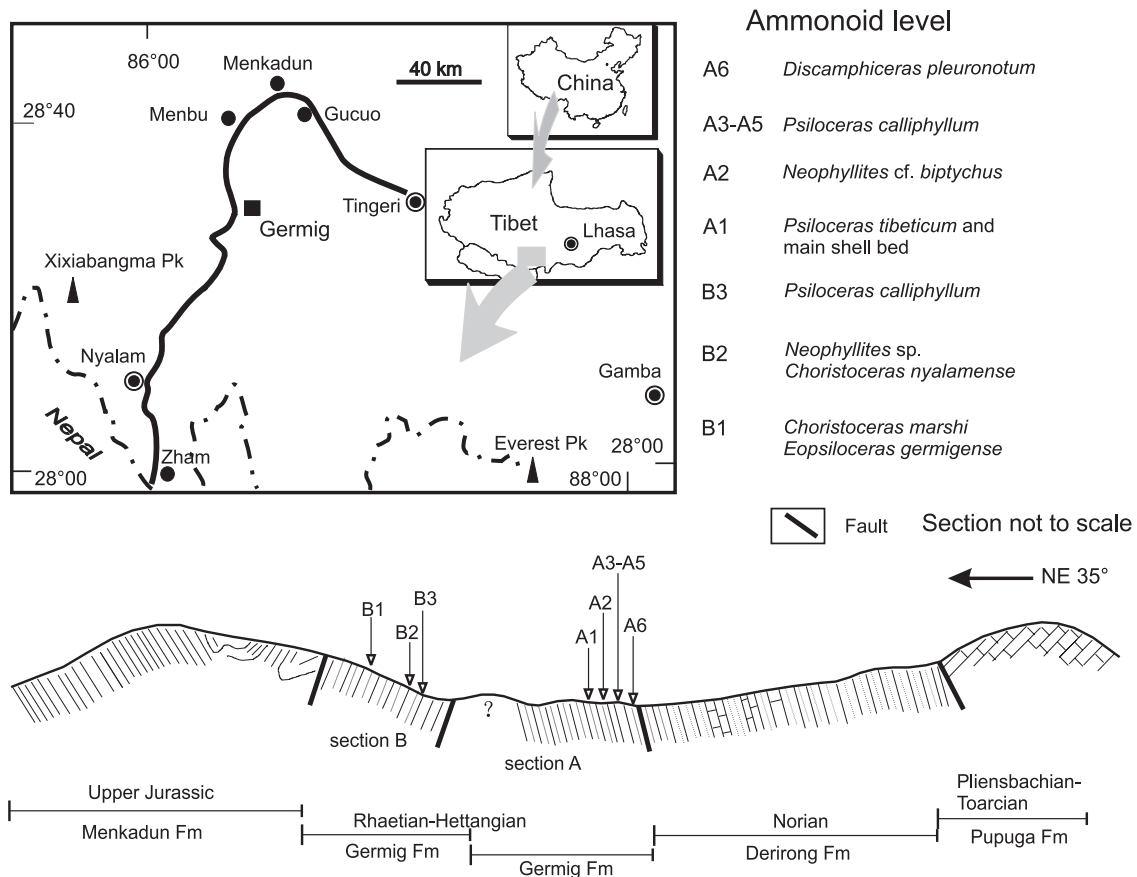
cies have been recently described (Yin and McRoberts 2006).

BIOSTRATIGRAPHY

Ammonoids were collected from nine levels (six in Section A and three in Section B). The stratigraphic distribution of the 18 taxa allows recognition of four assemblage zones, namely the Upper Rhaetian Marshi, the Lower Hettangian Tibeticum and Calliphyllyum, and the Middle Hettangian Pleuronotum zones.

Marshi Zone

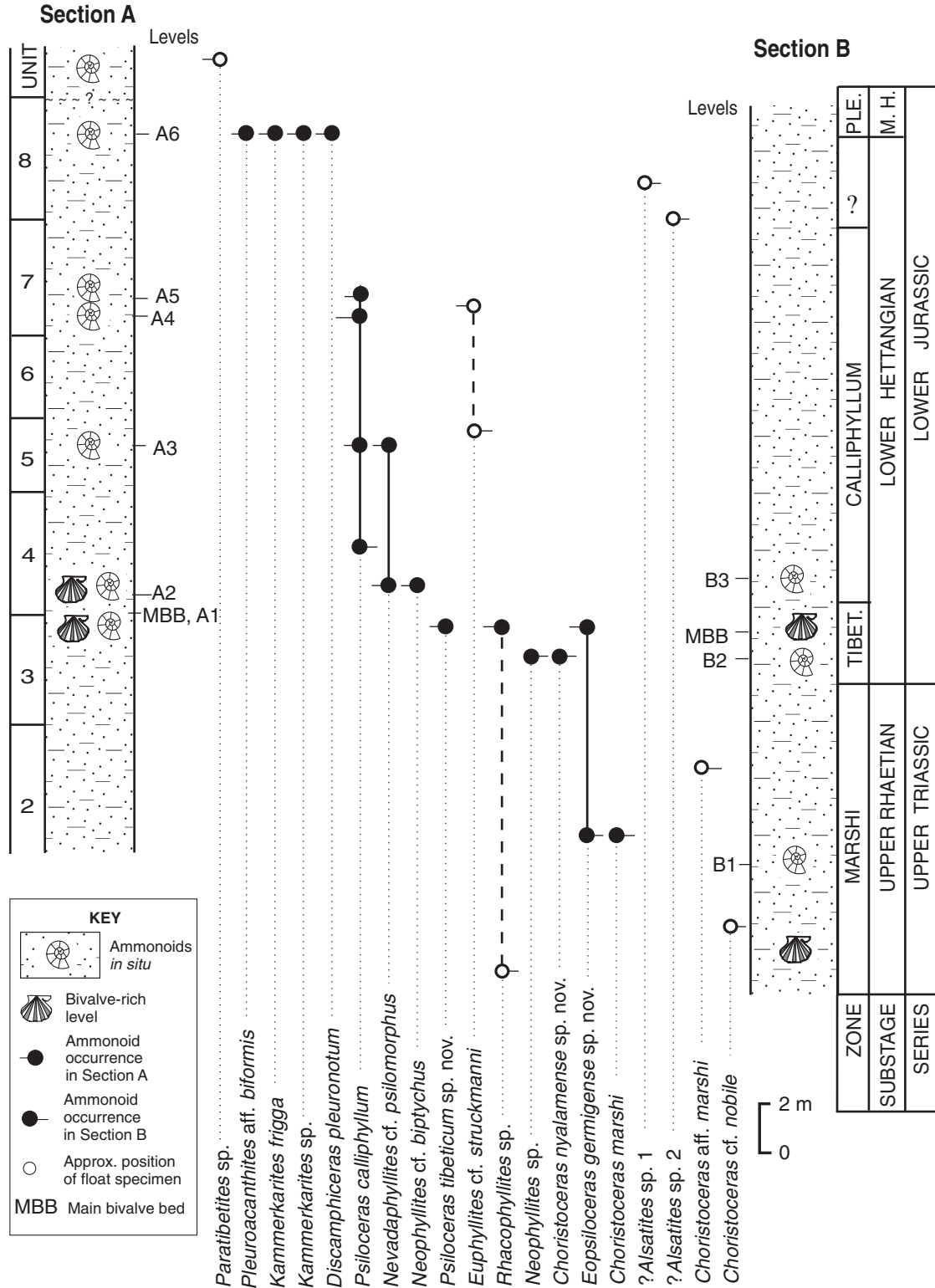
This zone is recognized in the lower part of Section B (level B1) where one bed yielded *Choristoceras marshi* and *Eopsiloceras germigense* sp. nov. A float specimen of *Choristoceras* aff. *marshi* was also found about 4 m above this bed. Below level B1, Upper Triassic bivalves such as *Krumbeckiella*, *Unionites*, *Palaeocardita* and *Cassianella* are abundant. The ammonoids *Tragorhacoceras* cf. *cylindricum*, *T.* cf. *psilo-*



TEXT-FIG. 1. Location of the Germig site and a schematic cross-section as seen from the China–Nepal highway.

morphum, *Placites* sp., *Arcestes* sp. and *Choristoceras* cf. *nobile* were collected as float specimens, but probably originated from these bivalve beds (Text-fig. 2).

In Europe, choristoceratids are known only from the Mediterranean Province. In the Koessen Formation of the Northern Calcareous Alps two ammonoid zones are dis-



TEXT-FIG. 2. Ammonoid biostratigraphy of the Germig sections in southern Tibet. Abbreviations: MBB., main bivalve bed; TIBET., Tibeticum Zone; PLE., Pleuronotum Zone; M. H., Middle Hettangian.

tinguished: the *Vandaites stuerzenbaumi* and *Choristoceras marshi* zones (Krystyn 1990). *Choristoceras marshi*, the index of the topmost Triassic, has not been collected previously from the Himalayas. In one aspect of ribbing, namely the ribs being inflated on the ventral shoulder, some specimens are similar to *Choristoceras crickmayi* Tozer (1979, p. 134, pl. 16.1, figs 4–6) from the topmost Triassic of western North America (Tozer 1979, 1994). In the Marshi Zone of Section B, one specimen with body chamber, referred to as *Choristoceras* aff. *marshi*, is more similar to the Austrian holotype of *Choristoceras marshi*, except for its nodose ribs on the inner whorls. A few fragmentary choristoceratid whorls in Section B show a tendency to uncoil and are compared with *Choristoceras nobile* (Mojsisovics 1893, p. 547, pl. 133, fig. 21; pl. 134, figs 9–14).

A new form, *Eopsiloceras germigense* sp. nov., is associated with *Choristoceras marshi* in Section B (Pl. 1, figs 28–30). It shows similar suture lines to, but is more evolute than, *Eopsiloceras planorboides* (Gümbel 1861, p. 410). According to Wiedmann (1970), *E. planorboides* ranges from the Upper Norian to the Rhaetian in Alpine Europe. In the Germig sections it is possible that *Eopsiloceras germigense* ranges from the Rhaetian up into the basal Hettangian, as is the case in Nevada (Guex 1995).

The ammonoid assemblage described above indicates the Marshi Zone of the uppermost Triassic; the subjacent Stuerzenbaumi Zone has not been proven. The uppermost part of the Marshi Zone, which is about 10 m thick, yielded a float specimen of *Choristoceras* aff. *marshi*.

Tibeticum Zone

This new local ammonoid zone, 4 m thick, is named after *Psiloceras tibeticum* sp. nov., with the base of the zone defined by the appearance of *Choristoceras nyalamense* and *Neophyllites* sp. indet., above the range of *Choristoceras marshi*.

It is characterized by an endemic assemblage of mostly new species found in both Sections A and B (Text-fig. 2), namely *Psiloceras tibeticum* sp. nov., *Neophyllites* sp. indet., *Choristoceras nyalamense* sp. nov., *Eopsiloceras germigense* sp. nov. and *Rhacophyllites* sp. The base of the Tibeticum Zone is defined only in section B, marked by the appearance of *Neophyllites* sp. and *Choristoceras nyalamense* above the disappearance of *Choristoceras marshi*.

The lower of the two ammonoid-bearing levels (B2 in Text-fig. 2) assigned to this zone occurs 8 m above the *Choristoceras*-bearing bed of the Marshi Zone (B1 in Text-fig. 2) and about 4 m above the highest float speci-

men of *C.* aff. *marshi*. The level occurs 1 m below the main bivalve bed in Section B and yields *Choristoceras nyalamense* sp. nov. and *Neophyllites* sp., marking the base of the Tibeticum Zone. The shell bed itself has not yielded any ammonites. The specimen attributable to *Neophyllites* sp. is identified by its suture line. Significantly, it was found together with the distinctive and endemic *C. nyalamense* in the same hand sample. Elsewhere in the world, *Neophyllites* occurs stratigraphically above *Choristoceras*, except in North America where, in the New York Canyon section, Nevada (USA), for example, *Choristoceras minutum* is associated with *Psiloceras* and (probably) *Neophyllites* (Guex *et al.* 2004).

The next higher ammonoid assemblage, which consists of *Psiloceras tibeticum* sp. nov., *Eopsiloceras germigense* sp. nov. and *Rhacophyllites* sp., occurs in the main bivalve bed of Section A.

The upper and lower assemblages differ in their taxonomic composition but share the co-occurrence of genera with latest Triassic and earliest Jurassic affinities. The two assemblages are stratigraphically situated between assemblages that correlate with the latest Triassic Marshi Zone and earliest Jurassic Calliphyllum Zone of the Western Tethys (Northern Calcareous Alps). A similar overlap of alleged Triassic and Jurassic forms in an equivalent stratigraphic position is known in New York Canyon (Guex 1995) and the Queen Charlotte Islands, British Columbia, Canada (Longridge *et al.* 2007); it is assigned to the Minutum Zone (*Minutus* Zone *auct.*) of the North American succession (Taylor *et al.* 2001).

The main bivalve bed in Sections A and B yields a rich, strongly endemic bivalve fauna that consists of 20 species (Yin and McRoberts 2006). This fauna is dominated by *Plagiostoma giganteum*, *Ctenostreon newelli* and *Persia hallami*. Triassic bivalve taxa found in the Marshi Zone (e.g. *Krumbeckiella*, *Palaeocardita*, *Cassianella* and *Unionites*) and the lower part of the Tibeticum Zone (e.g. *Palaeocardita*) do not range upward into the main bivalve bed. Significantly, some forms known from the basal Jurassic of England (e.g. *Chlamys valoniensis* and *Plagiostoma giganteum*) also occur in the main bivalve bed in the Tibeticum Zone and the basal Calliphyllum Zone (e.g. *Chlamys valoniensis*) in Section A. The lower part of the Tibeticum Zone is the only stratigraphic interval thus far known in the world where Triassic bivalves overlap with a psiloceratid form (*Neophyllites*), with exception of a tiny probable *Psiloceras* in the British Penarth Group (Donovan *et al.* 1989).

Calliphyllum Zone

The Calliphyllum Zone is represented by four ammonite-bearing horizons in Section A and one in Section B. It is

about 14 m thick and yields *Psiloceras calliphyllum* (Neumayr 1879), *Neophyllites* cf. *biptychus* (Lange 1941), *Nevadaphyllites* cf. *psilomorphus* (Neumayr 1879) and *Phylloceras* sp.

The lowermost ammonite horizon is situated 0.8 m above the main bivalve bed (with *Psiloceras tibeticum*) in Section A. Its fauna consists of *Neophyllites* cf. *biptychus* and *Nevadaphyllites* cf. *psilomorphus* in association with the bivalves *Liostrea tibetica* Yin and McRoberts, 2006 and *Chlamys valoniensis* (Defrance, 1825). *Psiloceras calliphyllum* does not appear at this level but Triassic bivalve taxa are missing. Suture lines are not preserved on the specimen of *Neophyllites* cf. *biptychus* so that the generic assignment is based on morphological characters only. *Nevadaphyllites psilomorphus* is an Alpine species known from the Calliphyllum Zone of the Alps.

Psiloceras calliphyllum first appears 2 m above the main bivalve bed in Section B (B3 in Text-fig. 2). In Section A, three horizons yield this species: at 6.5 m, 11 m and 12 m above the main bivalve bed (A3, A4 and A5 in Text-fig. 2). At the lowest level here (A3), *Psiloceras calliphyllum* is associated with *Nevadaphyllites* cf. *psilomorphus*.

The presence of *Psiloceras calliphyllum* identifies the Calliphyllum Zone both at Germig and in the Alps. A notable difference is the low diversity of the ammonite fauna in the Germig area compared with the highly diverse fauna of the Alpine Calliphyllum Zone. The apparent high diversity in the Alps could result from condensation. If this were so, other Alpine elements of the Calliphyllum Zone should be expected higher in the Germig section but they have not been found. Their absence could be a result of a stratigraphic gap but, more probably, there are ecological reasons. In contrast to the sedimentary environment represented in the Alpine sections, the lithology of the Germig sections indicates shallow marine conditions (Hallam *et al.* 2000).

The occurrence of the Marshi and Calliphyllum zones in the Germig sections suggests that the intervening Tibeticum Zone is an independent, new ammonoid zone for the eastern Tethys that corresponds to the transitional interval between the Marshi and Calliphyllum zones in the Alps where no ammonites are known thus far.

Uncertain interval

Above *Psiloceras calliphyllum* in Section B, three float specimens of evolute, densely ribbed ammonites have been found. Suture lines are not visible; therefore, a confident generic assignment is difficult. Morphologically, *Alsatites* s.l. seems to be more probable than *Caloceras* and this would indicate the Alpine Megastoma Zone (mainly Middle Hettangian). These ammonites may represent a higher interval whose stratigraphic position is still unknown.

Pleuronotum Zone

This zone is proposed for the ammonoid assemblage collected from a single, 0.3-m-thick bed at the top of unit 8 in Section A. This level yielded an ammonite fauna that consists of *Discamphiceras pleuronotum* (Canavari 1882), *Pleuroacanthites* aff. *biformis* (Sowerby 1831), *Kammerkarites frigga* (Wöhner 1884) and *Kammerkarites* sp. This fauna indicates the Middle Hettangian.

A tiny ammonite specimen from the *D. pleuronotum*-bearing bed is compared with *Pleuroacanthites biformis*. The type region of *P. biformis* is La Spezia in Italy (Canavari 1882, 1888) where the ammonite fauna is mainly Upper Hettangian. In the Alps, the species occurs in the Megastoma Zone (Middle and basal Upper Hettangian, Wöhner 1895, p. 252) and in Nevada it is known from the Middle Hettangian (Guex 1995). In Tibet, *Kammerkarites frigga* occurs in the same bed as *Pleuroacanthites* aff. *biformis*, as does a larger form of *Kammerkarites*. The genus *Kammerkarites* is a characteristic element of the Middle Hettangian Megastoma Zone in the Alps.

Significance of biostratigraphical results

In summary, the ammonite fauna of the Germig sections undoubtedly represents the uppermost Triassic and lowest Jurassic. The Upper Rhaetian, the Lower and at least a part of the Middle Hettangian are represented by the Marshi, Tibeticum, Calliphyllum and Pleuronotum zones. The ammonite fauna shows strong affinity to that of the Mediterranean Province, particularly the Alps, but its diversity is strikingly low and most species are represented by only one or two specimens. Of course, further collecting in this remote area is likely to yield more taxa and shed more light on correlation details.

The sections studied yield the first ammonite fauna spanning the T/J boundary interval in the Tethyan Realm that is not condensed. Of particular significance is the new Tibeticum Zone, which as yet has no equivalent in the Western Tethys. The co-occurrence of *Choristoceras* and *Neophyllites*, and the first appearance of *Psiloceras* immediately above, implies that this zone approximates the T/J boundary in the sections. Although probably represented by endemic species in Tibet, all three genera offer significant correlation potential with T/J boundary sections elsewhere in the world. *Psiloceras* and *Neophyllites* are the earliest Hettangian genera in both Europe and North America, whereas *Choristoceras*, traditionally regarded as youngest Triassic in age, is now known to occur together with *Psiloceras* in both North and South America (Hillebrandt 2000; Guex *et al.* 2004; Longridge *et al.* 2007). Although no internationally accepted boundary stratotype (GSSP) for the base of the Jurassic has yet been agreed

upon, we tentatively regard the Tibeticum ammonoid zone as a basis for recognizing the T/J boundary in the Himalayas.

SYSTEMATIC PALAEOLOGY

The fossils described in this paper are housed in the museum collection of the China University of Geosciences in Beijing (CUGB). The quality of preservation varies considerably but many specimens are preserved in fine-grained sandstone as both internal and external moulds, original shell material having been dissolved. Ammonoid specimen measurements (Tables 1–4), in millimetres, follow the terminology of Smith (1986). N, specimen catalogue numbers (all are prefixed by A2004CUGB); D, shell diameter at which measurements were made; UD, umbilical diameter; $U = UD/D$; WW, whorl width; WH, whorl height; $WWWH = WW/WH$; PRHW, primary ribs per half whorl.

Order AMMONOIDEA Zittel, 1884

Suborder CERATITINA Hyatt, 1884

Superfamily CHORISTOCERATOIDEA Hyatt, 1900

Family CHORISTOCERATIDAE Hyatt, 1900

Genus CHORISTOCERAS Hauer, 1865

Type species. *Choristoceras marshi* Hauer, 1865.

Choristoceras marshi Hauer, 1865 Plate 1, figures 1–9; Text-figure 3C; Table 1

- * 1865 *Choristoceras marshi* Hauer, p. 654, pl. 1, figs 1–8.
1893 *Choristoceras marshi* Hauer; Mojsisovics, p. 560, pl. 135, figs 13–29; pl. 136, figs 6–8.
1895 *Choristoceras marshi* Hauer; Pompeckj, p. 13L, pl. 1, figs 3a–c, 4a–b, 5a–b.
1973 *Choristoceras marshi* Hauer; Wiedmann, p. 237, pl. 1, fig. 4a–c, text-fig. 2.

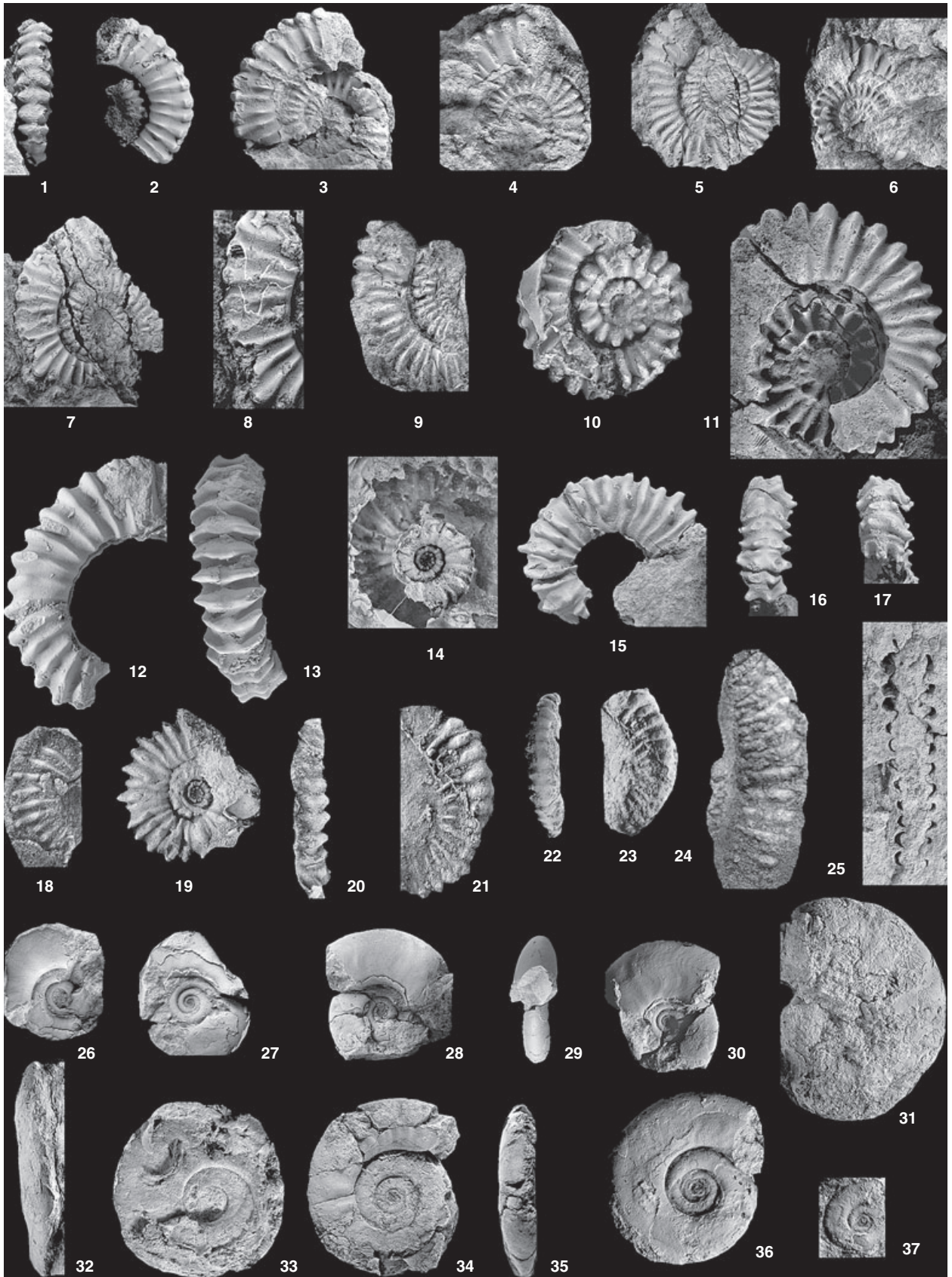
Material. Seven specimens, including two phragmocones.

Description. Evolute and compressed, planispirally coiled, the flanks are rather flat, whorl height consistently exceeds whorl width during ontogeny. Ribs are straight, rectiradiate to slightly rursiradiate, crossing the venter where there is a median depression. On the umbilical part of the flank, ribs are sharp and narrow; they become blunt and broader on the ventral part and are conspicuously inflated on the ventrolateral shoulder. The interspaces between the ribs are usually wider than the ribs. The number of ribs per half a whorl varies between 14 and 18. The body chamber is slightly more than half a whorl long, and no tendency of uncoiling is observed. The suture line consists of external, lateral and umbilical lobes; the saddles are rounded and undivided; only the lateral lobe has a single large indentation on the middle and outer whorls.

EXPLANATION OF PLATE 1

- Figs 1–9. *Choristoceras marshi* Hauer, 1865, Marshi Zone, Level B1, Section B. 1–3, 1011. 1, ventral view of body chamber. 2, lateral view of body chamber. 3, lateral view of body chamber and inner whorls. 4, 1012, lateral view. 5, 1013 (latex cast), lateral view of external mould. 6, 1014 (latex cast), lateral view. 7–8, 1015. 7, lateral view. 8, detail of whorl showing suture; $\times 2$. 9, 1016, lateral view.
- Figs 10–13. *Choristoceras* aff. *marshi* Hauer, 1865, Marshi Zone, *ex situ* above Level B1, Section B, 1017. 10, lateral view of inner whorls (latex cast). 11, lateral view of body chamber and external mould of inner whorls (= Yin and Enay 2000, fig. 2/11). 12, lateral view of body chamber. 13, ventral view of body chamber.
- Figs 14–19. *Choristoceras nyalamense* sp. nov., Tibeticum Zone, Level B2, Section B. 14, 10181, paratype (latex cast), lateral view of inner whorls. 15–17, 1018, holotype. 15, lateral view of body chamber (= Yin and Enay 2000, fig. 2/13). 16, ventral view of body chamber. 17, ventral view showing the last suture. 18, 10121, paratype (latex cast), lateral view of whorl fragment. 19, 10120, paratype (latex cast), lateral view of inner whorls.
- Figs 20–25. *Choristoceras* cf. *nobile* Mojsisovics, 1893, Marshi Zone, *ex situ* below Level B1, Section 1. 20–21, 10122 (latex cast). 20, ventral view of whorl fragment (= Yin and Enay 2000, fig. 2/16). 21, lateral view (= Yin and Enay 2000, fig. 2/17). 22–23, 10123 (latex cast). 22, ventral view of whorl fragment. 23, lateral view. 24, 10125 (latex cast), lateral view of a whorl fragment (= Yin and Enay 2000, fig. 2/17). 25, 10124, ventral view of a whorl fragment, cut by a fracture plane.
- Figs 26–30. *Eopsiloceras germigense* sp. nov., Tibeticum Zone, Level A1, Section A. 26, 2011, paratype (latex cast), lateral view. 27, 2012, paratype (latex cast), lateral view. 28–30, 2015, holotype, Marshi Zone, Level B1, Section B. 28, 30, lateral views. 29, ventral view.
- Figs 31–32. *Nevadaphyllites* cf. *psilomorphus* (Neumayr, 1879), Calliphyllum Zone, Level A2, Section A, 2016. 31, lateral view of phragmocone. 32, ventral view.
- Fig. 33. *Rhacophyllites* sp., Tibeticum Zone, Level A1, Section A, 2018 (latex cast), lateral view of phragmocone (= Yin *et al.* 1999, fig. 3/1).
- Figs 34–35. *Neophyllites* cf. *biptychus* Lange, 1941, Calliphyllum Zone, Level A2, Section A, 2021. 34, lateral view (= Yin and Enay 2000, fig. 2/9). 35, ventral view (= Yin and Enay 2000, fig. 2/8).
- Figs 36–37. *Neophyllites* sp. indet., Tibeticum Zone, Level B2, Section B, 2020. 36, lateral view (= Yin and Enay 2000, fig. 2/15); $\times 2$. 37, lateral view (latex cast of external mould).

Specimen numbers prefixed A2004CUGB. All $\times 1$ except where stated.



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Remarks. The Germig material compares well with the holotype of *Choristoceras marshi* from Austria. The coiling is similar and so is the suture line (see Wiedmann 1973, p. 11, figs 2, 4). The lateral lobes are indented on the middle and outer whorls, but unindented on the inner whorls.

The Tibetan *C. marshi* differs from *C. crickmayi* Tozer of western North America mainly by the ribbing on its outer whorls (Tozer 1994, p. 267, pl. 147, figs 19–22; p. 644, fig. 120a–c). On the inner whorls, however, the suture lines as well as the number of ribs are similar to *C. crickmayi*, so that small specimens are possibly confused. In the eastern Tethys, choristoceratids have been known since the work of Welter (1914). Two species of *Choristoceras* were described from Timor [*C. indoaustralicum* Welter and *C. cf. ammonitifforme* Gümbel (Welter 1914)] but both appear to be more involute than the Tibetan form, and their ribs are sharper and less densely spaced (Welter 1914, pl. 28, figs 5–6, 8–10; pp. 145–147). *Choristoceras marshi* is different from *C. aff. marshi* (see below) because no nodose ribbing is developed on the inner whorls, where, instead, slender and straight ribs are present.

Occurrence. Level B1, Section B (Marshi Zone)

Choristoceras aff. marshi Hauer, 1865

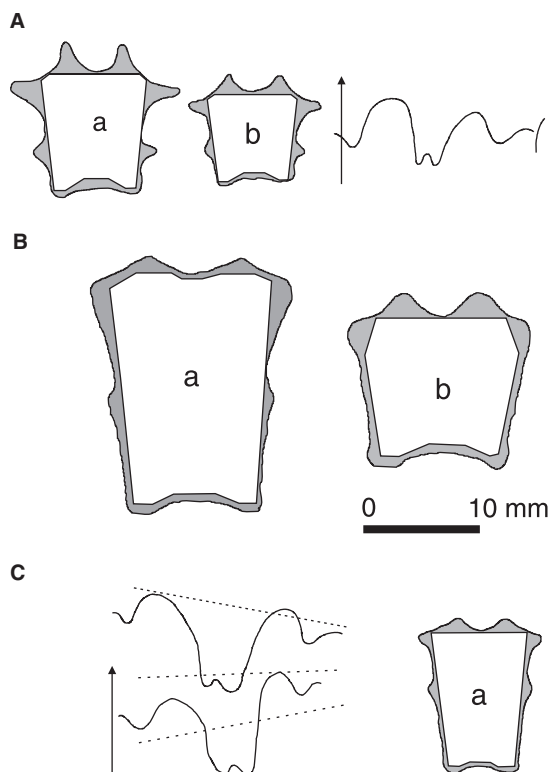
Plate 1, figures 10–13; Text-figure 3B; Table 1

pars 2000 *Choristoceras cf. marshi* Hauer, 1865, Yin and Enay, p. 605, fig. 2/11–12; *non* p. 606, fig. 3/1–2.

Material. One float specimen, last whorl with body chamber, middle and inner whorls preserved as external mould.

Remarks. The body chamber of this specimen is well preserved but no suture line is visible. The middle and inner whorls (studied as a latex cast of the mould) exhibit stout, nodose ribs. The body chamber whorl is similar to that of the holotype of *Choristoceras marshi* (Wiedmann 1973, p. 11, fig. 4) in ribbing style but the density on the inner whorls is much less (7–8 ribs per half a whorl). During ontogeny, the outline of the whorl section varies from square to compressed rectangular (Text-fig. 3B). The present specimen was collected between the horizons of *Choristoceras marshi* and *C. nyalamense*. Judging from the ribbing patterns, *C. aff. marshi* seems to be an intermediate form between these two species. The other specimen referred to as *C. cf. marshi* in Yin and Enay (2000, p. 606, fig. 3/1–2) is misidentified; its suture line indicates *Kammerkarites* (see below).

Occurrence. Collected as a float specimen about 4 m above level B1 in Section B (Marshi Zone).



TEXT-FIG. 3. Whorl cross-section and suture line of *Choristoceras* from Section B at Germig. A, *Choristoceras nyalamense* sp. nov., 1018, holotype, suture drawn at WH = 7 mm. B, *Choristoceras aff. marshi*, 1017. C, *Choristoceras marshi*, 1015, suture drawn at WH = 9.5 mm. Cross-sections labelled 'a' drawn near to aperture, those labelled 'b' drawn at middle whorl. Specimen numbers prefixed A2004CUGB.

Choristoceras nyalamense sp. nov.

Plate 1, figures 14–19; Text-figure 3A; Table 1

2000 *Choristoceras* sp. n. indet., Yin and Enay, p. 605, fig. 2/13.

Derivation of name. After Nyalam, the region in southern Tibet where the type material was collected.

Types. The holotype is specimen A2004CUGB1018 (Pl. 1, fig. 15), which has a well-preserved body chamber but the inner whorls are preserved as an external mould. The specimens A2004CUGB10121 (Pl. 1, fig. 18) and 10120 (Pl. 1, fig. 19) are paratypes; the latter is an external mould that occurs in same piece of rock as *Neophyllites* sp. indet.

Type horizon. The holotype is from level B2 in section B.

Material. Only the type material is known.

Diagnosis. Relatively involute, ribbing irregular in strength and spacing, with scattered secondary ribs; two

rows of irregularly strong tubercles on either flank, lateral lobe strongly indented.

Description. The early whorls are coiled planispirally. The body chamber is slightly more than half a whorl long. The whorls are thick and strongly ribbed. The ribs are straight, rectiradiate to slightly rursiradiate and cross the venter; their strength varies. Interspaces between the ribs are also variable but narrower than the ribs; occasionally, the secondary ribs are intercalated and much more feeble. On the inner whorls, ribs are swollen and nodose, becoming sharper and stronger on the body chamber. There are four rows of tubercles on the flanks; the inner row of tubercles gradually shifts from the middle to the outer flank; the outer row of tubercles is on the ventrolateral shoulder. The ventral furrow is strong and bordered by ventrolateral tubercles. Whorl height is equal to whorl width in the body chamber; the outline of the whorl section is rounded-square, and becomes slightly compressed on the outer whorls (Text-fig. 3A). The septal suture line visible on the holotype consists of external, lateral and umbilical lobes; the lateral lobe is strongly indented.

Remarks. Taking into account the conspicuous rows of tubercles, stout ribs on earlier whorls and the sulcate venter, the specimens represent a new species of *Choristoceras* that differs from other choristoceratids occurring below the horizon of the new species (Text-fig. 3). The suture line of the specimen compares well with that of *C. marshi* from Section B (Text-fig. 3C).

Two species of *Choristoceras* are known from Timor: *C. indoaustralicum* Welter and *C. cf. ammonitifforme* Gümbel (Welter 1914). Both of these appear to be more involute than the Tibetan form, and the less densely spaced ribs on the inner whorls are sharper and not nodose (Welter 1914, pl. 28, figs 5–6, 8–10; pp. 145–147). *C. clamathense* Smith from California (Smith 1927, p. 97, pl. 59, figs 12–13) is also characterized by strong tubercles or spines, but it is more compressed and involute than the Tibetan species and, in contrast to the latter, the outer row of tubercles on the Californian specimen is much smaller.

Occurrence. Level B2 from 1 m below the main bivalve bed in Section B (Tibeticum Zone).

Choristoceras cf. nobile Mojsisovics, 1893

Plate 1, figures 20–25

- cf. 1893 *Choristoceras nobile* Mojsisovics, p. 547, pl. 133, fig. 21; pl. 134, figs 9–14.
 1985 *Choristoceras cf. nobile* Mojsisovics; Prinz, p. 168, pl. 1, fig. 6.
 cf. 1994 *Choristoceras nobile* Mojsisovics; Tozer, p. 268, pl. 148, figs 1–10.
 2000 *Choristoceras* sp.; Yin and Enay, p. 605, figs 16–17.

Material. Four specimens, three of which are external moulds.

Remarks. All specimens are fragments of detached body chambers so that no suture lines can be seen. Ribs are rectiradiate, sharp with tubercles on the ventrolateral area, and cross the nearly tabulate venter. Conspicuous detachment clearly differentiates these specimens from the other specimens of *Choristoceras* in Section B referred to *C. marshi*, *C. aff. marshi* and *C. nyalamense* sp. nov. Coiling and the presence of nodes in the Tibetan material are comparable with the Austrian *C. nobile* Mojsisovics (1893) but the poor preservation precludes confident identification.

Occurrence. Collected as float from below and near level B1 in Section B (Marshi Zone).

Suborder PHYLLOCERATINA Arkell, 1950
 Superfamily PHYLLOCERATOIDEA Zittel, 1884
 Family USSURITIDAE Hyatt, 1900

Genus EOPSILOCERAS Spath, 1930

Type species. *Ammonites planorboides* Gümbel, 1861.

TABLE 1. Measurements of *Choristoceras* species in mm.

Taxa	N	D	UD	U	WW	WH	WW/WH	PRHW	Figures
<i>Choristoceras marshi</i>	1011	30	14.5	0.48	8	11.5	–	–	Pl.1, fig. 1
	1012	28.5	15	0.52	–	–	–	–	Pl.1, fig. 4
	1013	36.5	18	0.49	–	11.5	–	19	Pl.1, fig. 5
	1014	28	15	0.53	–	9	–	–	Pl.1, fig. 6
	1015	32	18	0.56	6.5	10.5	0.62	18	Pl.1, fig. 7
<i>C. aff. marshi</i>	1017	47	22	0.47	12	14.5	0.83	16	Pl.1, figs 10–13
<i>C. nyalamense</i>	1018	30	11.5	0.38	10	11	0.91	11	Pl.1, fig. 15
	10121	27.5	11	0.4	–	9	–	12	Pl.1, fig. 18

Remarks. The allocation of *Eopsiloceras* to the Psiloceratidae by Guex (1995) seems unjustified on the basis of the lituid internal lobe of *Eopsiloceras* (Wiedmann 1970, pp. 934–935, text-fig. 4d).

Eopsiloceras germigense sp. nov.

Plate 1, figures 26–30; Text-figure 4A; Table 2

Derivation of name. After the village of Germig close to the outcrops where the type material was collected.

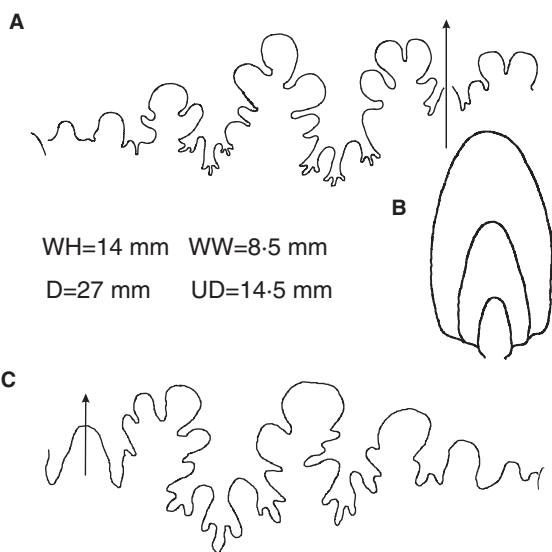
Types. The holotype is a nearly complete specimen with body chamber (A2004CUGB2015; Pl. 1, figs 28–30). The paratypes are external moulds (A2004CUGB2011, Pl. 1, fig. 26, and 2012, Pl. 1, fig. 27).

Type horizon. The holotype is from level B1 in section B.

Material. The three type specimens only.

Diagnosis. Smooth, involute, venter highly arched, umbilicus narrow, deep and steep.

Description. Shell is fairly inflated, thick, involute; body chamber is at least half a whorl; smooth except for feeble sinuous striae. The umbilicus is steep and deep. The whorl height exceeds width; inner whorls are more compressed than outer ones; the whorl section is rounded triangular in outline, the venter is smooth and arched. Septal suture line (at 8 mm whorl height) consists of external, lateral and three umbilical lobes. The lateral and first umbilical lobes possess accessory lobes that are further subdivided into three; the saddles are deeply indented.



TEXT-FIG. 4. Comparison of whorl cross-section and suture line of *Eopsiloceras germigense* sp. nov. and *Eopsiloceras planorboides* (Gümbel). A, A2004CUGB2015, holotype, suture line of *E. germigense*. B, whorl section of same specimen. C, suture line of *E. planorboides* after Wiedmann (1970).

Remarks. This is the first record of *Eopsiloceras* in Tibet. Its suture line compares well with the Austrian species *Eopsiloceras planorboides* (Gümbel, 1861), illustrated by Wiedmann (1970, pl. 4, figs 3–4) but the Tibetan specimen is more involute and the whorl section is more triangular. In particular, its inner whorl is more compressed than in the Austrian species.

Eopsiloceras was once thought to be restricted to the Norian (Arkell *et al.* 1957) but Wiedmann (1970) indicated that it also occurs in the Rhaetian. *Eopsiloceras germigense* in our material supports the Rhaetian occurrence of the genus, because it co-occurs with *Choristoceras marshi*. In Tibet, as in Nevada, it appears to range as high as the basal Hettangian (Guex 1995).

Occurrence. Level B1 (Type horizon), Section B (Marshi Zone) and Level A1, Section A (Tibeticum Zone).

Family DISCOPHYLLITIDAE Spath, 1927

Genus RHACOPHYLLITES Zittel, 1884

Type species. *Ammonites neojurensis* Quenstedt, 1846.

Rhacophyllites sp.

Plate 1, figure 33; Table 2

1999 *Rhacophyllites* sp.; Yin *et al.*, p. 128, fig. 3/1.

Material. Three specimens.

Remarks. Two specimens exhibit a juraphyllitid-style suture line with a diphylic first lateral saddle and a triphylic adjacent saddle. The figured specimen from Section A is relatively evolute and compressed; the whorl flank is flat and smooth. It is similar to the Italian *Rhacophyllites stella* (Sowerby, 1823) figured by Canavari (1888, p. 91, pl. 2, figs 1–5). Traditionally, *Rhacophyllites* is regarded as Triassic (Tozer 1981) but here, as also in Nevada (Guex *et al.* 1998), it occurs in transitional T/J faunas in beds considered to be Jurassic.

Occurrence. One specimen in the main bivalve bed (level A1) of Section A (Tibeticum Zone). Two specimens were found loose in Section B below level B1 (Marshi Zone).

Family JURAPHYLLITIDAE Arkell, 1950

Genus NEVADAPHYLLITES Guex, 1980

Type species. *Nevadaphyllites compressus* Guex, 1980.

Nevadaphyllites cf. *psilomorphus* (Neumayr, 1879)

Plate 1, figures 31–32; Table 2

cf. 1879 *Phylloceras psilomorphum* Neumayr, p. 21, pl. 2, fig. 4.*Material.* Two specimens.

Remarks. Both specimens are highly involute phragmocones with compressed whorls that are slightly convergent towards the venter; sculpture is lacking. The suture line is only partly preserved but undoubtedly phylloceratid. *Nevadaphyllites* was established on the basis of a North American species, but two Alpine species have also been included in the genus (Guex 1980). The present Tibetan specimens are closer to the Alpine *Nevadaphyllites psilomorphus* on the basis of the flanks that are convergent towards the venter.

Occurrence. Levels A2 and A3 in Section A (Calliphylum Zone).

Suborder LYTOCERATINA Hyatt, 1889

Superfamily LYTOCERATOIDEA Neumayr, 1875

Family PLEUROACANTHITIDAE Hyatt, 1900

Genus PLEUROACANTHITES Canavari, 1888

Type species. *Ammonites bififormis* Sowerby, 1831.

Pleuroacanthites aff. *bififormis* (Sowerby, 1831)

Text-figures 5E–G, 6; Table 4

- aff. 1831 *Ammonites bififormis* Sowerby, p. 333, fig. 67, non fig. 65.
 aff. 1882 *Lytoceras* (?) *biforme* Sowerby; Canavari, p. 156, pl. 17, figs 8–11.
 aff. 1882 *Lytoceras* (?) *subbiforme* Sowerby; Canavari, p. 157, pl. 17, fig. 12.
 aff. 1888 *Pleuroacanthites bififormis* (Sowerby); Canavari, p. 121, pl. 3, figs 8–12.

aff. 1894 *Pleuroacanthites bififormis* (Sowerby); Wähner, p. 34, pl. 3, fig. 2; pl. 4, figs 1–3; pl. 5, figs 1–7; pl. 9, figs 3–4.

aff. 1995 *Pleuroacanthites bififormis* (Sowerby); Guex, p. 42, pl. 23, figs 5–6, pl. 24, figs 13–14; text-fig. 17.
 1999 *Psilophyllites* sp.; Yin *et al.*, fig. 3/8.

Material. One external mould with part of an internal mould of a body chamber attached.

Description. This is a small external mould that shows a part of the body chamber whorl that is strongly depressed; it has nodes on the innermost whorls and a high umbilical wall (Text-fig. 5E–G). It is relatively evolute; whorl width significantly exceeds whorl height, and the flanks meet the venter at a rounded right angle. The almost flat venter is wide and smooth. The ribs are restricted to the umbilical part of the flanks. The lateral bulges are regularly and widely spaced. The inner bulges are more nodose, straight, and become narrow and sinuous on the outer whorls where they are widely spaced (c. 9–10 per complete whorl). The suture line is unknown.

Remarks. Among the Hettangian lytoceratids, *Pleuroacanthites* is the only genus that includes dwarf forms. *Pleuroacanthites bififormis* was first described from La Spezia, Italy (Canavari 1882, 1888), then from the Northern Alps (Wähner 1894) and at Fonsjoch in Austria (Lange 1952, pl. 11, fig. 4); it is now also known from North America (Guex 1995). The Tibetan specimen is more similar to the small forms from the Northern Alps (Wähner 1894, pl. 5, figs 3–5). In comparison with the Italian specimens (Canavari 1882, pl. 17, figs 8–12) the whorl is more depressed. The North American *P. bififormis* shows the same ribbing (Guex 1995, p. 42, pl. 23, figs 5–6) but is much larger than the Tibetan *P. aff. bififormis*, and its venter is not as flat. The Tibetan specimen was incorrectly referred to *Psilophyllites* sp. in an earlier work (Yin *et al.* 1999). *Psilophyllites* differs from *Pleuroacanthites* by its smooth and compressed shell.

This is the first record of *Pleuroacanthites* from the eastern Tethys. It may be interpreted as a biogeographical link between the western Tethys and the eastern Pacific, indicating migration via the Himalayan basin of the eastern Tethys.

TABLE 2. Measurements of three species in mm.

Taxa	N	D	UD	U	WW	WH	WW/WH	PRHW	Figures
<i>Eosiloceras</i>	2011	23.5	8.5	0.36	–	–	–	–	Pl.1, fig. 26
<i>germigense</i>	2012	22.5	9	0.4	–	–	–	–	Pl.1, fig. 27
	2015	27	14.5	0.54	8.5	14	0.61	–	Pl.1, fig. 28
<i>Nevadaphyllites</i> cf. <i>psilomorphus</i>	2016	46	–	–	8.5	–	–	–	Pl.1, fig. 31
<i>Rhacophyllites</i> sp.	2018	34.5	11	0.32	–	–	–	–	Pl.1, fig. 33



TEXT-FIG. 5. A–D, *Euphyllites* cf. *struckmanni* (Neumayr), A2004CUGB4025, Calliphyllum Zone (?), *ex situ*, Section B. A, lateral view of specimen with body chamber. B, ventral view of middle whorl. C, lateral view of middle whorl. D, lateral view of fragment of middle whorls. E–G, *Pleuroacanthites* aff. *biformis* (Sowerby), A2004CUGB3026 (latex cast), Pleuronotum Zone, Level A6, Section A. E, lateral view of nucleus. F, lateral view; $\times 3$. G, ventral view; $\times 3$. All $\times 1$ except where stated.

Occurrence. Level A6, Section A (Pleuronotum Zone).

Suborder AMMONITINA Hyatt, 1889
 Superfamily PSILO CERATOIDEA Hyatt, 1867
 Family PSILO CERATIDAE Hyatt, 1867

Genus NEOPHYLLITES Lange, 1941

Type species. *Psilophyllites antecedens* Lange, 1931.

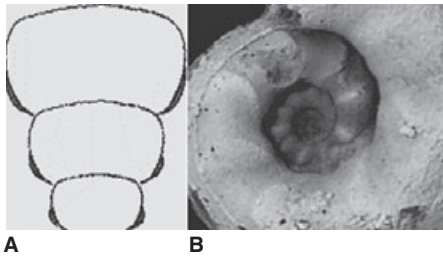
Neophyllites sp. indet.

Plate 1, figures 36–37; Text-figures 7, 8A; Table 3

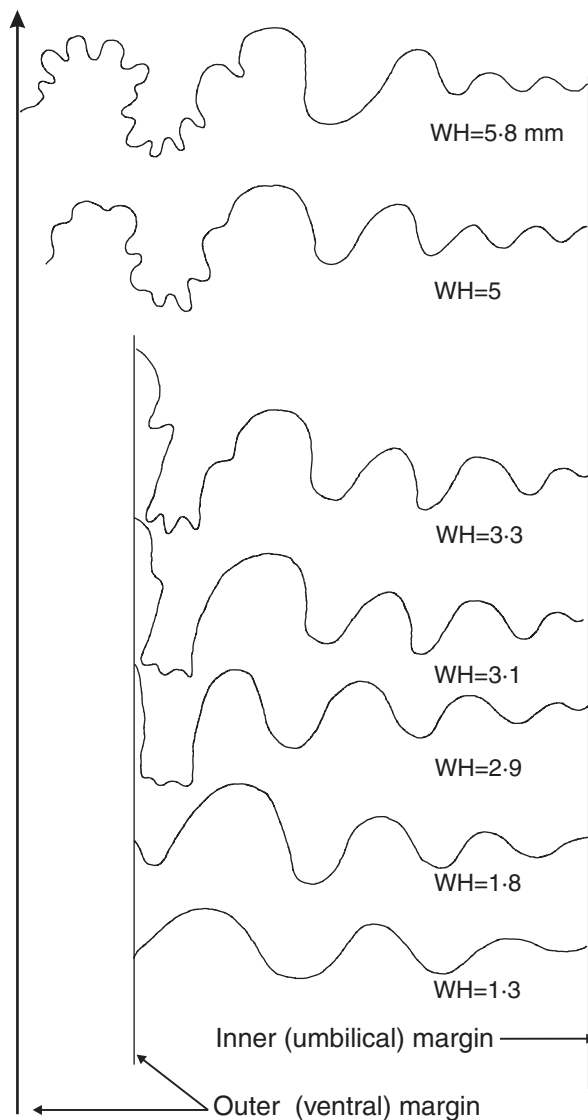
2000 *Neophyllites* sp.; Yin and Enay, pp. 604–605,
 fig. 2/15.

Material. One specimen, A2004CUGB1016.

Description. The specimen is small (16.5 mm in diameter), relatively involute and appears fairly compressed, although com-



TEXT-FIG. 6. *Pleuroacanthites* aff. *biformis* (Sowerby), A2004CUGB3026. A, whorl cross-section. B, ribbing on nucleus at $D = 8.5$ mm, $UD = 4.0$ mm.



TEXT-FIG. 7. Suture lines of *Neophyllites* sp. indet., A2004CUGB2020.

pression has probably been secondarily enhanced slightly. The body chamber is about three-quarters of the whorl. The flanks are flat and smooth, the umbilical wall is steep, and whorl height exceeds whorl width.

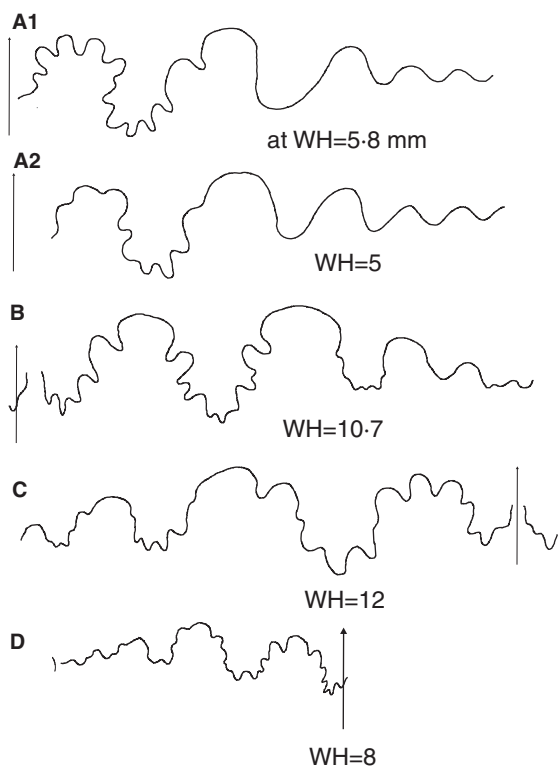
A series of suture lines from the inner whorls to the end of the phragmocone can be observed (Text-fig. 7). They consist of two indented saddles and one indented lateral lobe, and the rest of the suture line is completely smooth. The ventral lobe is incompletely preserved but may be shallower than the lateral lobe. Both the lateral saddle and the lobe exhibit only shallow indentations; the second saddle shows only one indentation; it is higher than the first lateral saddle.

Remarks. Formerly, *Neophyllites* was regarded as a synonym of *Psilophyllites* (Arkell *et al.* 1957) but *Psilophyllites* appears later than *Neophyllites*, and there are conspicuous differences between these two genera. Therefore, Schindewolf (1962), Wiedmann (1970) and Bloos (1999) regarded *Neophyllites* as a valid genus. *Psilophyllites* can be ruled out for our specimen on the basis of the indented saddles.

It is difficult to distinguish smooth, basal Hettangian *Psiloceras* from *Neophyllites* without knowledge of the suture line. Bloos (1999, 2004) has given a detailed description and discussion of the morphology and suture lines of *Neophyllites*, *Psilophyllites* and *Psiloceras*, and the criteria for distinguishing these genera.

The suture line of the Tibetan specimen is significantly similar to European *Neophyllites* in possessing a simply indented first lateral saddle and lobe (Text-fig. 8). The specimen is small and its immaturity hinders identification; only generic determination is possible. More specimens, particularly those representing later ontogenetic stages, must be collected before confident species assignment is possible, but we suspect that a new species is represented.

The association of *Neophyllites* sp. indet. with *Choristoceras nyalamense* might suggest that this species is earlier than the *Neophyllites* of Europe. However, an association of *Choristoceras* and *Neophyllites*? has also been reported from the lowermost Jurassic of Nevada by Guex (1995; Guex *et al.* 2002, 2004). Suture lines are lacking but the wide umbilicus and the lack of nodes on the innermost whorls are in keeping with *Neophyllites*. Because of the crushed state and the different size, exact comparison with the Tibetan *Neophyllites* sp. indet. is difficult, but the latter appears to be slightly more involute and more rapidly expanding. *Choristoceras* and *Neophyllites*? have also been reported in association in the Queen Charlotte Islands (Longridge *et al.* 2007). The co-occurrence of *Choristoceras* and *Neophyllites* characterizes the Minutum Zone of the North American succession (Taylor *et al.* 2001) and suggests a correlation with the Tibeticum Zone of Tibet, established herein.



TEXT-FIG. 8. Comparison of suture lines of *Neophyllites* sp. indet. with European species of *Neophyllites* (data from Bloos 1999, 2004). A1–2, *Neophyllites* sp. indet. B, *N. neumayri*. C, *N. imitans*. D, *N. antecedens*.

Occurrence. Level B2, Section B (Tibeticum Zone).

Neophyllites cf. *biptychus* Lange, 1941
Plate 1, figures 34–35; Table 3

- cf. 1941 *Neophyllites biptychus* Lange, p. 60, pl. 2, figs 1–2.
cf. 1970 *Neophyllites biptychus* Lange; Wiedmann, p. 1011,
pl. 10, fig. 3.

2000 *Psiloceras* ex gr. *pacificum* Guex; Yin and Enay,
p. 604, fig. 2/8–9.

Material. One specimen.

Description. The specimen is evolute and very slender. Its ribbing is irregular in spacing and thickness; occasionally the ribs seem to be bifurcated. The inner whorls are almost smooth; the ribbing is best developed on the last whorl. Nodes are not developed on the innermost whorls. The ribs are restricted to the umbilical half of the flank and are strongest near the umbilicus.

Remarks. Suture lines, the best character for the generic recognition of *Neophyllites*, are lacking but the morphological features justify the assignment to this genus. Essentially the same features are found in *N. biptychus* Lange, 1941 and *N. neumayri* Lange, 1952, the other ribbed species of *Neophyllites*. The Tibetan specimen is most similar to *Neophyllites biptychus* Lange from north-west Europe (Lange 1941). The umbilicus in Lange's specimen is somewhat wider and the ribbing somewhat denser, but unfortunately he did not provide information on the range of variability within this species.

In the Alpine species *Neophyllites neumayri*, the umbilicus is wider, the ribbing is considerably denser and the ribs are thinner (Bloos 2004, fig. 2), but all of the other characters of ribbed *Neophyllites* mentioned above are the same.

The characters of *Psiloceras* are quite different from *Neophyllites*. *Psiloceras* specimens from the Alps, as well as those from North and South America, show essentially the same features: nodes on the innermost whorls; ribbing best developed on the inner whorls, weakening and disappearing on the outer whorls; ribs strongest on the middle of the flank, fading out towards the venter and to the umbilicus.

The Tibetan specimen was incorrectly assigned to *Psiloceras* ex gr. *pacificum* by Yin and Enay (2000). In addition to the differences between *Neophyllites* and *Psiloceras*

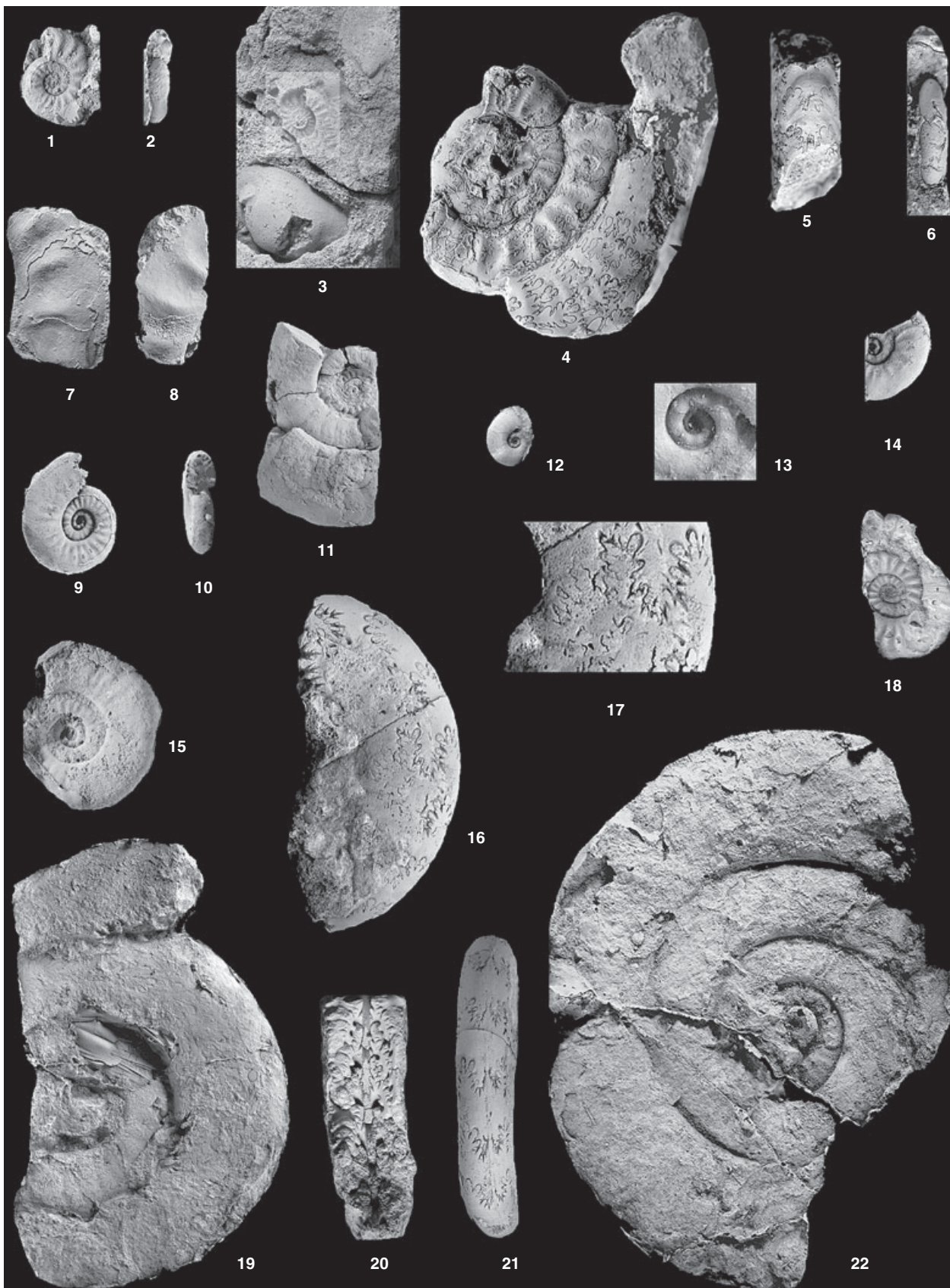
EXPLANATION OF PLATE 2

Figs 1–8. *Psiloceras tibeticum* sp. nov., Tibeticum Zone, Level A1 (main bivalve bed), Section A. 1–3, 2025, paratype. 1, inner whorls (latex cast), lateral view; $\times 2$. 2, aperture and ventral view; $\times 2$. 3, external mould (highlighted) in association with bivalves. 4–6, 2026, holotype. 4, lateral view. 5, ventral view. 6, ventral view of inner whorl. 7, 2023 (latex cast), lateral view of inner whorl fragment. 8, 2024 (latex cast), lateral view of inner whorl fragment.

Figs 9–18, 20–22. *Psiloceras calliphyllum* Neumayr, 1879, Calliphyllum Zone, Level A3–5, Section A. 9–10, 3015 (latex cast). 9, lateral view (= Yin and Enay 2000, fig. 2/1). 10, ventral view. 11, 3021, incomplete specimen in lateral view. 12–13, 3017 (latex cast). 12, lateral view. 13, lateral view of innermost whorls with nodes; $\times 4$. 14, 3019 (latex cast), lateral view. 15, 3020 (latex cast), lateral view (= Yin *et al.* 1999, fig. 2/13). 18, 3016 (latex cast), lateral view (= Yin *et al.* 1999, fig. 3/9). 20, 3012, dorsal view of phragmocone with suture line. 16–17, 21–22, Level B3, Section B, 3011. 16, lateral view of phragmocone fragment. 17, detail of whorl showing suture line; $\times 2$. 21, ventral view. 22 (latex cast), lateral view of entire specimen (= Yin and Enay 2000, fig. 2/3).

Fig. 19. *Euphyllites* cf. *struckmanni* (Neumayr, 1879), Level A4?, Section A, 3025 (latex cast), lateral view.

Specimen numbers prefixed A2004CUGB. All $\times 1$ except where stated.



described above, *P. pacificum* has much thicker whorls than species of *Neophyllites*.

Guex *et al.* (2002, fig. 2C) figured one Nevadan specimen, referred to as *Neophyllites* aff. *biptychus*. It differs from the Tibetan form in having ribs that are sinuous on the flank and even seem to cross the venter, and ornamentation that is at odds with ribbed *Neophyllites*. It might, in fact, belong to the *Psiloceras marcouxii* group.

There is some similarity with *Psiloceras marcouxii* Guex (Guex 1995, pl. 1, figs 1–2; species introduced in Guex *et al.* 1998) but the umbilicus is narrower than in the Tibetan form. The ribbing of *P. marcouxii* is weaker on the inner whorls and no nodes are observed on the innermost whorls, characters that could indicate affinities to *Neophyllites*.

Occurrence. Level A2, Section A (Calliphyllum Zone), in association with *Nevadaphyllites* cf. *psilomorphus*, two aulacoceratid fragments, and the bivalves *Chlamys valoniensis* and *Liostraea tibetica* Yin and McRoberts, 2006.

Genus PSILO CERAS Hyatt, 1867

Type species. *Ammonites planorbis* Sowerby, 1824.

Psiloceras tibeticum sp. nov.

Plate 2, figures 1–8; Text-figure 9; Table 3

Derivation of name. After Tibet where the type material was collected.

Types. The holotype is specimen A2004CUGB2026 (Pl. 2, figs 4–6). The paratype (A2004CUGB2025) is an external mould of a juvenile specimen (Pl. 2, figs 1–3).

Type horizon. Level A1 in Section A.

Material. Five specimens including the type material and two additional body chamber fragments.

Diagnosis. Evolute, compressed, early whorls bearing short, regular, widely spaced ribs that become more densely spaced and weaker on the last whorl. Body chamber almost smooth.

Description. Evolute, compressed; umbilicus shallow, umbilical wall low, indistinct, whorls are slightly arched; ribs which appear on the innermost whorl are distant, rectiradiate on the flank and bent forward at the ventral margin in early ontogeny (Pl. 2, figs 1–2); later the ribs are restricted to the umbilical part of the flank; body chamber tends to be smooth. Whorl height consistently exceeds whorl width; the cross-section is compressed and elliptical in outline (Pl. 2, figs 2, 6; Text-fig. 9).

On the holotype, the suture lines are well preserved; saddles and lobes are relatively narrow, high and slender as in most Alpine *Psiloceras* of the *calliphyllum* group; the umbilical part of the suture line is, however, less retracted than is usual in the *calliphyllum*-type. The space between the two last suture lines is reduced, indicating that the holotype is adult.

Remarks. *P. tibeticum* differs from *Neophyllites* cf. *biptychus*, which occurs a little higher in the section, by the well-ribbed inner whorls and the ribs being more pronounced on the flank rather than near the umbilicus.

In coiling and ribbing, the most similar form is the north-west European species *Psiloceras plicatulum* (Quenstedt, 1883), which also occurs rarely in the Alps (Bloos 2004). However, in this form the elements of the suture line are low and the indentations are shallow, as is usual in the *psilonotum*-type sutures. Moreover, *P. plicatulum* does not become smooth on the body chamber.

A similar Alpine form with *calliphyllum*-type suture line is *Psiloceras costosum* Lange, 1952. This species differs by its wider umbilicus and a denser ribbing. Two other ribbed Alpine species of *Psiloceras*, *P. naumanni* (Neumayr, 1879) and *P. trochoeides* Lange, 1952 differ in the same way.

Some specimens of the very variable North American species *Psiloceras polymorphum* Guex, 1980 are broadly similar in sculpture and suture line (Guex 1995, pls 7–9; text-fig. 11A–B) but in this species the ribbing on the inner whorls is generally denser and less projected on the venter (Guex 1995, pl. 9, fig. 9). However, the main difference is the greater whorl thickness and different outline of the whorl section of *P. polymorphum* in comparison with *P. tibeticum* (Guex 1995, pls 7–9).

Occurrence. Level A1 (type horizon), Section A (Tibeticum Zone).

Psiloceras calliphyllum (Neumayr, 1879)

Plate 2, figures 9–18, 20–22; Text-figure 10; Table 3

1879 *Aegoceras calliphyllum* Neumayr, p. 27, pl. 4, fig. 5.

1884 *Aegoceras calliphyllum* Neumayr; Wöhner, p. 137, pl. 15, fig. 4.

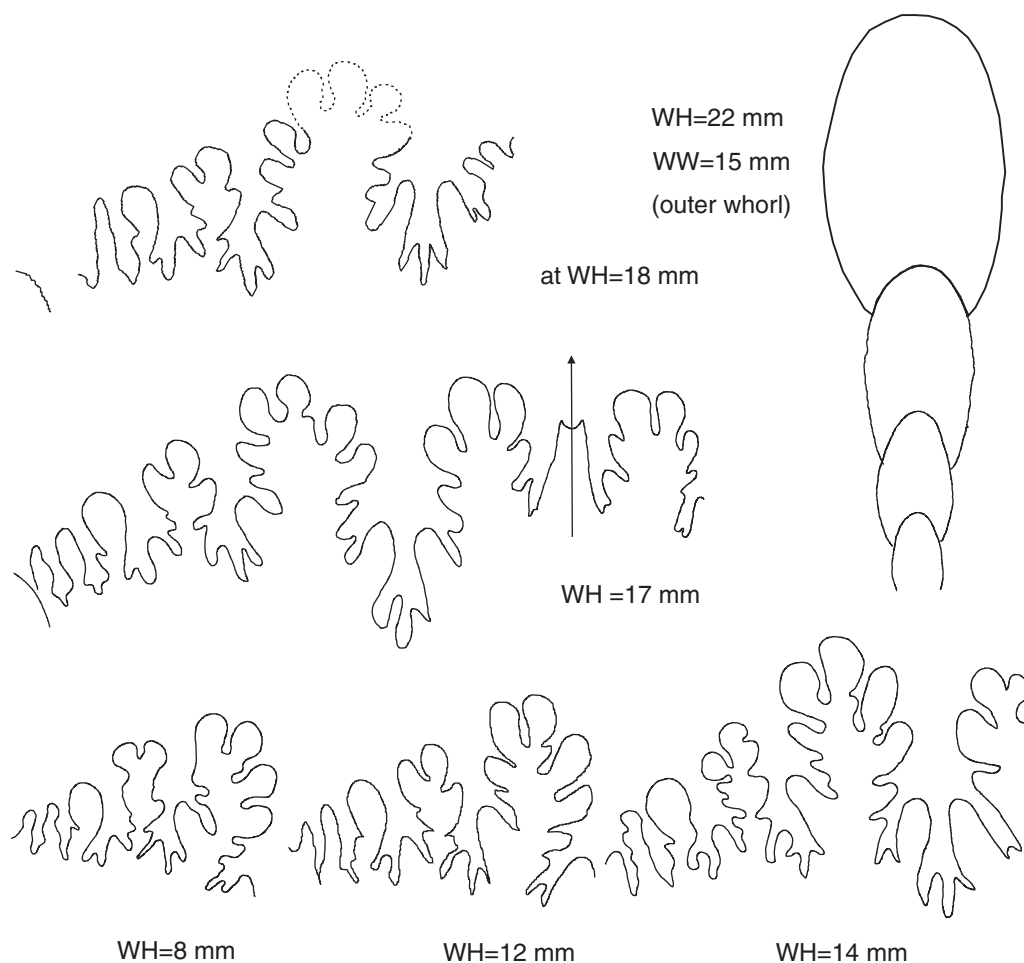
1963 *Psiloceras calliphyllum* Neumayr; Blind, p. 46, pl. 1, fig. 3.

1982 *Psiloceras* (*Paraphylloceras*) *calliphyllum* (Neumayr); Tozer, p. 390, fig. 57/4.

1994 *Psiloceras calliphyllum* Neumayr; Schlatter, p. 6, fig. 2.

1999 *Psiloceras* cf. *pacificum* Guex; Yin *et al.*, p. 128, fig. 3/6.

1999 *Psiloceras* cf. *polymorphum* Guex; Yin *et al.*, p. 128, fig. 3/7, 13.



TEXT-FIG. 9. Whorl cross-section and suture lines of *Psiloceras tibeticum* sp. nov., A2004CUGB2026, holotype.

- 1999 *Caloceras crassicoatum* Guex; Yin *et al.*, p. 128, fig. 3/9.
 2000 *Caloceras crassicoatum* Guex; Yin and Enay, p. 604, fig. 2/1.
 2000 *Psiloceras* cf. *pacificum* Guex; Yin and Enay, p. 604, fig. 2/2–4.
 2000 *Psiloceras* ex gr. *pacificum* Guex; Yin and Enay, p. 604, fig. 2/10.

Material. Four specimens (one relatively well preserved and three fragments) from Section B, and nine specimens (external moulds and fragments) from Section A.

Description. This species is a rather large form among the psiloceratids of Tibet (Pl. 2, fig. 22). It is evolute and shows a slender, high-oval whorl section (Text-fig. 10). The innermost whorls show nodes (Pl. 2, figs 9, 11–15, 18). Subsequent whorls are ribbed but the ribbing fades out early and the middle and outer whorls are smooth (Pl. 2, figs 19, 25). The suture line is well preserved in the largest specimen. Its elements are slender, high and deeply indented; the umbilical part is strongly retracted (Text-fig. 10).

Remarks. The Tibetan form compares well with the Alpine *Psiloceras calliphyllum* (Neumayr 1879) in regard to size, shape, ribbing and suture line. With respect to the early ribbing, there are close similarities to other psiloceratids from north-west Europe (*P. erugatum* Buckman, 1921), North America (*P. pacificum* Guex, 1980) and South America (*P. pressum* Hillebrandt, 2000; *P. planocostatum* Hillebrandt, 2000). However, all of these forms differ in other characters. The American forms are thicker, and *P. erugatum* is smaller and has a different whorl shape and a particularly different suture line. Inner whorls (Pl. 2, figs 9, 15, 18) of the Tibetan form have been previously confused with *Caloceras crassicoatum* Guex, 1995 because of the well-developed ribbing. The narrower whorls and the early weakening and disappearance of ribbing clearly differentiate these small specimens from *Caloceras*. Two of the specimens were incorrectly referred to *Psiloceras* cf. *polymorphum* Guex by Yin *et al.* (1999, p. 128, fig. 3/7, 13), but they differ from *P. polymorphum* in having narrower whorls.



TEXT-FIG. 10. Whorl cross-section and suture line of *Psiloceras calliphyllum* (Neumayr).

Tibetan *Psiloceras* specimens have been mentioned before by Wang and He (1981) who figured three from Longzi, which they referred to *Psiloceras psilonotum* (Quenstedt 1883). One is a whorl fragment with preserved suture line (Wang and He 1981, fig. 3) that is of the *Psiloceras* type. However, the specimen was not illustrated so the species cannot be determined and even its generic affinities are uncertain because *Caloceras*, *Waehneroceras* and other genera also display suture lines of this type. For its whorl height (15.7 mm), the suture line is very simple. The indentations of the saddles show almost no second-order subdivisions. The saddles are slightly more slender than those normally seen in *Psiloceras psilonotum* and related species (e.g. *P. plicatulum*), which means that *Psiloceras calliphyllum* is not very likely. The second specimen is densely ribbed (Wang and He 1981, pl. 2, figs 3–4), rather thick and involute, suggesting that it is not a *Psiloceras*. The third specimen (Wang and He 1981, pl. 2, fig. 5) is badly preserved but strongly ribbed, rather involute, and certainly not a *Psiloceras*.

Occurrence. Levels A3, A4 and A5 in Section A, and level B3 in Section B (Calliphyllum Zone).

Genus EUPHYLLITES Wöhner, 1898

Euphyllites cf. *struckmanni* (Neumayr, 1879)

Plate 2, figure 19; Text-figures 5A–D, 11; Table 4

cf. 1879 *Aegoceras?* *struckmanni* Neumayr, p. 36, pl. 6, fig. 5a–c.

cf. 1898 *Euphyllites struckmanni* Neumayr; Wöhner, p. 170, pl. 22, figs 1–8.

2000 ?*Discamphiceras* sp.; Yin and Enay, p. 606, fig. 3/7–9.

Material. Three specimens collected as float: inner whorls with part of the body chamber. Two specimens are fragments of large individuals; one is an external mould from which a latex cast was made.

Description. The specimens, consisting of parts of the body chamber and inner whorls (Text-fig. 5A–D), have a broad venter and flat or slightly arched, smooth flanks. The ornamentation, only preserved on the body chamber, is an irregular, weak undulation. The suture line (Pl. 2, fig. 19; Text-fig. 11A–C) is complex with conspicuously high and narrow elements. The external lobe is subdivided into at least five accessory lobes; the lateral

TABLE 3. Measurements of *Neophyllites* and *Psiloceras* species in mm.

Taxa	N	D	UD	U	WW	WH	WW/WH	PRHW	Figures
<i>Neophyllites</i> cf. <i>biptychus</i>	2021	36	17	0.47	9	11.5	0.78	9	Pl.1, fig. 34
<i>Neophyllites</i> sp. indet.	2020	16.5	6	0.36	–	6.5	–	–	Pl.1, fig. 37
<i>Psiloceras tibeticum</i>	2025	13	6.5	0.5	3	4	0.75	10	Pl.2, fig. 1
<i>Psiloceras</i>	2026	57	32	0.56	15	22	0.68	–	Pl.2, fig. 4
<i>Psiloceras calliphyllum</i>	3017	12	4	0.33	–	–	–	–	Pl.2, fig. 13
	3020	29	13.5	0.47	–	–	–	–	Pl.2, fig. 15
	3015	24	8.5	0.35	–	8.5	–	11	Pl.2, fig. 12
	3011	112	60	0.54	12	18	0.67	–	Pl.2, fig. 16
	3016	24	11	0.47	–	–	–	–	Pl.2, fig. 18

lobe has three-folded accessory lobes; saddles are high, narrow and deeply subdivided. The umbilical part of the suture line is strongly retracted.

Remarks. The large fragments compare well with *Euphyllites struckmanni* (Neumayr, 1879) in shape, sculpture and suture line. The only difference is that the flanks of the Alpine species are flat and not arched, resulting in a whorl with a different cross-section (Neumayr 1879, pl. 6, fig. 5b). The second specimen is similar to smooth Alpine specimens (Wöhner 1898, pl. 22, figs 1, 3).

Occurrence. Two float specimens 4–6 m above level B3 in Section B (A2004CUGB4025 and 4044); one float specimen found between levels A5 and A6 in Section A (A2004CUGB3025).

Genus ALSATITES Haug, 1894

Type species. *Ammonites liasicus* d'Orbigny, 1844.

?*Alsatites* sp. 1

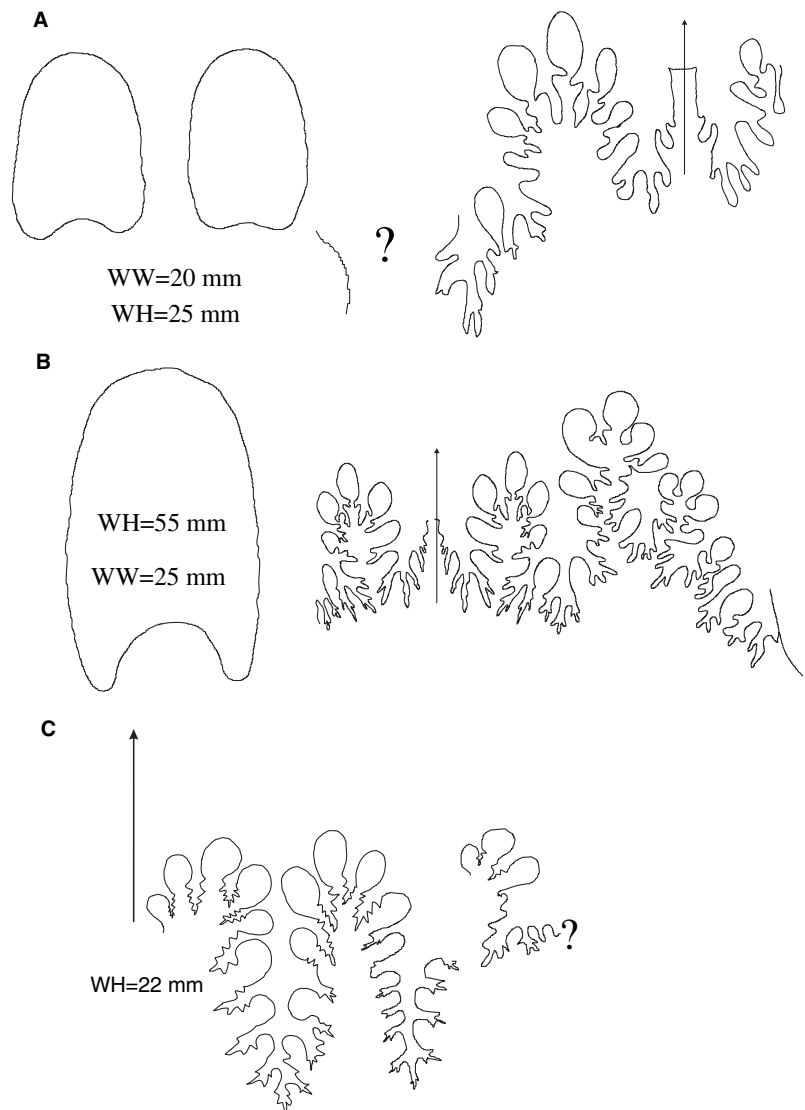
Plate 3, figures 1, 3–4; Text-figure 12A; Table 4

2000 *Psiloceras distinctum* Pompeckj; Yin and Enay, p. 607, fig. 3/6.

Material. Two specimens, not *in situ*.

Description. The venter is arched and smooth but the cross-section is not circular; the maximum width of the whorl is attained

TEXT-FIG. 11. Whorl cross-sections and suture lines of *Euphyllites* cf. *struckmanni* (Neumayr). A, two cross-sections and suture line of A2004CUGB4025, inner whorl. B, cross-section and suture line of the same specimen, outer whorl. C, suture line of A2004CUGB3025 (latex cast of exterior mould).



in the lower third of the whorl height from where the flanks converge to the venter (Pl. 3, fig. 4). The suture line is unknown.

Remarks. In regard to ribbing and the venter, there are similarities to *Caloceras* so that this genus cannot be definitely ruled out. However, the ribs are low, blunt and rather short whereas in *Caloceras* they are generally sharper, higher and longer. Notable exceptions occur such as the blunt ribbing in *Caloceras torus hercynum* figured by Lange (1952, pl. 13, fig. 1). *Caloceras* and convergent forms of *Alsatites* can be best distinguished by characteristic differences in suture line (see numerous examples in Lange 1941, 1952). Thus, for confident identification, better specimens will be needed from the Germig sections. Of the two Tibetan alsatitid forms, that referred to as ?*Alsatites* sp. 1 differs from ?*A.* sp. 2 by its less irregular, straighter ribbing. Moreover, in ?*A.* sp. 2, there is a tendency for the ribs to become rursiradiate; ?*A.* sp. 1 is considerably less evolute than ?*A.* sp. 2.

Occurrence. Not in place; collected stratigraphically high above level B3 in Section B.

?*Alsatites* sp. 2

Plate 3, figure 2; Text-figure 12B; Table 4

Material. One float specimen.

Description. The specimen is extremely evolute, the whorl section is circular (Text-fig. 12B), and the venter is rounded. The ribbing is rather dense, blunt, low, and irregular in thickness and spacing; the ribs are inclined backwards and cross the flanks in a concave arch. The suture line is unknown.

Remarks. The absence of a suture line and the shape of the venter makes generic allocation difficult. The very low expansion rate and the irregular and concave ribbing are different from *Caloceras*. It is most probably a form of *Alsatitinae* (*Alsatites s.l.*). In Alpine *Alsatitinae*, a ventral keel is

usually developed later in ontogeny but on the inner whorls it is almost lacking, so that the cross-section can be nearly circular [e.g. *Alsatites proaries* (Neumayr) in Wöhner 1886, pl. 29, fig. 1b; *Alsatites liasicus* morphotype *subliasicus* (Reynès) in Guérin-Franiatte 1990, pl. 5, fig. 2, pl. 7, fig. 2]. The Tibetan specimen differs in being less densely ribbed.

Occurrence. Not in place; collected stratigraphically high above level B3 in Section B.

Genus DISCAMPHICERAS Spath, 1924

Type species. *Ammonites kammerkarensis* Gümbel, 1861.

Discamphiceras pleuronotum (Canavari, 1882)

Plate 3, figures 5–6, 8–11; Plate 4, figures 1–5, 10–11, 15; Text-figure 13; Table 4

1882 *Aegoceras pleuronotum* Canavari, p. 169, pl. 19, figs 2, 4–5.

1884 *Aegoceras pleuronotum* Canavari; Wöhner, p. 110, pl. 25, figs 1–3.

1888 *Psiloceras pleuronotum* Canavari; Canavari, pl. 29, p. 149, pl. 19, figs 2a–c, 4a–b; non 5a–d.

1999 *Kammerkarites haploptychus* (Waehner); Yin *et al.*, figure 3/10–12.

1999 *Discamphiceras* sp.; Yin *et al.*, figure 3/14.

2000 *Discamphiceras* cf. *silberlingi* Guex; Yin and Enay, p. 604, fig. 2/5–7.

Material. About 28 specimens from Section A, at the top of unit 8, and several additional float specimens from Section B.

Description. Slightly evolute form, whorls compressed and flat; the outline of the whorl section is high elliptical; the body chamber whorl is slightly more inflated than the phragmocone whorls (Text-fig. 13). The umbilical wall is steep and shallow. The diameter of specimens with body chambers ranges from 60 to 200 mm. The ribs are straight and low, and generally restric-

EXPLANATION OF PLATE 3

Figs 1, 3–4. ?*Alsatites* sp. 1, *ex situ*, Sections A and B. 1, 5013 (latex cast), lateral view. 3–4, 5012 (latex cast). 3, lateral view (= Yin and Enay 2000, fig. 3/6). 4, aperture and ventral view.

Fig. 2. ?*Alsatites* sp. 2, *ex situ*, Section B, 5011, lateral view.

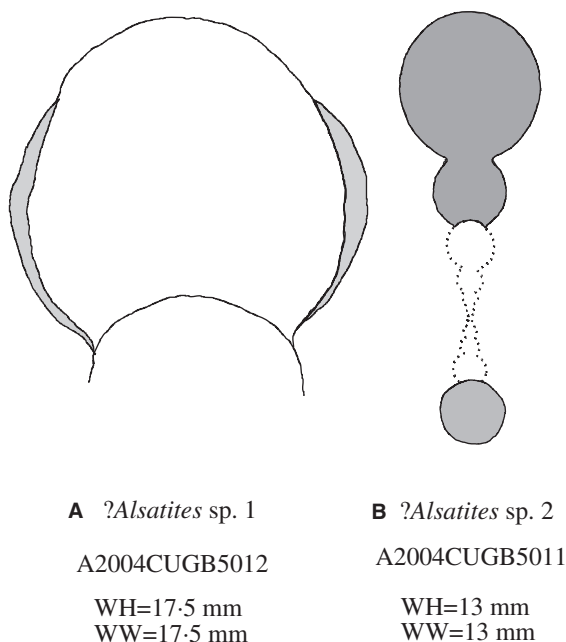
Figs 5–6, 8–11. *Discamphiceras pleuronotum* (Canavari, 1882), Pleuronotum Zone, Level A6, Section A. 5, 7027 (latex cast), lateral view. 6, 9, 7017. 6, ventral view of body chamber. 9, lateral view; note last septum. 8, 7018 (latex cast), lateral view. 10, 7088 (latex cast), lateral view of entire specimen, same individual as 7017 (6 and 9). 11, 7020, lateral view.

Figs 7, 12. *Kammerkarites* sp., Pleuronotum Zone, Level A6, Section A. 7, 5015 (latex cast), lateral view (= Yin and Enay 2000, fig. 3/5). 12, 5016 (latex cast), lateral view.

Specimen numbers prefixed A2004CUGB. All $\times 1$.



YIN *et al.*, Triassic/Jurassic boundary ammonoids



TEXT-FIG. 12. Whorl cross-sections of ?*Alsatites* spp.

ted to the lower two-thirds of the flank. They are highest at the middle of the flank, gradually fading out towards both the umbilicus and the venter (Pl. 3, figs 6, 9; Pl. 4, figs 5, 15). They become weaker on the body chamber (Pl. 4, fig. 15). The suture line (Text-fig. 13A–B) is of the *calliphylum*-type, as usual in most Tethyan psiloceratids.

Remarks. *Discamphiceras pleuronotum*, which was first described from Italy by Canavari (1882), has not been reported from the eastern Tethys before. The Tibetan specimens were previously determined as either *Kammerkarites haploptychus* (Wöhner 1882) or *Discamphiceras* sp. and *D. cf. silberlingi* (Yin *et al.* 1999; Yin and Enay 2000). However, *D. silberlingi* is more involute and thicker, and its ribbing is denser and stronger. Meister *et al.* (2002) suggested that the Tibetan *Discamphiceras* could be related to *D. asiaticum* Meister, Vu Khuc and Tran Huyen, 2002 from the Sinemurian of Vietnam.

However, the Tibetan *D. pleuronotum* differs from *D. asiaticum* by its less dense ribbing and more evolute shell. *Discamphiceras asiaticum* is also thicker, the whorl section is more depressed, and the ribbing is stronger and weakens on the body chamber. In La Spezia, Tuscany, the type region of *D. pleuronotum*, other ammonites indicate the upper part of the Hettangian; a Middle Hettangian age has not been proved with certainty (Canavari 1882, 1888; Venturi 1985). In the Alps, *D. pleuronotum* occurs in the Megastoma Zone (Middle and basal Upper Hettangian; Wöhner 1886, 1894). In North America (Nevada; Guex 1995) and in South America (Peru; Hillebrandt 2000), *Discamphiceras* occurs in the Middle Hettangian. Another species from Viet Nam, *Discamphiceras tongdzuyi* (Vu Khuc and Cariou, 1998) differs markedly by its more triangular whorl section and the sharper venter of the adult shell.

Occurrence. Level A6, Section A (Pleuronotum Zone).

Family SCHLOTHEIMIIDAE Spath, 1924

Genus KAMMERKARITES Spath, 1924

Type species. *Aegoceras diploptychum* Wöhner, 1882.

Kammerkarites frigga (Wöhner, 1884)

Plate 4, figures 6–9, 12–14; Table 4

- 1884 *Aegoceras frigga* Wöhner, p. 106, pl. 23, figs 1–3.
- 1941 *Storthoceras frigga* (Wöhner); Lange, p. 41.
- 1993 *Kammerkarites frigga* (Wöhner); Rakús, p. 22, pl. 2, figs 2–4, pl. 3, figs 2–5.
- 1995 *Kammerkarites frigga* (Wöhner); Guex, p. 32, pl. 17, figs 5–14.
- 1999 *Kammerkarites?* cf. *frigga* (Wöhner); Pálffy *et al.*, p. 1541, fig. 4B, E–F, H.
- 2000 *Choristoceras* sp.; Yin and Enay 2000, p. 607, fig. 3/1–2.

EXPLANATION OF PLATE 4

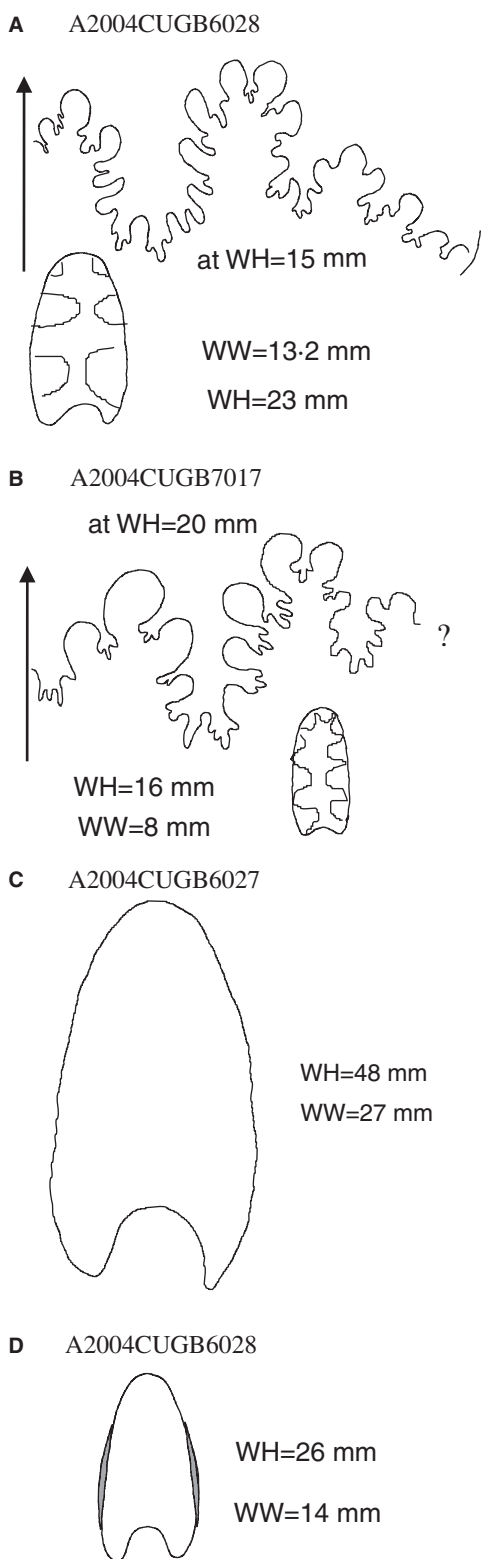
Figs 1–5, 10–11, 15. *Discamphiceras pleuronotum* (Canavari, 1882), Pleuronotum Zone, Level A6, Section A. 1, 6017 (latex cast), lateral view of innermost whorls. 2, 6020, lateral view of innermost whorls. 3, 6021, lateral view of inner whorls. 4, 7078 (latex cast), lateral view. 5, 10, 6028. 5, lateral view of body chamber fragment. 10, ventral view. 11, 15, 6027. 11, ventral view of body chamber. 15, lateral view.

Figs 6–9, 12–14. *Kammerkarites frigga* (Wöhner, 1884), Pleuronotum Zone, Level A6, Section A. 6–7, 7009 (latex cast). 6, view of venter and whorl section. 7, lateral view. 8–9, 7007 (latex cast). 8, ventral view. 9, lateral view. 12–14, 7008 (latex cast). 12, lateral view of inner whorls (= Yin and Enay 2000, fig. 3/2). 13, lateral view of body chamber and external mould of inner whorls (= Yin and Enay 2000, fig. 3/1). 14, ventral view.

Specimen numbers prefixed A2004CUGB. All $\times 1$.



YIN *et al.*, *Discamphiceras*, *Kammerkarites*



TEXT-FIG. 13. Whorl cross-sections and suture line of *Discamphiceras pleuronotum* (Canavari).

Material. Three specimens preserved as external moulds.

Description. All specimens are small and moderately evolute. The whorls are compressed; the outline of the whorl section is rounded (Pl. 4, fig. 6). The ribbing is strong and dense; the ribs are simple, slightly concave on the flanks and projected at the ventral margin; they pass across the venter without interruption, forming a ventral chevron (Pl. 4, figs 8, 14). The suture can be traced in part.

Remarks. Previously, the float specimen illustrated in Plate 4, figures 12–14 was confused with *Choristoceras* (Yin and Enay 2000, p. 607, fig. 3/1–2) but re-examination of the partly preserved suture line of this specimen revealed a deeply indented lateral saddle and lobe that is not in keeping with choristoceratid affinities.

Occurrence. Level A6, near the top of Section A (Pleuronotum Zone).

Kammerkarites sp.

Plate 3, figures 7, 12; Table 4

2000 *Kammerkarites* cf. *haploptychus* (Wöhner); Yin and Enay, pp. 606–607, fig. 3/5.

Material. Two specimens.

Description. Rather large, midvolute form. Whorls are slender; outline of whorl sections is elliptical; ribbing is straight, strong, moderately dense and slightly inclined forward, weak on the body chamber. The ribs are extended over the whole flank, short only on the body chamber; their thickness increases from the umbilical wall to the ventral margin where they are highest and broadest. The suture line is incompletely preserved in one of the specimens; it seems to be simple; the umbilical part is somewhat retracted.

Remarks. By its relatively involute coiling, the Tibetan material resembles *Discamphiceras*. However, the ribbing is similar only on the body chamber; on the other whorls it is conspicuously different, indicating *Kammerkarites*. Our specimen is less evolute than the Alpine forms of this genus. The suture line seems to be simpler than in *Discamphiceras*, but this cannot be determined with certainty.

Similar, narrowly coiled, forms of *Kammerkarites* occur in Nevada, including *K. diploptychoides* Guex, 1980 and *K. rectiradiatus* Guex, 1980, but their shell shape and ribbing ontogeny are different.

Occurrence. Level A6, Section A (Pleuronotum Zone).

TABLE 4. Measurements of seven species in mm.

Taxa	N	D	UD	U	WW	WH	WW/WH	PRHW	Figures
<i>Euphyllites</i> cf.	3025	90	53	0.59	—	22	—	—	Pl. 2, fig. 19
<i>struckmanni</i>	4025	—	—	—	36	58	0.62	—	Text-fig. 5A–D
<i>Pleuroacanthites</i>	3026	8.5	4	0.47	6	3	2	—	Text-fig. 5E–G
aff. <i>biformis</i>									
? <i>Alsatites</i> sp. 1	5013	29	14	0.48	—	9.5	—	13	Pl. 3, fig. 1
	5012	80	49	0.61	17.5	17.5	1	26	Pl. 3, fig. 3
? <i>Alsatites</i> sp. 2	5011	48	32	0.67	13	13	1	20	Pl. 3, fig. 2
<i>Discamphiceras</i>	7027	78	32	0.41	—	25	—	—	Pl. 3, fig. 5
<i>pleuronotum</i>	7018	—	—	—	13	27	0.48	—	Pl. 3, fig. 8
	7088	66	26	0.39	13	23	0.57	16	Pl. 3, fig. 10
	6017	8	—	—	—	—	—	—	Pl. 4, fig. 1
	7078	93	45	0.48	14	24	0.58	—	Pl. 4, fig. 4
	6028	—	—	—	15	25	0.6	—	Pl. 4, fig. 5
	6027	192	98	0.51	30	57	0.53	18(?)	Pl. 4, fig. 15
<i>Kammerkarites</i>	7009	20	9	0.45	7.5	7.5	1	—	Pl. 4, fig. 7
<i>frigga</i>	7007	16	6	0.38	6	6	1	13	Pl. 4, fig. 9
	7008	38	18	0.47	10	12	0.83	—	Pl. 4, fig. 12
<i>Kammerkarites</i> sp.	5016	—	—	—	—	41	—	—	Pl. 3, fig. 12

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