

CONODONTS OF THE LOWERMOST TRIASSIC OF SPITI, AND NEW ZONATION BASED ON *NEOGONDOLELLA* SUCCESSIONS

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Riassunto. Sono descritti i conodonti del Triassico basale degli strati a *Otoceras woodwardi* e adiacenti della regione di Spiti. Inoltre sono confrontati con le faune del limite Permo-Trias (P-T) di altre regioni. Viene introdotta una nuova zonazione per il pelagico basata sul genere *Neogondolella*: l'intervallo caratterizzato da *N. carinata* - *N. taylorae* è suddiviso in tre parti sulla base delle comparse successive, in ordine ascendente, di *N. meishanensis*, *N. krystyni* Orchard n. sp. e di *N. discreta* Orchard & Krystyn n.sp. Lo sviluppo di queste specie griesbachiane comporta un cambio morfologico successivo nella configurazione della parte assiale (lama, carena, cuspidi) degli elementi pettiniformi. La zonazione su conodonti pelagici è calibrata con le zonazioni basate sulle specie di *Hindeodus* e di *Isarcicella*, e con le faune ad ammonoidi di Spiti, di altre località himalayane e dell'Artico. La Zona a *meishanensis* comprende la Zona a *parvus* e parte della soprastante Zona a *staeschei*. Gli strati con *O. woodwardi* in Spiti contengono gli indici delle zone a *staeschei* e *krystyni*. La fauna a conodonti associata con gli *Otoceras* differisce da quella del Permiano terminale del Changshing Limestone della Cina, ma assomiglia a quella degli strati di transizione P-T a Meishan, dove una Zona a *meishanensis*, qui considerata con uno spettro più ristretto, si rinviene già sotto il datum a *parvus*. Il cambio faunistico che introduce le specie di *Neogondolella* caratteristiche della fauna a *N. carinata* - *N. taylorae* si trova alla base degli strati di transizione di Meishan, che è lo stratotipo proposto del limite P-T. Poco sopra questo orizzonte, la scomparsa di molte specie di *Neogondolella* e la comparsa di nuove specie di *Hindeodus* coincide con un cambio nella biofacies a conodonti, piuttosto che con un evento di estinzione. Nelle sezioni di Spiti, la fauna a *N. carinata* - *N. taylorae*, associata all'inizio con *H. parvus* (come a Selong in Tibet) persiste attraverso l'intero Griesbachiano. Gli indici delle tre zone a *Neogondolella* sono riconosciuti anche nel Salt Range e nell'Artico Canadese. Infine sono descritte quattro nuove specie di conodonti: *Neogondolella discreta*, *N. kazi*, *N. krystyni*, e *N. nassichuki*.

Abstract. Conodonts from the lowermost Triassic *Otoceras woodwardi* beds and adjacent strata of Spiti are described and compared with Permian-Triassic (P-T) boundary bed faunas from elsewhere. A new pelagic zonation based on *Neogondolella* is introduced: the interval characterized by *N. carinata*-*N. taylorae* is subdivided into three parts based on successive first appearances of *N. meishanensis*, *N. krystyni* Orchard n. sp. and *N. discreta* Orchard and Krystyn n. sp., the nominal species of three successive zones. The development

of these Griesbachian species involves a progressive morphological change in the configuration of the axial part (blade-carina-cusp) of the pectiniform elements. The pelagic conodont zonation is intercalibrated with the parallel zonation based on species of *Hindeodus* and *Isarcicella*, and with ammonoid faunas from Spiti, other Himalayan localities, and the Arctic. The *meishanensis* Zone embraces the *parvus* Zone and part of the overlying *staeschei* Zone. Strata containing *O. woodwardi* in Spiti carry the indices to the *staeschei* and *krystyni* zones. The *Neogondolella* conodont fauna associated with *Otoceras* differs from that of the latest Permian Changshing Limestone of China, but resembles that from the P-T boundary transition beds at Meishan, where a *meishanensis* Zone of restricted scope occurs beneath the *parvus* datum. The faunal change which introduces the characteristic *Neogondolella* species of the *N. carinata*-*N. taylorae* fauna occurs at the base of the P-T boundary transition beds at Meishan, the proposed boundary stratotype. Slightly above this level, the disappearance of most *Neogondolella* species and the introduction of new *Hindeodus* species coincides with a change in conodont biofacies rather than an extinction event. In the Spiti sections, the *N. carinata*-*N. taylorae* fauna, associated at first with *H. parvus* (as in Selong, Tibet), persists through the entire Griesbachian. Indices of the three *Neogondolella* zones are also recognized in the Salt Range and the Canadian Arctic. Four new conodont species are described: *Neogondolella discreta*, *N. kazi*, *N. krystyni*, and *N. nassichuki*.

Introduction.

Conodonts from the lowermost Triassic strata of the Himalaya have been at the forefront of discussions concerning biostratigraphic correlation around the Permian-Triassic (P-T) boundary. This follows a century of controversy about the biochronological significance of *Otoceras*, which was first discovered at Shalshal Cliff (Griesbach, 1880) and subsequently at many other Himalayan localities. Eventually, Diener (1912) drew the P-T boundary at the base of the Himalayan *Otoceras woodwardi* Zone. With the advent of conodont studies, the relative age of *Otoceras*-bearing beds again became a controversial issue. Late Permian, «Dzhulfian to Dorashamian ...or Wuchiapingian to Changshingian» conodonts were reported with *Otoceras* from several sections in Spiti, Zanskar, and Kumaun, as well as in Kashmir

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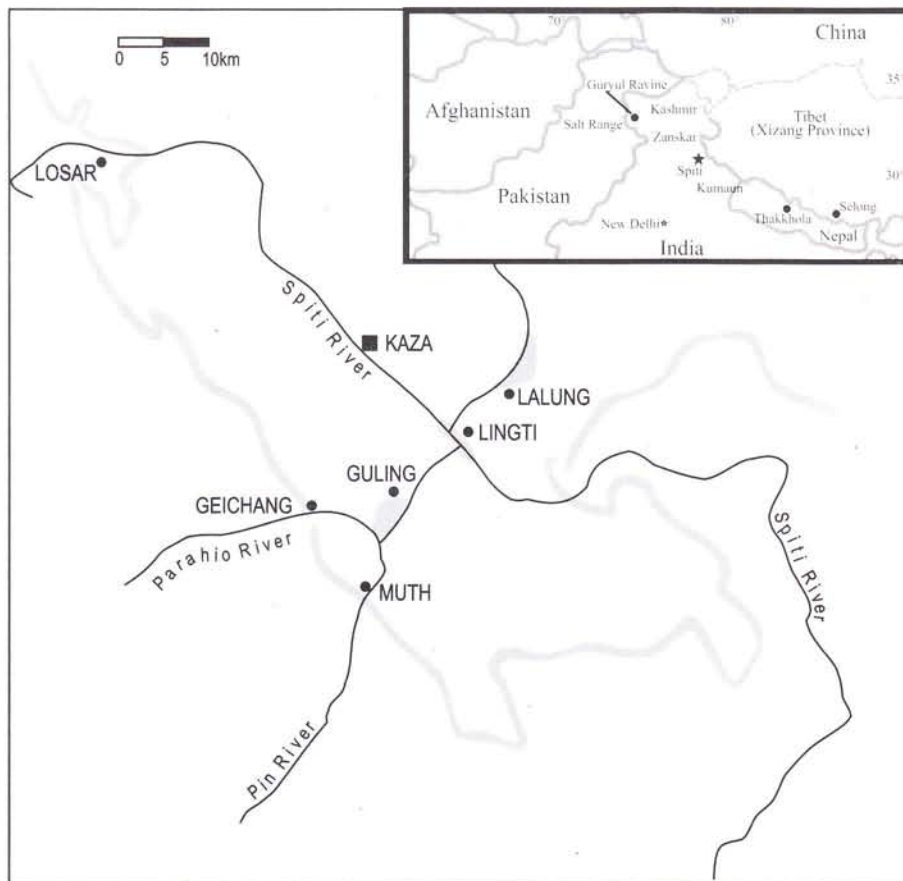


Fig. 1 - Lowermost Triassic outcrop and location of Spiti sections and (inset) general location of other Himalayan lowermost Triassic conodont sites mentioned in the text.

boundary transition beds at Meishan, South China (Zhang et al., 1995; Wang, 1995; Mei, 1996). The present account of *Neogondolella* faunas from the lowermost Triassic should facilitate comparison of similar faunas and lead to a better understanding of conodont faunal changes and correlation around the P-T boundary.

Previous work.

Conodonts from the *Otoceras-Ophicerus* beds at Guling, Spiti (Fig. 1) were first described by Goel (1977), who reported *Neogondolella carinata* and *N. planata* but found no *Hindeodus*. Bhatt & Joshi (1978) listed both *N. carinata* and *Hindeodus typi-*

(Bhatt & Arora 1984, p. 724), and Sweet (1979, 1992) claimed the contemporaneity of Changshingian and *Otoceras woodwardi*-bearing strata through the application of graphic correlation.

Conodonts are now known from many *Otoceras* localities and other P-T boundary sections both in the Himalayas and elsewhere. These are composed of varying proportions of two principal conodont stocks, the *Hindeodus-Isarcicella* group and species of *Neogondolella* (= *Clarkina*). Recently, the focus has been on the *Hindeodus-Isarcicella* group, from amongst which *H. parvus* has been widely favoured as the index for the systemic boundary (e.g., Yin et al., 1996). In the conodont collections recovered from ammonoid-bearing lowermost Triassic strata in Spiti, pelagic *Neogondolella* predominates. Although some *Neogondolella* species have been regarded as long-ranging through P-T boundary strata, those from Spiti sections have a stratigraphic distribution that provides the basis for a refined pelagic zonation for the lowermost Triassic. The relationship between this zonation and that of the *Hindeodus/Isarcicella* species, and the intercalibration with ammonoid faunas is discussed below. The description and illustration of large, diverse, and relatively well preserved *Neogondolella* conodont faunas from Spiti supplements recent descriptions of new species from the *Otoceras latilobatum* Zone of Selong, Tibet (Orchard et al., 1994), and from the P-T

calis as the principal elements of the basal Triassic bed in the Spiti River section. These species were earlier reported with *Otoceras* at Guryul Ravine, Kashmir (Sweet, 1970a). Subsequently, Bhatt et al. (1981a, b) and Bhatt & Arora (1984) presented a different interpretation of the conodont fauna from several *Otoceras* and other lowermost Triassic localities in the Himalayas (Kashmir, Kumaun, Spiti, Zaskar), namely an association of *Neogondolella subcarinata*, *N. changxingensis*, *N. carinata*, *N. orientalis*, *N. planata*, *N. deflecta* subsp., *N. behnkeni* and *N. sp. A* (Bhatt & Arora, 1984, p. 724); many of these species were only known from unequivocal Upper Permian strata elsewhere. Contemporary reports from Kashmir (Matsuda, 1981, 1984), the Zaskar area (Nicora et al., 1984), and the Thakkhola valley of Nepal (Hatlberg & Clark, 1984) recognized only the generalized *N. carinata-H. typicalis* fauna in basal Triassic strata.

Recently, Garzanti et al. (1995) reported conodonts from the «First limestone band» of the Tamba Kurkur Formation of Spiti (Lingti, Guling, Losar, Gechang). These included several of the species differentiated by Orchard et al. (1994) from the *Otoceras latilobatum* Zone in Selong, Tibet, from which the conodonts had formerly been regarded as Changshingian in age. Orchard et al. (1994) regarded the Selong conodont fauna as wholly distinct from that of the Changshing

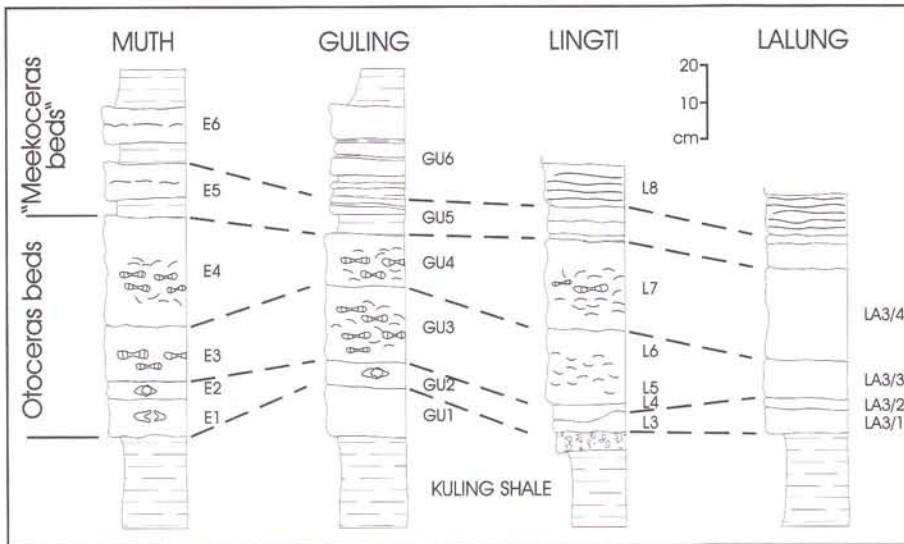


Fig. 2 - Correlation of stratigraphic sections for the lowermost Triassic at four Spiti sections showing bed numbers (=conodont samples) and ammonoid-bearing intervals.

Limestone, and recorded *Hindeodus parvus* throughout the bed. Mei (1996) confirmed these findings, although contemporary reports of conodonts from late Griesbachian «unit A» of the Tamba Kurkur Formation in the Thakkhola area continued to identify species typical of the Changshing Limestone (Belka & Wiedmann, 1996). The new Himalayan data presented here were summarized in a preliminary way by Krystyn & Orchard (1996). Fossil data from four Spiti sections are documented in this report, namely Muth, Guling, Lingti, and Lalung (Figs. 1, 2). Ammonoid faunas collected from the first three sections are summarized in Fig. 3, which also presents the ammonoid zonation for Spiti (after Krystyn).

Beyond the Himalayas, *Otoceras* is well known from the Arctic region (Dagys 1994; Tozer, 1994), but precise correlation between the Arctic ammonoid faunas and those from the Himalayas is uncertain (Fig. 3). Boreal P-T boundary conodont faunas are also far less abundant than those from Spiti and are largely undescribed. Both Henderson (1993) and Kozur (in Wignall et al., 1996, p. 44) have reported typical Changshingian *Neogondolella* ex gr. *subcarinata* from the Lower Griesbachian (=Otoceras beds), of respectively Ellesmere Island and Greenland, but these records cannot yet be fully evaluated. Limited data provided by Henderson and Baud (1997) suggest that the *Otoceras* beds from the Canadian Arctic correlate with the P-T boundary transition beds of Meishan, China (Orchard & Tozer, 1997).

Until recently, conodont zonation of the P-T boundary interval was based on a mixture of *Neogondolella* species (especially in the Upper Permian) and species of *Hindeodus-Isarcicella* (in the lowermost Triassic) (e.g., Zhang et al., 1996). The recognition of different conodont biofacies about the P-T boundary (see Orchard, 1996) has led to separate zonations for «shallow water» (*Hindeodus*) and «pelagic» (*Neogondolella*) facies (Wang & Wang, 1997), although neither are well docu-

mented. Indices of the former biofacies have received far more attention however and the species *Hindeodus parvus* has been strongly favoured as a P-T boundary index (Yin et al., 1996). The *Neogondolella* biofacies has been relatively poorly known in spite of the predominance of the nominal genus in many faunas. Kozur et al. (1995, pp. 182-3) have argued that morphological variability in this group, which has been commonly referred to Clarkina, precludes their use as reliable index fossils for the P-T boundary. This paper presents evidence to the contrary.

Spiti conodont faunas (MJO).

More than 12,000 conodont elements have been recovered from lowermost Triassic samples collected by L. Krystyn from four Spiti sections: Muth, Guling, Lingti, and Lalung (Figs. 1, 2). All these collections are dominated by *Neogondolella* pectiniform elements (85%), with fewer specimens of *Hindeodus-Isarcicella* (<4%) and ramiform (<12%) elements. In common with conodont faunas from the *Otoceras latilobatum* Zone in Selong (corresponding percentages: 68, 19, 13), those from Spiti represent a predominantly pelagic *Neogondolella* biofacies (Fig. 4A, B). As at Selong (Orchard et al., 1994), the key indices *Hindeodus parvus* and *Isarcicella staeschei* constitute only 0.5% of the conodont fauna from Spiti, but these key elements are nevertheless crucial in establishing correlations with other areas where a *Hindeodus-Isarcicella* biofacies predominates.

Paleoecological controls on P-T boundary conodont distribution have recently been discussed by Kozur (1996, pp. 84-87), who suggested very specific controls to explain observed anomalies. Orchard (1996, p. 36) pointed out that, in general, the relative abundances of *Hindeodus* and *Neogondolella* varied in an onshore-offshore relationship, with the former more common in shallower water habitats. Although faunal partitioning was rarely absolute (the exclusively *Hindeodus*-bearing Werfen Formation in the Alps being one exception, and many *Neogondolella*-bearing deep-water radiolarian cherts being another), key *Hindeodus* species may be very rare or absent in small collections of pelagic conodont faunas. This is precisely the situation in the Hima-

DIENERIAN	SPITI	MUTH	GULING	LINGTI	CANADA
	Zones				Zones
	<i>Pleurogyronites planidorsatus</i>	<i>P. planidorsatus</i> <i>S. ellipticum</i> <i>Proptychites</i> n. sp. 1 <i>Kymatites</i> sp. E6	<i>P. planidorsatus</i> <i>S. ellipticum</i> <i>A. cf. lilangensis</i> <i>Proptychites</i> sp. GU6	<i>Proptychites</i> sp. L8	<i>Proptychites candidus</i>
?	"unnamed interval"	<i>Meekophiceras</i> ? sp. E5	<i>Pleurogyronites</i> ? sp. <i>M. ?varaha</i> <i>Proptychites</i> ? sp. <i>Kymatites</i> sp. GU5	(gap)	? (<i>Bukkenites strigatus</i>)
GRIESBACHIAN	<i>Ophiceras tibeticum</i> [+ <i>Discophiceras</i> cf. <i>wordiei</i>]	<i>D. cf. wordiei</i> <i>O. sakuntula</i> <i>O. tibeticum</i> E4	<i>Bukkenites</i> sp. <i>D. cf. wordiei</i> <i>O. sakuntula</i> <i>O. tibeticum</i> <i>O. cf. bandoi</i> GU4	<i>O. cf. tibeticum</i> L7	<i>Ophiceras commune</i>
	<i>Otoceras woodwardi</i>	<i>O. cf. tibeticum</i> <i>O. bandoi</i> <i>Ophiceras</i> n. sp. 1 <i>O. woodwardi</i> E3	<i>O. bandoi</i> <i>Ophiceras</i> n. sp. 1 <i>O. woodwardi</i> GU3	<i>O. cf. bandoi</i> L5-L6	
	[+ <i>Ophiceras bandoi</i>]	<i>O. woodwardi</i> E2	<i>O. bandoi</i> <i>O. woodwardi</i> GU2	_____	?
		<i>O. bandoi</i> <i>O. woodwardi</i> E1	_____	_____	L3

Fig. 3 - Composition and succession of ammonoid faunas (with bed numbers) in the lowermost Triassic at three Spiti sections and equivalent Canadian ammonoid zones. See Fig. 5 for conodont-based correlation of beds.

layan sections where the presence of *H. parvus* in the *Otoceras* beds was long disputed.

Hindeodus-Isarcicella successions.

Key P-T boundary species of *Hindeodus* and *Isarcicella* have been related within a 'morphocline' that has been interpreted as comprising the successive species *Hindeodus typicalis*, *H. latidentatus*, *H. parvus*, *Isarcicella turgida*, and *I. isarcica* (Kozur, 1990a, p. 390; Yin et al., 1996; Ding et al., 1996). Recently, the lineage has been revised as *Hindeodus latidentatus praeparvus* - *H. parvus* - *Isarcicella turgida* - *I. i. staeschei* - *I. i. isarcica* (Kozur, 1996, pp. 94, 100), and as *Hindeodus latidentatus* - *H. parvus* - *Isarcicella staeschei* - *I. isarcica* with an independent *Hindeodus priscus* - *H. turgidus* line (Wang & Wang, 1997). In this paper, *Hindeodus latidentatus* sensu stricto is not viewed as directly ancestral to *H. parvus*, but as a separate development from *H. typicalis* in the latest Permian. Most elements formerly included in *H. latidentatus* are now assigned to *H. praeparvus*, which includes more probable precursors of *H. parvus*. Variants of *H. typicalis* are also candidates as ancestors of *H. parvus*. Sweet (1988, p. 120) has also suggested a quite different origin for *Isarcicella* in *Diplognathodus*. The phyletic position of *H. turgidus* is uncertain, not least because of uncertainty about an ecological control on element thickness (Kozur, 1995, p. 72). Species of *Isarcicella* (as used herein) show progressive acquisition of accessory lateral nodes and are valuable indices.

Lai (1998), in a very recent review of the *Hindeodus-Isarcicella* group, continued to employ a very broad

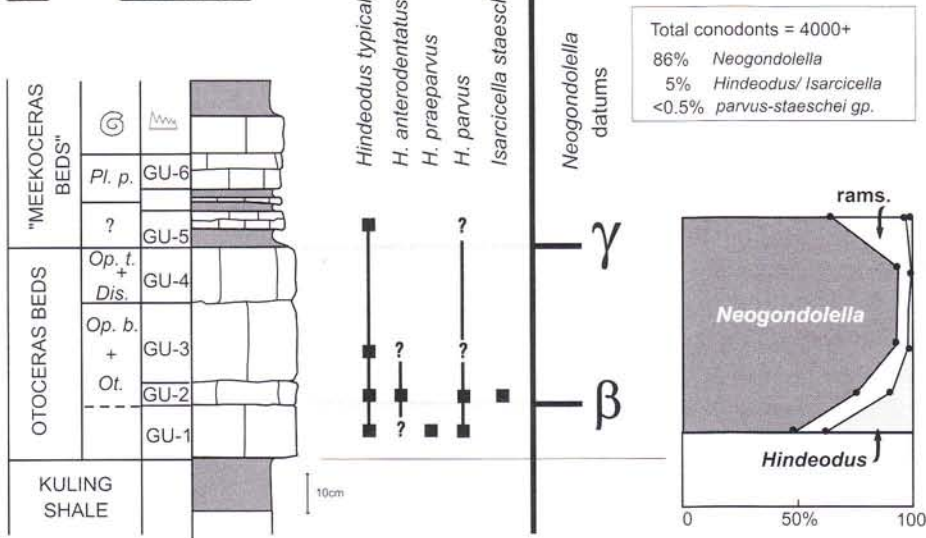
interpretation of *H. latidentatus*, and furthermore submerged *H. staeschei* in *I. isarcica*. The question of the ancestry of *H. parvus* was also discussed by Lai (1998) as well as by Yin (1998). The present author fully agrees that it is of little consequence whether the prospective antecedent *H. typicalis* or *H. praeparvus* (*H. latidentatus* of authors) cooccurs with *H. parvus*. In spite of statements to the contrary (Kozur, 1996, p. 94), Orchard (in Krystyn & Orchard, 1996) made

no such assertion. Rather, in pointing out that *H. praeparvus* (= *H. n. sp. X* sensu Orchard, = *H. latidentatus* emend sensu Kozur partim, not = *H. latidentatus*) cooccurs with *H. parvus*, Orchard (op. cit., p. 19) wished to show that *H. praeparvus* should not be regarded as definitive for Permian strata, as has been implied by Kozur et al. (1995, p. 184).

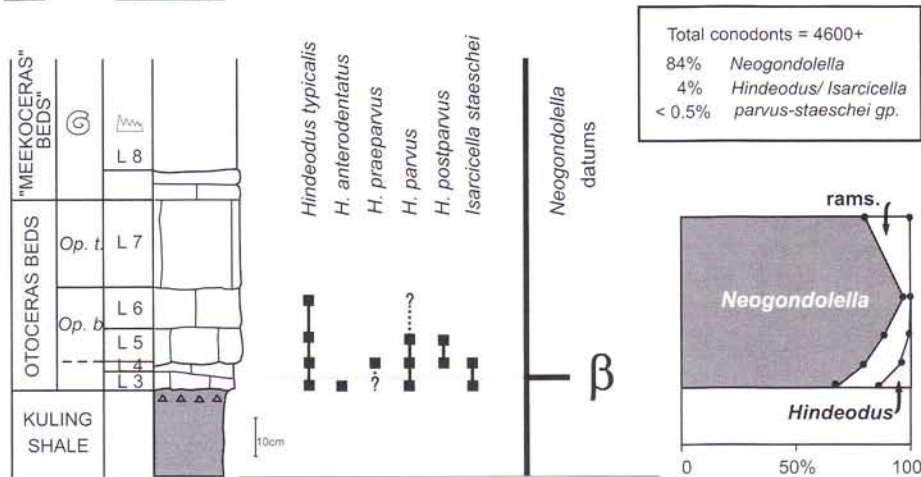
Regarding the identity of the single specimen of *Hindeodus* reported from bed 25 at Meishan (Zhang et al., 1995), Orchard (1996, p. 37-38) viewed this specimen as typical of neither *H. latidentatus* nor *H. parvus*, but preferred an alignment with the latter. Yin (1998, p. 19) states that some Chinese researchers have concluded that the specimen in question represents *H. latidentatus* rather than *H. parvus* because it has a compressed rather than a rounded cusp, although this criterion has not previously been widely used to differentiate the two species. The Meishan specimen from bed 25 differs from *H. latidentatus* in its prominent cusp, a feature that according to the «arbitrary definition» introduced by Kozur et al. (1995, p. 184) would result in the assignment of this specimen to *H. parvus*. However, rather than attach great significance to this single occurrence, the specimen is here taxonomically isolated as *H. aff. parvus* (Fig. 4C).

In Spiti, the most common *Hindeodus* species by far is the conservative and long-ranging *H. typicalis* (Table 1). This is the only *Hindeodus* species in samples from Muth, where the genus is uncommon. Strictly interpreted, the section at Muth could be referred to the *typicalis* Zone, a generalized boundary interval that precedes the *H. parvus* datum (e.g., Zhang et al, 1996).

4A GULING



4B LINGTI



4C MEISHAN

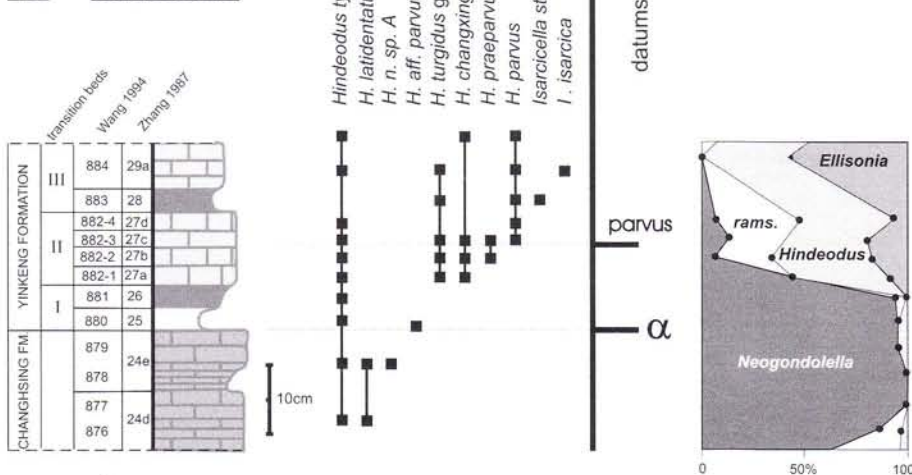


Fig. 4 - Occurrence of *Hindeodus* and *Isarcicella* species, *Neogondolella datums*, and their relationship with conodont biofacies in sections at A) Guling, B) Lingti, and C) Meishan. Ammonoid faunas of the Spiti sections abbreviated (see Fig. 3). For Meishan, relative abundance data is derived from Wang (1995, p. 141), and the occurrence of selected species is modified from recent reports by Wang (1994, 1995), Kozur et al. (1995), Kozur (1996), Yin et al. (1996), and Zhang et al. (1996). The *H. turgidus* group embraces *H. turgidus*, *H. cf. turgidus* and *H. priscus*.

However, the Muth samples are younger than this because they contain *Neogondolella* species of the *krystyni* Zone (see below), which implies that both *H. parvus* and *I. staeschei* were extant but absent due to either unfavourable biofacies or collection failure.

Hindeodus parvus is present throughout the lower parts of the sections at Guling, Lingti, and Lalung, and is accompanied by small numbers of *Isarcicella staeschei* except at the base of the Guling section, where rare *H. praeparvus* cooccur with *H. parvus* (but no ammonoids). The basal bed of the Guling section (Figs. 4A, 5) is therefore referred to the *parvus* Zone, whereas the basal beds of other Spiti sections are referred to the younger *staeschei* Zone *sensu* Wang (1996) (Fig. 5). Kozur (1996, p. 100) reported very rare *H. staeschei* from the uppermost *parvus* Zone too, but such occurrences should be assigned to the *staeschei* Zone. All but one of the 14 specimens of *I. staeschei* in the Spiti collections have a single lateral node, and this morphotype appears prior to more denticulate forms, both in Spiti and elsewhere (Wang, 1996; Kozur, 1996).

Several specimens of *Hindeodus anterodentatus* occur in

the collections from Guling and Lingti (Table 1), implying the *isarcica* Zone sensu Kozur (1996, p. 96), which embraces the *staeschei* Zone sensu Wang (1996). *Isarcicella isarcica* sensu stricto, which defines a zone above the *staeschei* Zone according to Wang (1996), is unknown in the Spiti collections. However, isolated specimens resembling the even younger zonal index species, *H. postparvus*, are recorded from Lingti (Fig. 4B). Kozur (1996, p. 98) stated that this species first occurred in the *isarcica* Zone below its main occurrence in the overlying *postparvus* Zone, but definition of the latter zone (Wang & Wang, 1997) would also designate such occurrences as lying within the *postparvus* Zone. These anomalies aside, there is insufficient material to clearly identify the *isarcica* or *postparvus* zones in Spiti, or to delimit the upper ranges of the key species (Fig. 6).

In Spiti, virtually all of the occurrences of *Hindeodus* and *Isarcicella* fall within the *Otoceras woodwardi* (+*Ophiceras bandoi*) beds and subjacent strata (Figs. 3, 4A, B; Table 1). At Guryul Ravine, a part of the

woodwardi Zone occurs below both *I. staeschei* and *H. parvus*, but too few conodonts occur in these strata (Khunamuh Formation, E2) to confidently identify a zone. In view of the succession at Selong where *Otoceras latilobatum* underlies the *O. woodwardi* Zone, it is likely that the lower *Otoceras* beds in Kashmir correspond to the *parvus* Zone (Fig. 5), in spite of the absence of the nominal conodont species. The strata above the Woodwardi Zone in Spiti contains *Ophiceras tibeticum* (+*Discophiceras* cf. *wordiei*) but are devoid of *Hindeodus/Isarcicella*, presumably reflecting some ecological filter. This contrasts with the situation at Guryul Ravine where most of the *I. staeschei* specimens (which are mostly 'advanced' forms with more than one lateral denticle) originated in strata referred to the Tibeticum Subzone (Matsuda, 1981, table 10). Kozur (1996) also reported *H. postparvus* from the *Ophiceras tibeticum* Zone. The calibration of the younger *Hindeodus/Isarcicella* zones with the Lower Triassic ammonoid faunas remain uncertain (Fig. 5).

	Guling					Lingti					Lalung				Muth			Selong		
	1	2	3	4	5	3	4	5	6	7	1	2	3	4	1	2	4	l	m	u
<i>H. anterodentatus</i>	?	3	?			4														?
<i>H. parvus</i>	22	5	?		?	12	5	1	?		2	3						4	4	15
<i>H. postparvus</i>							1	1												
<i>H. praeparvus</i>	2					?	1													
<i>H. typicalis</i> + <i>H. sp. ind.</i>	205	64	4		1	134	43	9	2		30	20	3		2	1		39	400	95
<i>I. staeschi</i>		2				4	5				2		1							1
<i>N. carinata</i>	R	A	A	A	C	A	A	A	A	C	P	A	A	A	A	A	C	C		R
<i>N. discreta</i>					A															
<i>N. kazi</i>								P	C											
<i>N. krystyni</i>		A	A	A	R		P	A	A	C			P	A	P	C	C			?
<i>N. meishanensis</i>	C	A	C	R		P	P	C	C		R	P	P	R	R	R	R	C	P	C
<i>N. nassichuki</i>	R	R				R	R	R	R		R	P	P		R	R	R	R	R	R
<i>N. nevadensis</i>		R	R	R					R	R				R		R	R			
<i>N. orchardi</i>	C	P				C	C	P	P		P	P	P	P	R	R		A	A	A
<i>N. planata</i>	R	A	C	A	P	A	A	A	A	C	A	A	A	A	P	C	P	A	A	A
<i>N. taylorae</i> - alpha	P	A	A	A	C	P	P	A	A	C	A	A	C	C	C	P	A	A	C	C
- beta	R	R	C	C		R	R	R	P		R	R			R	R	P	R	R	R
- gamma		R	P	P	P	R	P	R	P			R	R		P					
<i>N. tulongensis</i> - alpha	P	P	P	C	R	C	P	C	C	P	C	P	R	R	P	R	P	A	P	C
- beta		P	C	P			R		R		R	R	R			R	P	R	R	
- gamma	R	R	P	P			R	R	R		P	R		R			R	P	R	R
<i>N. zhejiangensis</i>	C	R	R			C	P	P	R		R	P						R	R	R
<i>N. sp. A</i>			R	R				P	P			R				R		P	R	R

Tab. 1 - Occurrence of conodont taxa in the Spiti and Selong sections. Numbers are given for *Hindeodus* and *Isarcicella* species, whereas only relative abundances are provided for the much more numerous (though often incomplete) *Neogondolella* species. R=rare (1-3 specimens), P=present (4-9), C=common (10-20), A=abundant (21+).

erable morphological variation, which has been rationalized by classifying specimens into thirteen morpho-species, four of which are newly named (Table 2). *Neogondolella taylorae* and *N. tulongensis* occur throughout the studied sections; *N. carinata* and *N. planata* are almost as wide-ranging; *N. meishanensis*, *N. nassichuki*, *N. orchardi*, and *N. zhejiangensis* occur through much of the sections but disappear earlier; and *N. krystyni* is widespread and appears later than most of the other species, sometimes associated with uncommon *N. kazi* and *N. sp. A*. A further new species, *N. discreta*, is reported only from the higher part of the Guling section, immediately preceding *Neospathodus kummeli*. A synthetic range chart for the species is shown in Fig. 6, which also incorporates known occurrences of the species in the *Otoceras latilobatum* bed of Selong (Orchard et al., 1994), the transition beds at Meishan (see Fig. 4C), and the lowermost Blind Fiord Formation in the Canadian Arctic (Henderson & Baud, 1997).

The range interval of *Neogondolella taylorae*, which was named in Selong and occurs in all the studied Spiti collections, has been termed the *taylorae* Zone (Orchard, in Krystyn & Orchard, 1996). The nominal species occurs also in Kashmir (Matsuda, 1984) and in Arctic Canada (Henderson and Baud, 1997), commonly associated with *N. carinata*. The interval characterized

by the two species is here subdivided and superceded by three new zones based on successive first appearances of *Neogondolella meishanensis*, *N. krystyni* and *N. discreta*. The development of these species, and of different morphotypes of associated species, is seen as a progressive morphological change in the configuration of the axial part (blade-carina-cusp) of the pectiniform elements (Orchard in Krystyn & Orchard, 1996). The *Neogondolella*-based subdivisions of the Griesbachian are defined below.

Neogondolella meishanensis Zone.

Base of zone: Appearance of *Neogondolella meishanensis*.

Top of zone: Appearance of *Neogondolella krystyni*.

Reference section: Meishan, China.

Occurrence: *Otoceras concavum* and *O. boreale* zones, Ellesmere Island; *O. latilobatum* Zone, Selong; *O. woodwardi* Zone, Guling, Lingti, Lalung, and Guryul Ravine; transition beds I and ?II, Meishan; Kathwai Dolomite, Salt Range.

The *meishanensis* Zone corresponds to or approximates the former Lower *taylorae* Zone, the interval lying above the alpha datum of Orchard (in Krystyn & Or-

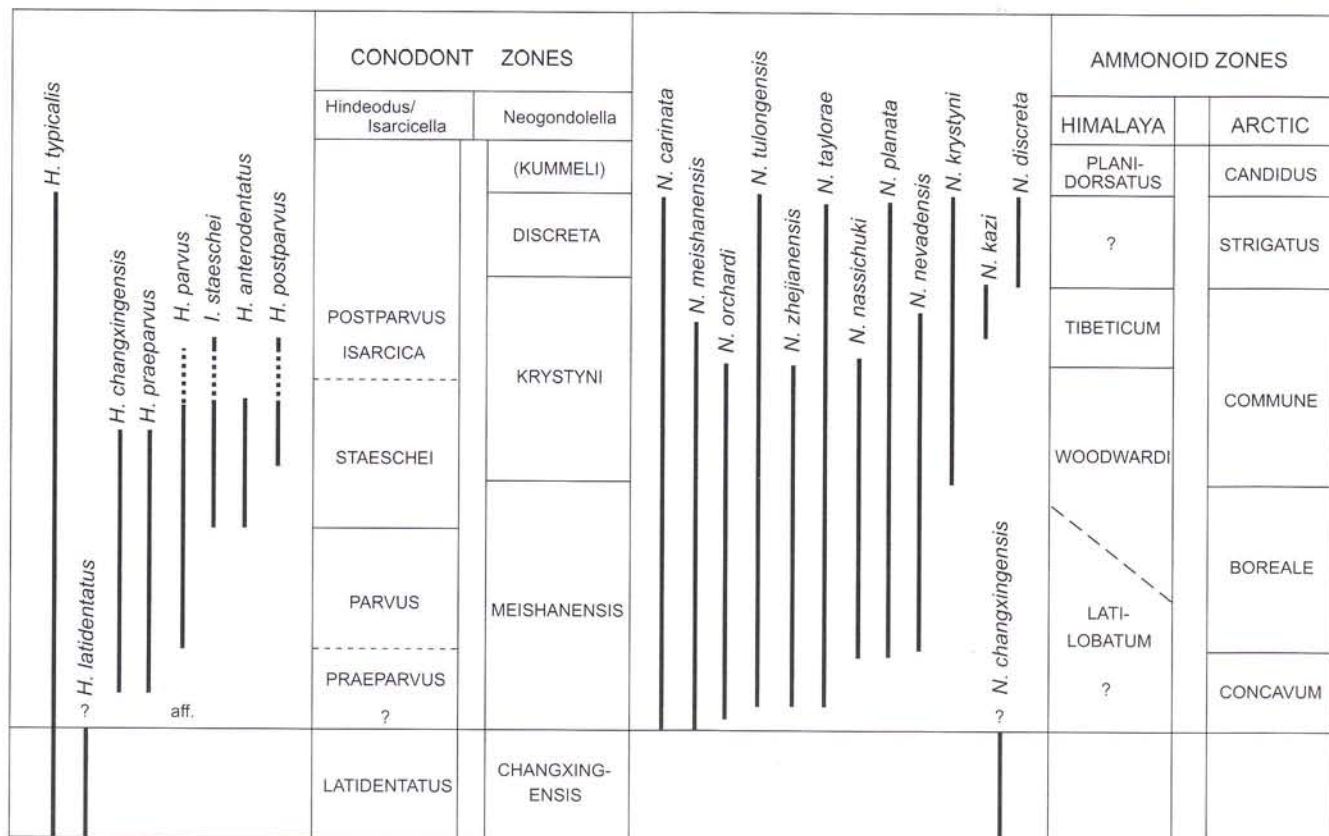


Fig. 6 - Conodont and ammonoid zonation of the lowermost Triassic and synthetic ranges of conodont taxa based on successions showed in Fig. 5. Note the appearance of 'typical' Griesbachian conodont taxa within the lower transition beds at Meishan; occurrences of 'typical' Permian conodont taxa (e.g., *N. changxingensis*, *H. latidentatus*) at this level are uncertain.

<i>N. carinata</i>	broad platform, maximum width medially, posteriorly indented.
<i>N. discreta</i>	narrow platform; high discrete carinal denticles.
<i>N. kazi</i>	broad posteriorly rounded platform; high and fused carinal denticles.
<i>N. krystyni</i>	platform margins parallel to undulose; elevated posterior carina.
<i>N. meishanensis</i>	upturned platform margins, straight carina, high terminal cusp.
<i>N. nassichuki</i>	narrow, evenly tapered platform with maximum width medially.
<i>N. nevadensis</i>	broad platform, maximum width near posterior end; carina extends to or beyond posterior end.
<i>N. orchardi</i>	narrow, curved and pointed platform with terminal cusp.
<i>N. planata</i>	broad, evenly tapered platform with maximum width medially.
<i>N. taylorae</i>	broad, rounded posterior margin, prominent cusp with posterior brim.
alpha	- as holotype; length:width ratio = 2:1.
beta	- relatively short bulbous platform due to anterior narrowing.
gamma	- relatively narrow, long platform; length:width ratio = 3:1.
<i>N. tulongensis</i>	subquadrate platform +/-sinuous margin.
alpha	- symmetrical quadrate platform.
beta	- platform with sinuous inner margin.
gamma	- form with strongly deflected posterior carina.
<i>N. zhejiangensis</i>	elongate-oval platform, rounded posterior margin, low carinal nodes, indistinct cusp +/-accessory posterior denticles.
<i>N. sp. A</i>	oblong platform, high carina, sinuous margin.

Tab. 2 - A summary of diagnostic morphological characteristics of *Neogondolella* species occurring in the lowermost Triassic.

chard, 1996). Above this datum, *Neogondolella* species are characterized by the diminution of the blade-carina and vertical growth of the cusp. One such species is *N. meishanensis*, a species based on material from the lower transition beds at Meishan (Fig. 4C, I) for which a biostratigraphic interval was named by Zhang et al. (1996). Although *N. taylorae* itself has not been described from Meishan, it may occur (see synonymy below) and certainly other commonly associated elements (including *N. meishanensis*) do. The *meishanensis* Zone, which is in direct superimposition with the *changxingensis* Zone at the reference section, is therefore employed as the conodont zone for the lowermost Griesbachian *Neogondolella* fauna (Figs. 5, 6). Associated conodont species characteristically have relatively low, discrete blade-carina denticles, and either a distinctive, upright cusp (*N. taylorae*, *N. tulongensis*, *N. carinata*, *N. nassichuki*), or, less commonly, an inconspicuous cusp (*N. zhejiangensis*). Some elements have subquadrate platforms, often with sinuous lateral margins (*N. tulongensis*). In many of these species, the cusp is surrounded by a platform brim whereas in *N. meishanensis* and *N. orchardi* the cusp is terminal.

The *meishanensis* Zone occurs in collections from the Guling (Gu-1), Lingti (L3), and Lalung (LA-1, -2) sections, none of which have associated ammonoids. It is also represented in the *Otoceras latilobatum* bed at Selong (Orchard et al., 1994) and apparently in the underlying «Changshingian» bed (Mei, 1996), which H. Geldsetzer (pers. comm., 1994) includes in the Triassic. The *meishanensis* Zone is equivalent to the *parvus* Zone and part of the *staeschei* Zone in Spiti and Selong. Elsewhere, some of the *Neogondolella* indices appear earlier than *H. parvus*, as for example in the Canadian Arctic (Henderson and Baud, 1997), and at Meishan, China (Fig. 4C). In these cases, the full complement of *Neogondolella* species seen in Selong and Spiti are also missing

from the relatively impoverished faunas so it is not clear whether all these species, including *H. parvus*, appear concurrently. In spite of these shortcomings at Meishan, the locality is chosen as the reference section for the base of the *meishanensis* Zone because the relationship with the older *changxingensis* Zone can be demonstrated, which it cannot elsewhere. The top of the *meishanensis* Zone has yet to be delineated at Meishan, but should be anticipated at about bed 28-29 (Fig. 4C), within the *staeschei* Zone.

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Neogondolella krystyni Zone.

Base of zone: appearance of *Neogondolella krystyni*.

Top of Zone: appearance of *Neogondolella discreta*.

Reference section: Guling, Spiti.

Occurrence: *Otoceras woodwardi* and *Ophiceras tibeticum* zones, Guling, Lingti, Lalung, and Muth; ?*Ophiceras commune* Zone, Ellesmere Island; topmost Kathwai Dolomite and Kathwai Limestone, Salt Range.

The *krystyni* (formerly the Middle *taylorae*) Zone lies above the beta datum of Orchard (in Krystyn & Orchard, 1996; Fig. 4A, B), which is marked by the development of *Neogondolella* species with accentuated posterior growth and often by greater fusion of the axial region. This morphology is best exemplified by *Neogondolella krystyni* which appears in the Lingti (L4, 5, 6, 7), Guling (Gu-2, 3, 4), Lalung (LA3-3, 4), and Muth (E1, 2, 4) sections. Other species that exhibit elevated carinas within the *krystyni* Zone are the advanced beta morphotype of *N. tulongensis*, *N. kazi*, and *N. sp. A*. Three species characteristic of the *meishanensis* Zone, that is *N. orchardi*, *N. nassichuki*, and *N. zhejiangensis*, occur only in the lower part of the *krystyni* Zone.

In Spiti, the major part of the *krystyni* Zone lies within the *Otoceras woodwardi* Zone, whereas the upper part of the conodont zone (above the disappearance of *N. orchardi*, *N. nassichuki*, and *N. zhejiangensis*) corresponds to the *Ophiceras tibeticum* Zone. In terms of the *Hindeodus-Isarcicella* zones, the *krystyni* Zone corresponds to part of the *staeschei* Zone and possibly also the younger *isarcica* and *postparvus* zones (Figs. 5, 6).

Neogondolella discreta Zone.

Base of zone: appearance of *Neogondolella discreta*.

Top of Zone: appearance of *Neospathodus kummeli*.

Reference section: Guling, Spiti.

Occurrence: unnamed interval below the *Pleurogyronites planidorsatus* Zone, Guling; *Bukkenites strigatus* Zone, Ellesmere Island; lower part of Lower Ceratite Limestone, Salt Range.

The *discreta* (formerly the Upper *taylorae*) Zone lies above the gamma datum of Orchard (in Krystyn & Orchard, 1996; Fig. 4A), which is characterized by the appearance of a species with a strongly elevated axial region and separation of the carinal denticles. In Spiti, the zone is recognized in the Guling section (Gu-5) where *Neogondolella discreta* occurs with several species that range from subjacent strata. *Neogondolella discreta* is the precursor of *Neospathodus kummeli* which has discrete carinal denticles and an almost entirely reduced platform.

The *discreta* Zone corresponds to Bed 5 at Guling, originally established as the lower part of the *Pleurogyronites planidorsatus* Zone of Spiti (Krystyn in Krystyn & Orchard, 1996), but supplementary ammonoid collections from Guling show most of the genera are new with intermediate ophiceratid-gyronitid morphology; true *Pseudogyronites* and *Protychites* are absent. The fauna of Bed 5 is therefore excluded from the previously adopted ammonoid zonal scheme (Krystyn & Orchard, 1996) and assigned to an informal unnamed interval between the *Ophiceras tibeticum* and *Pleurogyronites planidorsatus* zones (Fig. 3). The latter ammonoid zone starts with Bed 6 in Guling and Muth and with Bed 8 in Lingti, and is characterized in all cases by the appearance of the conodont *Neospathodus kummeli*, which occurs immediately above the *discreta* Zone both at Guling and at its type locality Chhidru A in the Salt Range (Fig. 5). The *discreta* Zone is also recognized in some collections from the *Bukkenites strigatus* Zone of the Canadian Arctic (Orchard & Tozer, 1997).

Summary.

Abundant conodont collections have been recovered from the lowermost Triassic strata in sections at Guling, Lingti, Muth and Lalung in Spiti. These strata contain a succession of ammonoids that are characterized as, in ascending order, the *Otoceras woodwardi*, *Ophiceras tibeticum*, an unnamed interval, and the *Pleurogyronites planidorsatus* zones.

Conodont collections from Spiti are dominated by pelagic *Neogondolella* with fewer *Hindeodus* specimens, most of which are conservative *H. typicalis*. Only a very small percentage of the fauna consists of short-ranging *Hindeodus* and *Isarcicella* species, and these taxa do not

occur at all in the *Ophiceras tibeticum* Zone. Ammonoid beds of the *Otoceras woodwardi* Zone carry conodonts of the *staeschei* Zone. The basal bed of the Guling section (without ammonoids) is referred to the older *parvus* Zone. There are too few representatives of the *Hindeodus/Isarcicella* group in the higher beds of the Spiti sections to delineate *Isarcicella* zones above the *staeschei* Zone. Evidence from elsewhere implies that the conodont indices were extant through the *Ophiceras tibeticum* Zone and their absence in Spiti probably results from unfavourable biofacies.

Three new *Neogondolella*-based zones are differentiated. The oldest interval (above α datum) is the *meishanensis* Zone, which occurs in the lowest beds of the Guling, Lingti and Lalung sections; it corresponds to the *parvus* and lower *staeschei* Zone. The next interval (above β datum) is the *krystyni* Zone, which starts within the *staeschei* Zone and is equivalent to the *O. woodwardi* and *O. tibeticum* zones. The youngest pelagic conodont zone (above γ datum) is assigned to the *discreta* Zone, corresponding to an unnamed interval beneath the *Planidorsatus* Zone, which itself is characterized by *Neospathodus kummeli*. Each of the new zones is recognized in the Salt Range (Fig. 5) and the Canadian Arctic (Henderson & Baud, 1997; Orchard & Tozer, 1997).

The *meishanensis* Zone also occurs in the *Otoceras latilobatum* bed in Selong and the transition beds at Meishan. In Guryul Ravine, Kashmir, the conodonts of the *Otoceras-Ophiceras* beds belong to an undetermined part of the *taylorae* Zone *sensu* Orchard (in Krystyn & Orchard, 1996). Relatively advanced specimens of *Hindeodus parvus* appear at about the middle of the Woodwardi Zone in Kashmir (Matsuda, 1981) and are associated with *Isarcicella staeschei*, albeit an atypical specimen; older examples of *H. parvus* should be anticipated beneath this level (Matsuda, 1981, fig. 2, bed 56), within the lower *O. woodwardi* beds where conodonts are uncommon.

In the Canadian Arctic, conodont species of the *meishanensis* Zone occur both within and below the *O. boreale* Zone, at the base of which *H. parvus* is reported to appear (Henderson and Baud, 1997). *Hindeodus* are rare in the lowermost Triassic of the Canadian Arctic and the delineation of the *H. parvus* Zone is problematic. In Greenland, *H. parvus* is reported to appear at the base of the *Ophiceras commune* Zone (Wignall et al., 1996, p. 44) but there is no available abundance data or information on associated gondolellids.

At Meishan, *Otoceras?* sp. occurs in bed 26 whereas *H. parvus sensu stricto* has not been found below bed 27c (Fig. 5). *Neogondolella* species of the *meishanensis* Zone occur in the lower transition beds at Meishan and the base of that zone is drawn at the top of the Changshing Limestone. Although a unique specimen of

Hindeodus aff. *parvus* occurs in bed 25, *Hindeodus* is rare below bed 27, the base of which appears to mark a conodont biofacies change rather than a conodont extinction event (Fig. 4C). Several new *Hindeodus* species appear in bed 27 at Meishan, including *H. praeparvus*, the apparently endemic *H. changxingensis*, and (10 cm higher) *H. parvus*. In northern Jiangxi, *H. parvus* is reported to occur immediately above the event-stratigraphic boundary (corresponding to base of bed 25 at Meishan) (Zhu et al., 1997), although this is disputed (Wang & Wang, 1997).

Conodonts from the *Otoceras woodwardi* Zone of Spiti are not Late Permian but are wholly younger than transition beds 25-27 of Meishan, China. Basal Triassic strata (lacking ammonoids) from Guling, Spiti correlate with (at least) transition bed 27c-d at Meishan, but also contain the same *Neogondolella* fauna as transition beds 25-26, as does the *Otoceras latilobatum* Zone at Selong, and apparently the *Otoceras* zones of the Arctic. *Hindeodus parvus* may appear coincident with (e.g., Selong) or later (e.g., Meishan, the Arctic) than the *Neogondolella* fauna. In those sections where *H. parvus* appears later, the impact of ecological exclusion and/or collection failure should be considered. It is concluded that the *Neogondolella* faunal change datum is close to, if not coincident (in a mixed biofacies) with the first appearance datums of both *Otoceras* and *Hindeodus parvus*, and each of these may serve in P-T boundary definition.

Taxonomy

The following excludes suprageneric hierarchy and descriptions of species are based only on pectiniform Pa elements. Synonymies are limited to key citations and are not intended to be comprehensive (see also occurrences). All specimens illustrated on Plates 1-6 are shown at a magnification of x80, a suitable standard for comparative study.

Genus *Hindeodus* Rexroad and Furnish, 1964

Type species: *Hindeodus cristulus* (Youngquist and Miller, 1949).

Remarks: *Hindeodus* has a seximembrate apparatus (Sweet, in Ziegler, 1977).

Hindeodus anterodentatus (Dai, Tian and Zhang, 1989)

Pl. 6, figs. 13, 15

- 1989 *Anchignathodus anterodentatus* Dai & Zhang, p. 428, pl. 45, fig. 14, 15; pl. 48, fig. 10, 11.
1996 *Hindeodus parvus anterodentatus* - Kozur, pp. 96-7, pl. 4, fig. 5 (cum syn.).

Diagnosis: The Pa element of this species has 1-3 denticles on the anterior edge of a cusp that is about two or more times higher than the posterior denticles, which are about equal in size and height.

Remarks: Kozur (1996) regarded this form as a short-ranging subspecies and derivative of *Hindeodus parvus*. The uncommon Spiti specimens have a moderately high and broad cusp and a derivation directly from *H. typicalis* through transitional forms (e.g., Pl. 6, fig. 14) is plausible.

Occurrence: *Otoceras woodwardi* Zone, Lingti and Guling. Worldwide in *isarcica* Zone (sensu lato) according to Kozur (1996).

Hindeodus latidentatus (Kozur, Mostler and Rahimi-Yazd, 1975)

Pl. 6, fig. 27, 28

1975 *Anchignathodus latidentatus* Kozur, Mostler and Rahimi-Yazd, pp. 4-5, pl. 2, fig. 6.

1994 *Hindeodus latidentatus* - Orchard et al., pl. 1, fig. 20.

1996 *Hindeodus latidentatus* - Mei, p. 146, pl. 18.2, fig. 5 (only).

1996 *Hindeodus typicalis* - Yin et al., pl. 1, fig. 1.

Diagnosis: The 3-4 posteriormost denticles of the blade of the Pa element are separated by broad 'U'-shaped spaces; the cusp is of moderate size.

Remarks: This is a distinctive species that became interpreted very broadly as *H. latidentatus* emend Kozur (1995). The species is here restricted to forms with the characteristic, ontogenetically stable, posterior denticulation. Kozur (1996) named such forms *H. l. latidentatus*, and distinguished a second subspecies, *H. l. praeparvus*, to accommodate most of the other specimens previously assigned to the emended species. The two forms have distinctive morphology and I see no basis for regarding them as subspecies of *H. latidentatus*.

Morphologically, *Hindeodus latidentatus* most closely resembles *H. parvus* rather than *H. typicalis* according to Yin (1998, p. 21) and Lai (1998, p. 27). However, the posterior denticles of both *H. parvus* and *H. typicalis* are generally more uniformly developed than in either *H. latidentatus* or *H. praeparvus*, both of which have carinal denticles of markedly different shape and size.

Occurrence: Red boundary clay, Kuh-e-Ali Bashi, Iran; Uppermost Changhsing Limestone, Meishan.

Hindeodus parvus (Kozur and Pjatakova, 1976)

Pl. 6, fig. 9, 16, 17, 20

1976 *Anchignathodus parvus* Kozur & Pjatakova, pp. 123-5, fig. 1a, b, e, h.

1981 *Hindeodus parvus* - Matsuda, pp. 91-3, pl. 5, fig. 1-3.

1981 *Hindeodus minutus* - Matsuda, pp. 78-84, pl. 1, fig. 28, 9-12 (only).

1994 *Isarcicella? parva* - Orchard et al., p. 833, pl. 1, fig. 21, pl. 2, fig. 5-7.

1996 *Hindeodus parvus* - Mei, pp. 145-6, pl. 18.2, fig. 2-4, 14.

1996 *Hindeodus parvus* - Kozur, pp. 94-97, pl. 2, fig. 5-8; pl. 3, fig. 1-10 (only); pl. 4, fig. 6 (only)(cum syn.).

1996 *Hindeodus parvus* - Yin et al., pl. 1, fig. 8a, b, 12; pl. 2, fig. 4-9.

1997 *Hindeodus parvus* - Wang & Wang, pl. 1, fig. 1-10; pl. 2, fig. 6-11.

Diagnosis: The cusp of the Pa element is more than twice the height of the posterior denticles, which are of subequal size and height except for several smaller ones that may be present on the posterior edge.

Remarks: Kozur (1990a, 1996) differentiated two morphotypes, later elevated to subspecies *erectus* and *parvus*, the former with a subvertical, usually adenticulate posterior edge, and the latter with a few denticles on the steeply inclined posteriormost blade. Mei (1996) added a third morphotype in which the posterior end was less inclined and denticulate. Each of these variants is here included in *H. parvus* although the holotype and most diagnostic forms are examples of *H. parvus erectus*, which has a profile typical of *Isarcicella* (Orchard, 1996). Two specimens included in *H. parvus erectus* by Kozur (1996) have only a moderately large cusp but feature large posterior denticles regarded here as diagnostic for *H. praeparvus*. A unique specimen of «*H. latidentatus*» from bed 25 at Meishan (Zhang et al., 1995, pl. 2, fig. 12) has an unusually large cusp, like *H. parvus*, although the posterior denticulation is similar to that of *H. latidentatus*. According to the definition introduced by Kozur et al. (1995, p. 184), this specimen could be assigned to *H. parvus*, some specimens of which it resembles (e.g., Wang & Wang, 1997, pl. 1, fig. 12). However, for reasons discussed earlier, this specimen is here referred to *H. aff. parvus*.

Occurrence: *Otoceras latilobatum* Zone, Selong; *O. woodwardi* Zone, Guling, Lingti, Lalung; *O. boreale* Zone, Ellesmere Island (Henderson & Baud, 1997); transition beds 25 (aff.), 27c, 27d, Meishan (Yin et al., 1996); beds 56-61 (E2-E3), Guryul Ravine (Matsuda, 1981); Kathwai Dolomite, Salt Range (Sweet, 1970b). Worldwide.

Hindeodus postparvus Kozur, 1990

Pl. 6, fig. 1

1990a *Hindeodus postparvus* Kozur, p. 400.

1996 *Hindeodus postparvus* - Kozur, pp. 98-99, pl. II, fig. 9, 10 (cum syn.).

Diagnosis: The Pa element has a large cusp, small anterior denticles, a distinctly arched upper profile, and strongly divergent posterior denticles.

Remarks: Only two incomplete elements of this species are identified from Spiti and neither are complete enough to show the arched upper profile, although both clearly have divergent posterior denticles.

Occurrence: *Otoceras woodwardi* Zone, Lingti. Lowermost Triassic, Eurasia.

Hindeodus praeparvus (Kozur, 1996)

Pl. 6, fig. 21?, 22, 23

1981b *Anchignathodus* cf. *latidentatus* - Bhatt et al., p. 200, pl. 2, fig. 20?, 24.

1994 *Hindeodus latidentatus* - Wang, pl. 1, fig. 9.

1995 *Hindeodus latidentatus* - Wang, pl. 2, fig. 4, 5.

1996 *Hindeodus* sp. X - Krystyn & Orchard, p. 19.

1996 *Hindeodus latidentatus* - Wignall, Kozur & Hallam, Fig. 1a.

1996 *Hindeodus latidentatus praeparvus* Kozur, pp. 93-4, pl. 1, fig. 10, 11; pl. 2, figs. 1-4 (cum syn.).

1996 *Hindeodus* cf. *parvus erectus* Kozur, pl. 3, fig. 11.

1996 *Hindeodus parvus erectus* Kozur, pl. 4, fig. 7.

1996 *Hindeodus latidentatus* - Yin et al., pl. 2, fig. 2, 3.

Diagnosis: The Pa element has a small to moderately large cusp and several posterior blade denticles which are distinctly larger than those of the anterior blade.

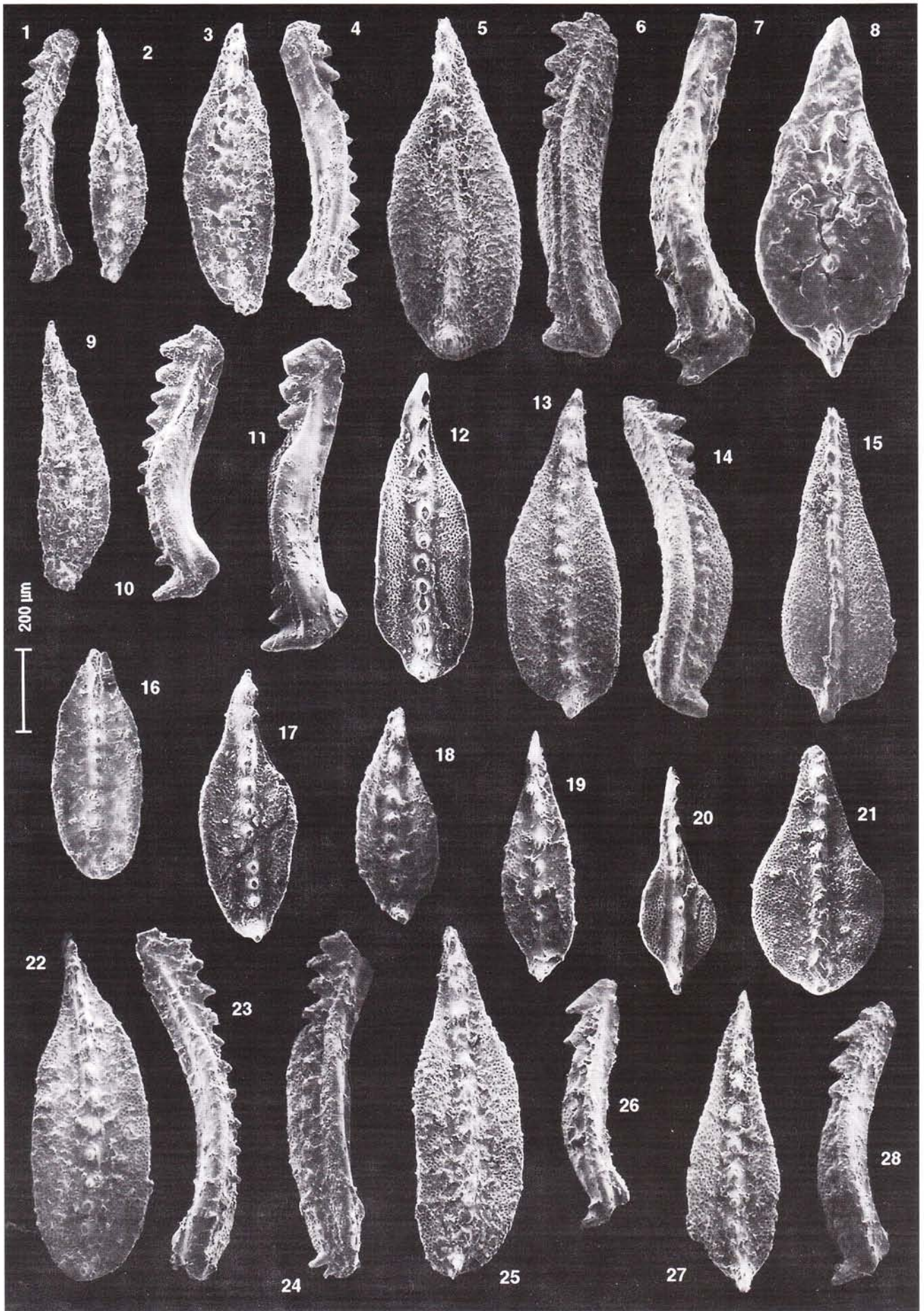
Remarks: Kozur (1996) introduced this species for elements that had formerly been submerged in *Hindeodus latidentatus* emend. Unlike *H. latidentatus*, the larger posterior denticles of *H. praeparvus* are closer together and separated by «V»-shaped spaces. Small specimens of *H. praeparvus* (from the Tesero Oolite) illustrated by Kozur (1996) have less distinctive denticulation compared with larger specimens originally assigned to *Hindeodus* sp. X by Orchard (in Krystyn & Orchard, 1996). Small specimens from Spiti (Pl. 6, fig. 21) are assigned to this species with question. Kozur (1996) distinguished two morphotypes of *H. praeparvus* which differ most conspicuously in the profile of the posterior end. Morphotype 1 is separated here as *Hindeodus* n. sp. A.

Occurrence: *Otoceras woodwardi* Zone, Guling and Lingti; Khunamuh Formation, E2, Guryul Ravine (Bhatt & Arora, 1984); lower and upper bed 27, Meishan (Wang, 1994, 1995; Yin et al., 1996). According to Kozur (1996), this species occurs worldwide in the uppermost Changhsingian and «rarely also in the lowermost Triassic». However, excluding lower bed 27 at Meishan (the age assignment of which is debated), only Triassic ages are confirmed here.

PLATE 1

Specimens are from Spiti except figs. 7-8 from Nevada, and fig. 9, 18, 21-22 from Selong. Magnification x 80.

- Fig. 1-4, 9 - *Neogondolella orchardi* (Mei, 1996). 1, 2) GSC 101687, Lingti 5. 3, 4) GSC 101688, Lingti 4. 9) GSC 101689, Selong U50.
- Fig. 5, 6 - *Neogondolella kazi* Orchard n. sp. GSC 101690, Lingti 6.
- Fig. 7, 8, 15, 20, 21 - *Neogondolella nevadensis* (Clark, 1959). 7, 8) Holotype, SUI 10172, Nevada; the specimen has an insoluble glue coating. 15) GSC 101691, Muth 4. 20) GSC 101692, Guling 2; juvenile. 21) GSC 101693, Guling 4.
- Fig. 10-14, 17, 18, 19, 26-28 - *Neogondolella meishanensis* (Zhang, Lai, Ding, and Liu, 1995). 10, 17) GSC 101694, Guling 2. 11, 12) GSC 101695, Guling 2. 13, 14) GSC 101696, Lingti 5. 18) GSC 101697, Selong L50. 19, 26) GSC 101698, Lingti 3. 27, 28) GSC 101699, Lingti 6.
- Fig. 16, 22-25 - *Neogondolella zhejiangensis* (Mei, 1996). 16) GSC 101700, Lingti 3. 22, 23) GSC 101675, Selong M50. 24, 25) GSC 101701, Lalung 3-2.



Hindeodus typicalis (Sweet, 1970)

Pl. 6, fig. 14, 18, 19, 25, 26

1970 *Anchignathodus typicalis* Sweet (a), pp. 7-8.1970 *Anchignathodus typicalis* - Sweet (b), pp. 222-3, pl. 1, fig. 13, 20.1981 *Hindeodus minutus* - Matsuda, pp. 78-84, pl. 1, fig. 1-7, ?8 (only).1996 *Hindeodus typicalis* - Mei, p. 146, pl. 18.2, fig. 6, 10, 11 (only) (cum syn.).1996 *Hindeodus typicalis* - Yin et al., pl. 1, fig. 13 (only); pl. 2, fig. 1.

Diagnosis: The Pa element has a large but not particularly high cusp and a posterior blade bearing 9-11 smaller subequal denticles that often gradually decline in height toward the posterior end.

Remarks: Mei (1996) distinguished three morphotypes of this species, but Morphotype 1 is here assigned to *H. n. sp. A*. Elements included in *H. typicalis* show a variable denticle morphology and posterior profile and some appear transitional to other *Hindeodus* species recognized in the *Otoceras* beds. The species is clearly the rootstock from which the other species developed.

Occurrence: *Otoceras latilobatum* Zone, Selong; *Otoceras woodwardi* and *Ophiceras tibeticum* zones, Guling, Lingti, Lalung, Muth, and Kashmir; unnamed interval at Guling. Upper Permian-Lower Triassic worldwide.

Hindeodus n. sp. A

Pl. 6, fig. 24

1981 *Hindeodus minutus* - Matsuda, p. 78-91, pl. 1, fig. 1 (only).?1996 *Hindeodus typicalis* - Mei, p. 146, pl. 18.2, fig. 8?, 9 (only).1996 *Hindeodus latidentatus praeparvus* Morphotype 1 Kozur, pp. 93-4.

Diagnosis: A large, short and high element with a cusp moderately larger than the 4-7 large and subequal posterior denticles; elements have a steep adenticulate posterior margin.

Remarks: Both Mei (1996) and Kozur (1996) regarded specimens such as these as ancestral to *H. parvus*, although they were assigned to separate species (see *H. praeparvus*). The Meishan specimens are large, that from Selong half the size. Specimens such as that illustrated (from Meishan) are unlikely precursors to *H. parvus*, but they do appear to have a narrow range about the P-T boundary.

Occurrence: Uppermost Changhsing Limestone; Meishan; ?*Otoceras latilobatum* Zone, Selong.

Hindeodus? n. sp. B

Pl. 6, figs. 2, 3.

Remarks: This unique carminiscaphate element has 5 or 6 narrow and discrete denticles, the anterior 2 of which are separated from the posterior ones. The basal cup is developed to the posterior of the anterior 2 denticles, which are upright and higher than the slightly inclined denticles on the posterior blade.

Occurrence: *Otoceras woodwardi* Zone, Lingti.

Genus *Isarcicella* Kozur, 1975

Type species: *Spathognathodus isarcicus* Huckriede, 1958

Remarks: *Isarcicella* is used here for carminiscaphate elements with a prominent cusp and denticulate lateral margins. This differs from Orchard (1996), who included all elements with a conspicuously elevated cusp in the genus. The multielement composition of *Isarcicella* is uncertain.

Isarcicella staeschei Dai and Zhang, 1989

Pl. 6, figs. 4-8, 10-12

1981 *Isarcicella isarcica* - Matsuda, pp. 93-4, pl. 5, figs. 4-7.1981 *Isarcicella?* sp. Matsuda, pp. 94-5, pl. 5, fig. 8.1989 *Isarcicella staeschei* Dai & Zhang, pp. 430-1, pl. 45, fig. 16-17; pl. 46, figs. 4-7, 11-13, 18, 19; pl. 53, figs. 13, 14.1994 *Isarcicella isarcica* - Orchard et al., pp. 832-3, pl. 2, fig. 13, 14.1996 *Isarcicella isarcica staeschei* - Kozur, p. 100, pl. 5, fig. 6a-c.1996 *Isarcicella isarcica* - Yin et al., pl. 1, fig. 15a, b.1997 *Isarcicella staeschei* - Wang & Wang, pp. 166-7, pl. 2, fig. 2-5 (cum syn.).

Diagnosis: An *Isarcicella* Pa element with 1-3 denticles on one side of the blade.

Remarks: The holotype has 2 denticles on one lateral margin, whereas the stratigraphically oldest specimens have only a single denticle. According to Kozur (1996), the more denticulate forms have the same range as *Isarcicella isarcica* sensu stricto, which has nodes on both sides of the blade. All but one specimen of *I. staeschei* from Spiti have a single lateral node and none have more than two. *Isarcicella isarcica* sensu stricto does not occur in the Spiti collections.

Occurrence: Upper *Otoceras latilobatum* Zone, Selong; *Otoceras woodwardi* Zone, Guling, Lingti, and Lalung; beds 56, 61, 63+ (Khunamuh Fm., E2, E3), Guryul Ravine, Kashmir (Matsuda, 1984).

PLATE 2

Specimens are from Spiti except figs. 10, 16-19 from Selong. Magnification x 80.

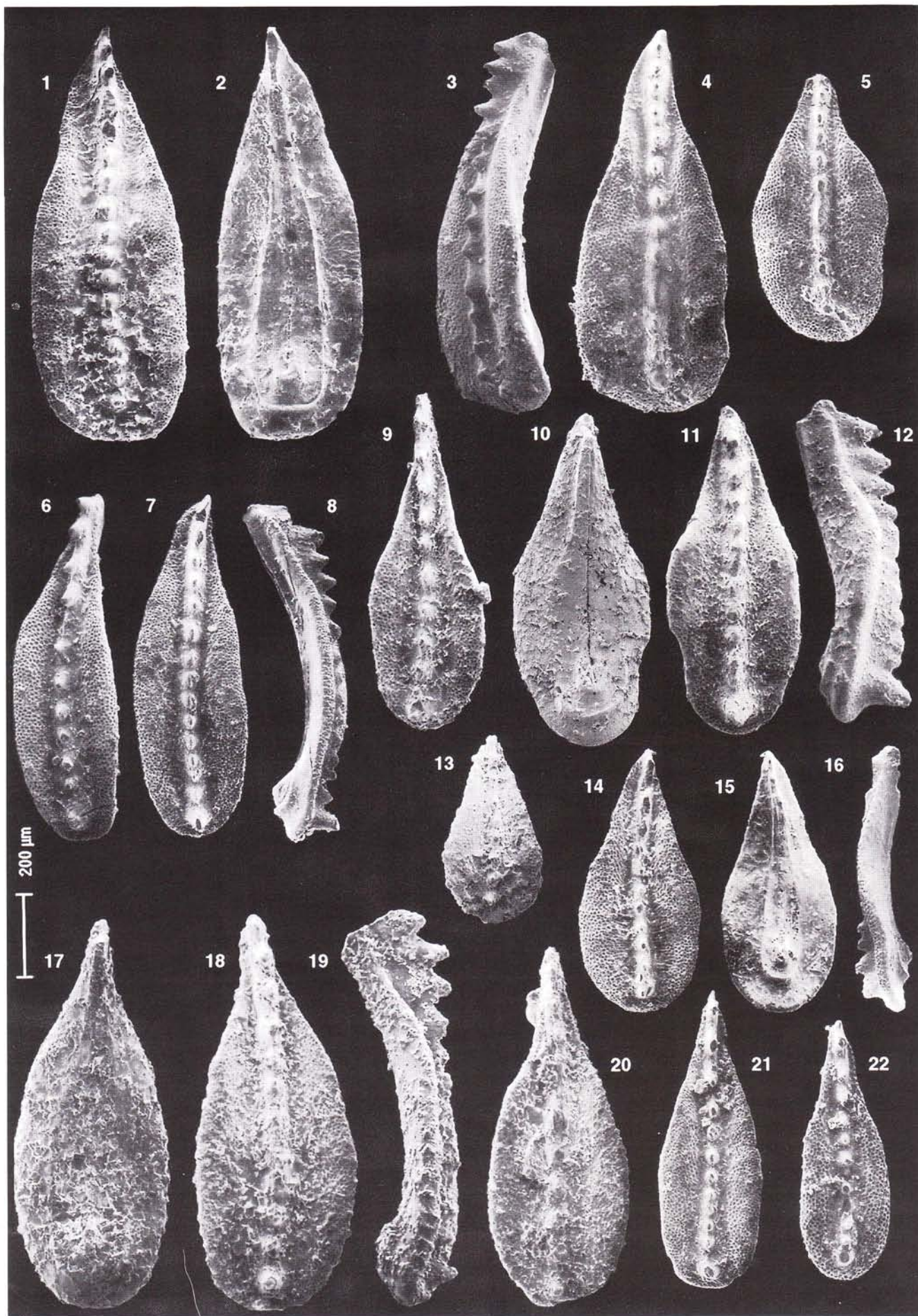
Fig. 1-9, 13-22 - *Neogondolella taylorae* Orchard, 1994.

Fig. 1-4, 17-22 - alpha morphotype. 1, 2) GSC 101702, Lingti 3. 3, 4) GSC 101703, Muth 4. 17-19) Holotype, GSC 101673, Selong U50. 20) GSC 101704, Selong M50. 21) GSC 101705, Guling 2. 22) GSC 101706, Guling 5.

Fig. 5, 9, 13-16 - beta morphotype. 5) GSC 101707, Guling 4. 9) GSC 101708, Lingti 3. 13) GSC 101709, Selong L50. 14-16) GSC 101710, Guling 4.

Fig. 6-8 - gamma morphotype. 6) GSC 101711, Lingti 4. 7, 8) GSC 101712, Guling 3.

Fig. 10-12 - *Neogondolella kazi* Orchard n. sp. Holotype, GSC 101713, Lingti 6.



Genus *Neogondolella* Bender and Stoppel, 1965Type species: *Gondolella mombergensis* Tatge, 1956

Diagnosis (new): *Neogondolella* has an octimembrate apparatus consisting of a total of 15 elements: Pa is segminiplanate (neogondolelliform), Pb is angulate (xaniognathiform), Sa is alate (hibbardelliform), Sb1 is breviform digyrate (enantiognathiform), Sb2 is dolobrate (grodelliform), Sc1 resembles tertiope date (cf. hindeodelliform with bifurcate anterior process), Sc2 is bipennate (cf. hindeodelliform), and M is breviform digyrate (cypridodelliform) (Orchard, in prep.).

Remarks: Many conodont workers assign the species described below to *Clarkina* Kozur 1990, although others use *Gondolella* Stauffer and Plummer, 1932 for all gondola-shaped form-genera. Kozur (1990b, p. 426) has regarded all gondolellid apparatuses as essentially the same, although none have been described in terms of the above diagnosis. Rather, gondolellid genera have generally been separated on the basis of Pa (platform) morphology combined with phylogenetic considerations. For example, the morphology of the Pa element of *Clarkina* is indistinguishable from younger *Paragondolella* and the separation of the genera is stratigraphic, arising from the assumed extinction of *Clarkina* early in the Triassic (Kozur, 1990b, p. 414). Pending a fuller understanding of gondolellid relationships, *Neogondolella* is retained for all the present species.

Neogondolella discreta Orchard and Krystyn n. sp.

Pl. 5, fig. 4-9

1996 *Neogondolella* n. sp. E - Krystyn & Orchard.1997 *Neogondolella* n. sp. E - Orchard & Tozer.**Holotype:** GSC 101749, Pl. 5, figs. 7-9.**Etymology:** The trivial name refers to the discrete carinal denticles.**Type stratum/ locality:** Bed 5, unnamed interval, Guling.

Diagnosis: The Pa element has a narrow biconvex platform strongly constricted at anterior and posterior ends and a blade-carina-cusp composed of high, discrete denticles. The inclined cusp, which is not strongly differentiated from adjacent denticles, is surrounded by a narrow platform brim in larger specimens. On the lower surface, the attachment surface surrounding the pit appears broad and flaring as a consequence of platform reduction.

Comparisons: This species differs from all others described herein by the configuration of the blade-carina although the platform shape is similar to *N. nassichuki* n. sp. and *N. krystyni* n. sp. *Neospathodus kummeli* has similar denticulation and may also include elements

with platform flanges, but these are not as well developed as in *N. discreta*, which has a narrow platform even in small specimens.

Occurrence: Bed 5, unnamed interval, Guling; Strigatus Zone, Ellesmere Island.

Neogondolella kazi Orchard n. sp.

Pl. 1, fig. 5, 6; Pl. 2, fig. 10-12

1996 *Neogondolella* n. sp. C - Krystyn & Orchard.**Holotype:** GSC 101713, Pl. 2, figs. 10-12.**Type stratum/locality:** Bed 6, *Otoceras woodwardi* Zone, Lingti.

Etymology: Named for Kazuharu Shimamura of Vancouver in tribute to his contributions to the application of geographical information systems to geological research in the Canadian Cordillera.

Diagnosis: The Pa element has a biconvex outline in upper view, a broadly rounded posterior end, a posterior platform brim, a moderately high and largely fused carina, and a prominent upright cusp.

Comparisons: The species has a platform outline similar to that of *N. taylorae*, which differs in its low and discrete carinal nodes. Unlike the more quadrate *N. meishanensis*, *N. kazi* has a subterminal cusp and high adjacent carinal denticles. *N. krystyni* has a narrower and more pointed platform and discrete denticles. Some elements of *N. tulongensis* may have fused carinas, but they have a different platform shape.

Remarks: The fused, ridge-like carina is a distinctive feature of this species. In the holotype it is markedly high, but it may also be lower in the centre of the platform. This type of carinal morphology characterizes many younger *Neogondolella* species, and *N. kazi* appears to be the oldest Triassic species to show it.

Occurrence: *Otoceras woodwardi* Zone, Lingti.

Neogondolella krystyni Orchard n. sp.

Pl. 4, fig. 25-28; Pl. 5, fig. 1-3, 10-17, 20, 21

1996 *Neogondolella* n. sp. D - Krystyn & Orchard.1997 *Neogondolella* n. sp. D - Orchard & Tozer.**Holotype:** GSC 101741, Pl. 5, fig. 1-3.

Etymology: Named for L. Krystyn of Vienna who collected the described conodont material.

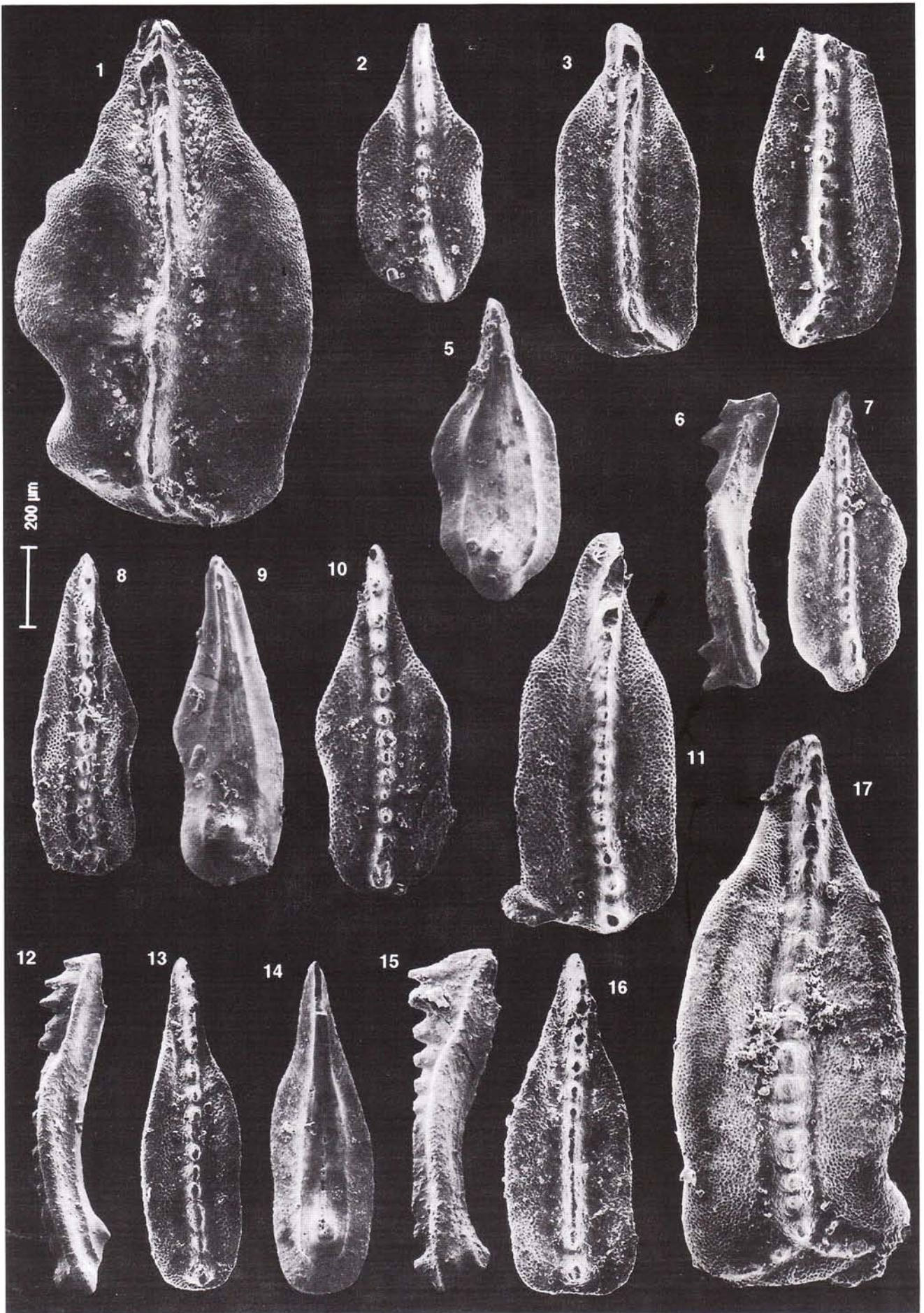
Type stratum/locality: Bed 3, *Otoceras woodwardi* Zone, Guling, Spiti.

Diagnosis: The Pa element has mid-platform margins that are straight to undulose and subparallel, whereas the anterior and posterior platform margins are tapered to a point. The blade-carina is composed of moderately high and subequal denticles that project strongly

PLATE 3

Specimens are from Spiti. Magnification x 80.

- Fig. 1-17 - *Neogondolella tulongensis* Tian, 1982.
 Fig. 1, 3, 4 - gamma morphotype. 1) GSC 101714, Guling 3. 3) GSC 101715, Guling 3. 4) GSC 101716, Guling 2.
 Fig. 2, 5-10 - beta morphotype. 2, 5) GSC 101717, Guling 4. 6, 7) GSC 101718, Muth 4; advanced form with high posterior carina. 8, 9) GSC 101719, Muth 2. 10) GSC 101720, Muth 4.
 Fig. 11-17 - alpha morphotype. 11) GSC 101721, Guling 4; specimen with secondary posterior process. 12-14) GSC 101722, Guling 2; specimen with partly fused carinal nodes. 15, 16) GSC 101723, Guling 2; specimen with carinal fusion. 17) GSC 101724, Guling 2; specimen with bifid posterior carina.



above the downturned posterior platform. The posterior carina terminates in an upright to posteriorly inclined cusp, which may be partly fused with adjacent denticles.

Comparisons: Carinal denticles are neither as high nor as discrete as in *N. discreta*, but are more developed than in most other contemporaneous species of *Neogondolella* with the exception of *N. kazi*, which has a broader and more rounded platform.

Remarks: Platform shapes are moderately variable but are commonly asymmetric. The cusp may or may not be well differentiated. The unifying feature of all specimens included here is the strongly developed posterior carina.

Occurrence: *Otoceras woodwardi* and *Ophiceras tibeticum* zones, Guling, Lingti, Lalung and Muth; Bed 5, unnamed interval, Guling; ?*Ophiceras commune* Zone, Ellesmere Island.

Neogondolella nassichuki Orchard n. sp.

Pl. 5, fig. 18-19, 22-30

1994 *Neogondolella* aff. *N. carinata* - Orchard et al., p. 833, pl. 3, fig. 16-19.

Holotype: GSC 101685, Pl. 5, fig. 28-30.

Type stratum/locality: Upper *Otoceras latilobatum* Zone, Selong, Tibet (GSC loc. C-301264).

Etymology: Named for W. Nassichuk who collected the conodont samples from Selong.

Diagnosis: The Pa element has a narrow, oval, slightly curved and arched platform. The low blade denticles descend to low and discrete carinal nodes which pass posteriorly to a moderately sized cusp surrounded by a narrow posterior platform brim.

Comparisons: The new species is narrower than *N. planata* and is more strongly tapered and less rounded posteriorly than *N. zhejiangensis*, but it has similar axial characteristics to both species. *N. sosioensis* and *N. xiangxiensis* (e.g. Tian, 1993a, pl. 5, fig. 10) have similar shapes but more strongly developed blades and anterior carinas. *N. nassichuki* may have developed from such forms through the suppression of axial denticulation, and then in turn given rise to *N. krystyni* through greater development of the posterior carina.

Occurrence: *Otoceras latilobatum* Zone, Selong; *Otoceras woodwardi* Zone, Guling, Lingti, Lalung, and Muth.

Neogondolella carinata (Clark, 1959)

Pl. 4, fig. 9, 11, 16, 17, 20

1959 *Gondolella carinata* Clark, pp. 308-9, pl. 44, fig. 15-19.

1977 *Neogondolella planata* - Goel, p. 1099, pl. 3, fig. 8, 9 (only).

1984 *Gondolella carinata* - Matsuda, pp. 119-122, pl. 1, fig. 7, 11.

1994 *Neogondolella carinata* - Orchard et al., p. 833, pl. 3, fig. 1-4, 10-14.

1995 *Gondolella carinata* - Garzanti et al., pl. 1, fig. 5 (only).

1996 *Neogondolella carinata* - Belka & Wiedmann, pl. 2, fig. 2?, 3.

Diagnosis: The Pa element has a broad flat platform with its maximum width at about midlength, and a marked constriction in front of the posterior cusp, which is surrounded by a platform brim. Blade-carina denticles are generally low and discrete, and the cusp generally well differentiated and upright.

Remarks: Orchard et al. (1994) reillustrated the holotype from the Dinwoody Formation in two views. The distinctive posterior indentation is here regarded as diagnostic although Sweet (1970b) and Matsuda (1984) included elements with a broad variety of platform shapes in this species. In younger populations of *N. carinata*, the carinal denticles become more pronounced.

Occurrence: The holotype is from about 10 m above the base of the Triassic Dinwoody Formation at Dinner Springs Canyon, Nevada. *Otoceras latilobatum* Zone, Selong; *Otoceras woodwardi* and *Ophiceras tibeticum* zones, Guling, Lingti, Lalung and Muth; unnamed interval beneath, and *Pleurogyronites planidorsatus* Zone, Guling; bed 64+ (Khunamuh Fm., E2), Guryul Ravine (Matsuda, 1984); Lowermost Triassic worldwide.

?Neogondolella changxingensis Wang and Wang, 1981

Pl. 4, fig. 21, 22

?1981 *Neogondolella subcarinata changxingensis* Wang & Wang, in Zhao et al., p. 80, pl. 5, fig. 6, 7, 10, 11.

1996 *Clarkina deflecta* - Zhang et al., pl. II.7, fig. 15 (only).

Remarks: Very rare specimens from Spiti have a platform shape and reduced posterior carina like that of *N. changxingensis* but the entire blade and carina appears more weakly developed than in typical specimens from the Changshing Limestone. In this respect, the elements have similar axial characteristics to contemporaneous species from Spiti.

Occurrence: *Otoceras woodwardi* Zone, Lingti; transition bed 26, Meishan (Zhang et al., 1996).

Neogondolella meishanensis

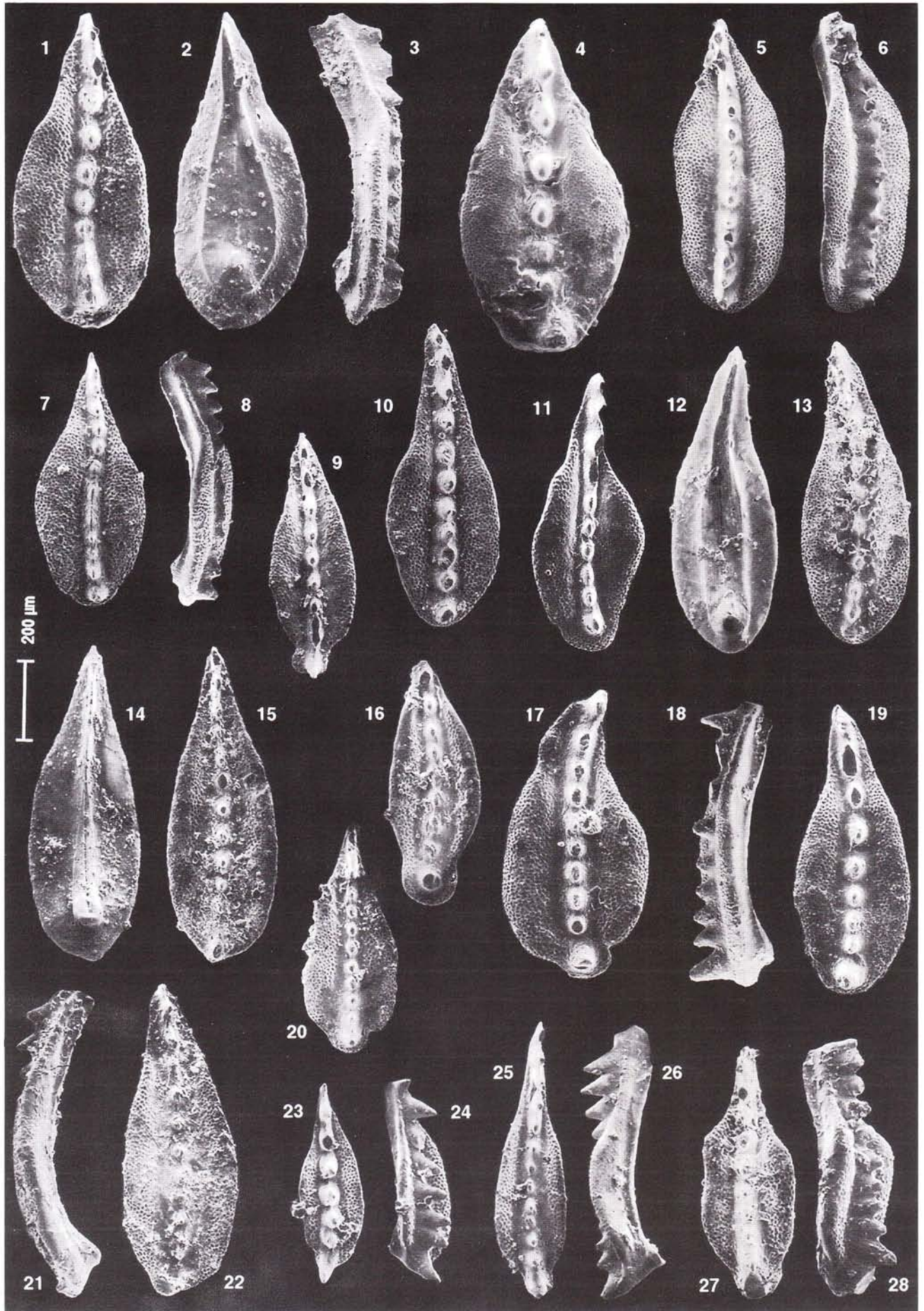
(Zhang, Lai, Ding, and Liu, 1995)

Pl. 1, fig. 10-14, 17, 18, 19, 26-28.

PLATE 4

Specimens are from Spiti except fig. 4 from Nevada. Magnification x 80.

- Fig. 1-4, 7, 8, 10, 12-15, 18, 19, 23, 24 -*Neogondolella planata* (Clark, 1959). 1-3) GSC 101725, Muth 4; advanced form with high posterior carina. 4) Holotype, SUI 10174, Nevada. 7, 8) GSC 101726, Guling 3. 10) GSC 101775, Guling 3. 12, 13) GSC 101727, Muth 2. 14, 15) GSC 101728, Guling 1; early form with poorly developed posterior carina. 18, 19) GSC 101729, Guling 3. 23, 24) GSC 101730, Muth 2; juvenile.
- Fig. 5, 6 - *Neogondolella* sp. A. GSC 101774, Muth 2.
- Fig. 9, 11, 16, 17, 20 - *Neogondolella carinata* (Clark, 1959). 9) GSC 101731, Guling 3. 11) GSC 101732, Guling 3. 16) GSC 101733, Muth 1. 17) GSC 101734, Guling 3. 20) GSC 101735, Muth 2.
- Fig. 21, 22 - ?*Neogondolella changxingensis* Wang and Wang, 1981. GSC 101736, Lingti 3.
- Fig. 25-28 - *Neogondolella krystyni* Orchard n. sp. 25, 26) GSC 101737, Muth 1; early form. 27, 28) GSC 101738, Muth 2; form with reduced platform development.



- 1995 *Clarkina* sp. nov. - Wang, pl. 1, fig. 2-4.
 1995 *Clarkina* sp. - Wang, pl. 1, fig. 11.
 1995 *Clarkina meishanensis* Zhang et al., p. 674, pl. 2, fig. 4, 5, 6.
 1995 *Gondolella taylorae* - Garzanti et al., pl. 2, fig. 3 (only).
 1995 *Gondolella carinata* - Garzanti et al., pl. 1, fig. 12?; pl. 2, fig. 10 (only).
 ?1996 *Clarkina carinata* - Zhang et al., pl. II.7, fig. 8, 11.

Diagnosis: The Pa element has a biconvex to parallel-sided platform, an often straight axis, generally low and discrete blade-carina nodes, and a prominent terminal cusp.

Remarks: The posterior platform of elements included here broadens with growth but the cusp remains at the posterior tip. Most of the specimens from Spiti have a straight axis and uniformly developed carinae nodes, as in the holotype. The paratypes from Meishan differ in being either curved, or having reduced posterior carinal nodes.

Occurrence: *Otoceras latilobatum* Zone, Selong; *Otoceras woodwardi* and *Ophiceras tibeticum* zones, Guling, Lingti, Lalung and Muth; transition beds 25, 26, 27d, Meishan (Wang, 1995; Zhang et al., 1996).

Neogondolella nevadensis (Clark, 1959)

Pl. 1, fig. 7, 8, 15, 20, 21

1959 *Gondolella nevadensis* Clark, p. 308, pl. 44, fig. 11-14.

Diagnosis: The Pa element has a broad and flat posterior platform and a long tapered anterior part. The cusp is terminal in position and may project posteriorly beyond the platform margin.

Remarks: The holotype of this species is reillustrated here (Pl. 1, fig. 7, 8). The bulbous posterior platform is diagnostic and is recognized in early growth stages. The species is generally rare in Spiti collections.

Occurrence: The holotype is from about 10 m above the base of the Triassic Dinwoody Formation at Dinner Springs Canyon, Nevada. *Otoceras woodwardi* and *Ophiceras tibeticum* zones, Guling, Lingti, Lalung, and Muth.

Neogondolella orchardi Mei, 1996

Pl. 1, fig. 1-4, 9

- 1994 *Neogondolella* aff. *changxingensis* - Orchard et al., p. 834, pl. 2, fig. 20, 21.
 1996 *Clarkina orchardi* Mei, p. 144, pl. 18, fig. 6-11 (12=*N. zhejiangensis*).
 1996 *Neogondolella* cf. *changxingensis* - Belka & Wiedmann, pl. 2, fig. 1?

Diagnosis: The Pa element is narrow and elongate, with evenly curved margins and carina. A low anterior blade passes posteriorly to low, moderately discrete carinal nodes, and a slightly larger terminal cusp.

Remarks: Both Orchard et al. (1994) and Mei (1996) compared this species with *N. changxingensis* and *N. taylorae*, between which it falls morphologically.

Occurrence: Upper *Otoceras latilobatum* Zone, Selong; *Otoceras woodwardi* Zone, Guling, Lingti, Lalung, and Muth; Griesbachian, Thini (Belka & Wiedmann, 1996).

Neogondolella planata (Clark, 1959)

Pl. 4, fig. 1-4, 7, 8, 12-15, 18, 19, 23, 24

- 1959 *Gondolella planata* Clark, p. 309, pl. 44, fig. 8-10.
 1977 *Neogondolella planata* - Goel, p. 1099, pl. 3, fig. 5 (only).
 1984 *Gondolella carinata* - Matsuda, pp. 119-122, pl. 1, fig. 4, 10 (only).
 1993a *Neogondolella planata* - Tian, pl. 5, fig. 19.
 1994 *Neogondolella planata* - Orchard et al., p. 835, pl. 3, fig. 5, 6.
 1995 *Clarkina planata* - Zhang et al., pl. 2, fig. 10.

Diagnosis: The Pa element has a broad, flat platform which has its maximum width at about midlength and is evenly tapered in both anterior and posterior directions. The cusp is subterminal on a relatively pointed posterior margin and may have a narrow posterior brim.

Remarks: This species has a more strongly tapered and narrower posterior platform, and a less distinct platform brim than *Neogondolella taylorae*. The holotype (reillustrated on Pl. 4, fig. 4) is a large specimen with relatively few (8) low carinal nodes whereas Spiti specimens are smaller and have more numerous (10-12) carinal nodes. Both 'primitive' forms with weak posterior carinal nodes (Pl. 4, fig. 14), and 'advanced' forms with elevated carinal nodes (Pl. 4, fig. 1) are recognized in the Spiti material.

Occurrence: The holotype is from about 10 m above the base of the Triassic Dinwoody Formation at Dinner Springs Canyon, Nevada. *Otoceras latilobatum* Zone, Selong; *Otoceras woodwardi* and *Ophiceras tibeticum* zones, Guling, Lingti, Lalung, Muth; Bed 5, unnamed interval, Guling; beds 63, 64+ (Khunamuh Fm., E3), Guryul Ravine (Matsuda, 1984); transition bed 29, Meishan (Zhang et al., 1995); lowermost Daye Formation, Hunan (Tian, 1993a); and elsewhere in the lowermost Triassic.

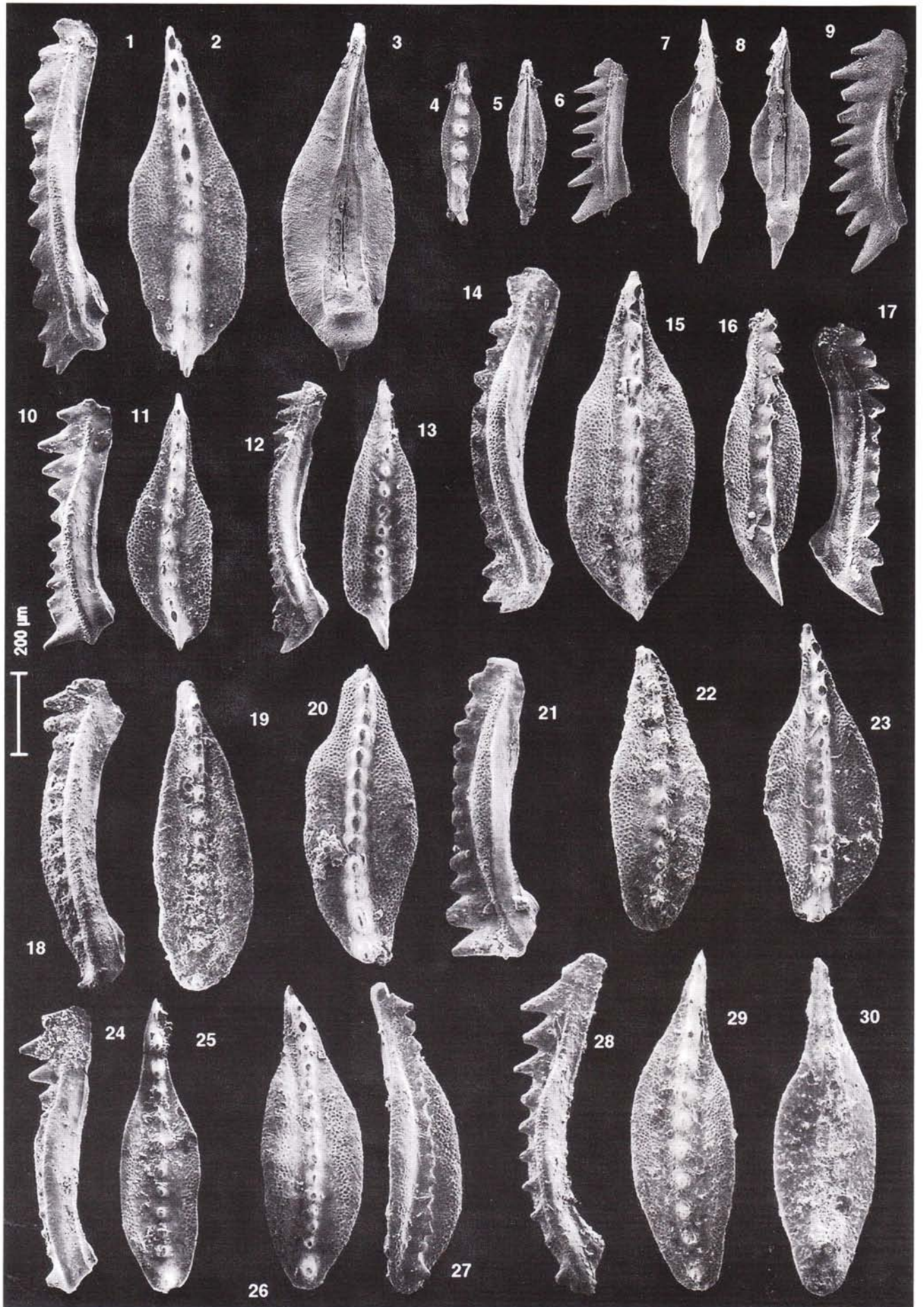
Neogondolella taylorae Orchard, 1994

Pl. 2, figs. 1-9, 13-22

PLATE 5

Specimens are from Spiti except figs. 25-27 from Selong. Magnification x 80.

- Fig. 1-3, 10-17, 20, 21 - *Neogondolella krystyni* Orchard n. sp. 1-3) Holotype, GSC 101739, Guling 3. 10, 11) GSC 101741, Guling 2. 12, 13) GSC 101740, Guling 4. 14, 15) GSC 101742, Guling 4. 16, 17) GSC 101743, Guling 3. 20, 21) GSC 101744, Guling 3.
 Fig. 4-9 - *Neogondolella discreta* Orchard n. sp. 4-6) GSC 101745, Guling 5; juvenile. 7-9) Holotype, GSC 101746, Guling 5.
 Fig. 18, 19, 22-30 - *Neogondolella nassichuki* Orchard n. sp. 18, 19) GSC 101747, Guling 2; atypical form. 22) GSC 101748, Lalung 3-2. 23) GSC 101749, Muth 4; form transitional to *N. krystyni*. 24, 25) GSC 101750, Lingti 4. 26, 27) GSC 101751, Muth 2. 28-30) Holotype, GSC 101685, Selong U50.



- 1981b *Gondolella orientalis* - Bhatt et al., p. 202, pl. 1, fig. 7, 8, 15, 16, 29, 30; pl. 2, fig. 1-3, 12, 13, 18, 19.
 1994 *Neogondolella taylorae* Orchard et al., p. 833, pl. 2, fig. 9-12, 15, 16; pl. 3, fig. 15.

Diagnosis: The Pa element has a broad, generally flattened platform with variably upturned anterior margins, is broadest between mid-length and the posterior one-third, and has a broadly rounded posterior margin. The blade-carinal denticles are generally low and moderately discrete and pass into a generally prominent upright cusp surrounded by a narrow posterior platform brim.

Remarks: This species is similar to *N. orientalis* as discussed by Orchard et al. (1994). Morphologically transitional forms between *N. taylorae* and several other species have been noted previously by both Orchard et al. (1994) and Mei (1996), and others are illustrated in Pl. 2. Several new morphotypes are introduced here.

alpha morphotype nov.

Pl. 2, figs. 1-4, 17-22

- 1977 *Neogondolella planata* - Goel, p. 1099, pl. 3, fig. 6, 7 (only).
 1993a *Neogondolella carinata* - Tian, pl. 5, fig. 18 (only).
 1994 *Neogondolella taylorae* Orchard et al., p. 833, pl. 2, fig. 9, 10, 15, 16; pl. 3, fig. 15.
 1995 *Gondolella taylorae* - Garzanti et al., pl. 1, fig. 4, 6, 7, ?11 (only).
 1995 *Gondolella carinata* - Garzanti et al., pl. 1, fig. 9 (only)
 ?1995 *Clarkina* cf. *planata* - Wang, pl. 1, fig. 13.
 ?1995 *Clarkina* sp. - Wang, pl. 1, fig. 10.
 1996 *Clarkina taylorae* - Mei, p. 145, pl. 18.2, fig. 12, 15.
 ?1996 *Clarkina deflecta* - Zhang et al., pl. II.7, fig. 18 (only).

Diagnosis: The platform of this morphotype has a length to width ratio of 2:1, and has gradually tapered to slightly constricted anterior platform margins.

Remarks: The alpha morphotype corresponds to the holotype of the species from Selong. Rare specimens (e.g., Pl. 2, fig. 1) may have a smaller cusp than is typical, or may have accessory posterior nodes (e.g., Pl. 2, fig. 4). In these respects, the specimens are transitional to *N. zhejiangensis*.

Occurrence: *Otoceras latilobatum* Zone, Selong; *Otoceras woodwardi* and *Ophiceras tibeticum* zones, Guling, Lingti, Lalung, Muth; Bed 5, unnamed interval, Guling; ?transition beds 26, 27a, Meishan (Wang, 1995; Zhang et al., 1996); lowermost Daye Formation, Hunan (Tian, 1993a). Bhatt et al. (1981b) reported similar forms from Spiti River, Shalshal Cliff-Kumaun, and Tagze-Zanskar.

beta morphotype nov.

Pl. 2, fig. 5, 9, 13-16

- 1994 *Neogondolella taylorae* Orchard et al., p. 833, pl. 3, fig. 15.
 1995 *Gondolella* aff. *taylorae* - Garzanti et al., pl. 2, fig. 7 (only).
 1996 *Clarkina* aff. *planata* - Mei, pl. 18.2, fig. 13.
 1996 *Neogondolella* n. sp. A - Krystyn & Orchard.

Diagnosis: A relatively short form in which the anterior one-third of the platform is strongly constricted and the posterior platform has a bulbous outline.

Remarks: This morphotype resembles *N. nevadensis* but differs in possessing a distinct posterior brim.

Occurrence: *Otoceras latilobatum* Zone, Selong; *Otoceras woodwardi* and *Ophiceras tibeticum* zones, Guling, Lingti, Lalung, Muth.

gamma morphotype nov.

Pl. 2, figs. 6-8

- ?1995 *Gondolella tulongensis* - Garzanti et al., pl. 1, fig. 10 (only).

Diagnosis: A relatively long and narrow morphotype with a length to width ratio of 3:1.

Remarks: This morphotype differs from moderately sized specimens of *N. tulongensis* alpha morphotype in its more rounded platform margins.

Occurrence: *Otoceras woodwardi* and *Ophiceras tibeticum* zones, Guling, Lingti, Lalung, Muth; Bed 5, unnamed interval, Guling.

Neogondolella tulongensis Tian, 1982

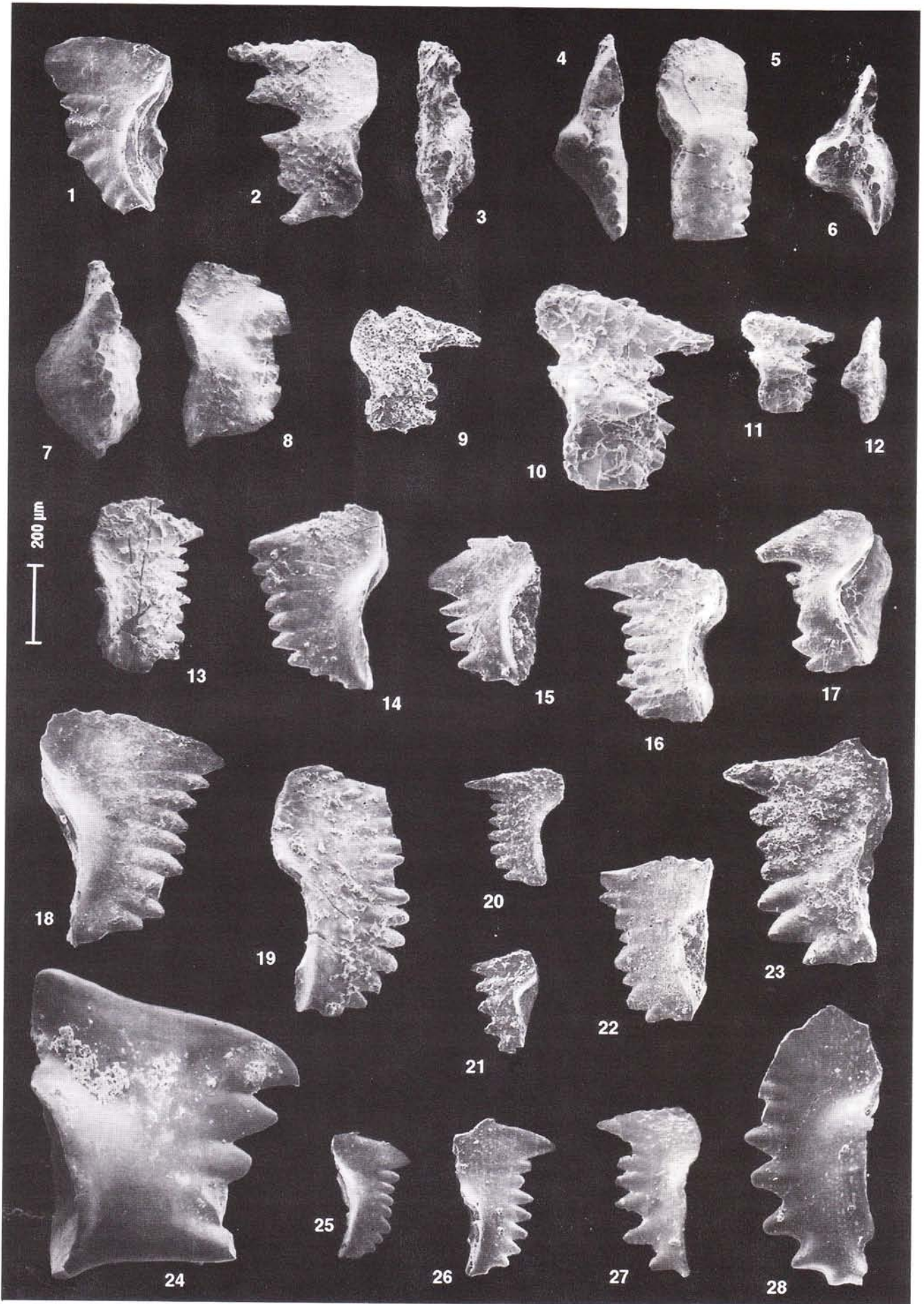
Pl. 3, fig. 1-17

- 1982 *Neogondolella tulongensis* Tian, p. 159, pl. 1, figs. 15, 17.
 1993b *Neogondolella tulongensis* - Tian, p. 372, pl. 79, figs. 9-11.

PLATE 6

Specimens are from Spiti except figs. 24, 27-28 from Meishan. Magnification x 80, except fig. 10.

- Fig. 1 - *Hindeodus postparvus* Kozur, GSC 101752, Lingti 4.
 Fig. 2, 3 - *Hindeodus?* n. sp. B. GSC 101753, Lingti 4.
 Fig. 4-8, 10-12 - *Isaricella staeschei* Dai and Zhang, 1989. 4, 5) GSC 101754, Lingti 3. 6) GSC 101755, Lingti 4; specimen with two lateral nodes. 7, 8) GSC 101756, Lingti 3; early form with tiny lateral node. 10-12) GSC 101757, Lingti 4; Fig. 10 x 160.
 Fig. 9, 16, 17, 20 - *Hindeodus parvus* (Kozur and Pjatakova, 1976).
 Fig. 9, 16, 17 - *Hindeodus parvus erectus* Kozur, 1996. 9) GSC 101758, Guling 1. 16) GSC 101759, Lingti 3. 17) GSC 101760, Guling 2.
 Fig. 20 - Morphotype 3 of Mei, 1996. GSC 101761, Lalung 3-1.
 Fig. 13, 15 - *Hindeodus anterodentatus* (Dai, Tian and Zhang, 1989). 13) GSC 101762, Lingti 3. 15) GSC 101763, Guling 2.
 Fig. 14, 18, 19, 25, 26 - *Hindeodus typicalis* (Sweet, 1970). 14) GSC 101764, Guling 3; specimen transitional to *H. anterodentatus*. 18) GSC 101765, Guling 2. 19) GSC 101766, Lingti 4. 25) GSC 101767, Guling 1; specimen transitional to *H. praeparvus*. 26) GSC 101768, Guling 1; specimen transitional to *H. parvus*.
 Fig. 21?, 22, 23 - *Hindeodus praeparvus* (Kozur, 1996). 21) GSC 101769, Lingti 3. 22) GSC 101770, Guling 1. 23) GSC 101771, Lingti 4.
 Fig. 24 - *Hindeodus* n. sp. A. GSC 101772, Meishan 12. Uppermost Changshing Limestone.
 Fig. 27, 28 - *Hindeodus latidentatus* (Kozur, Mostler and Rahimi-Yazd, 1975). 27) GSC 101664. 28) GSC 101773; both growth stages show characteristic posterior denticulation. Meishan 12. Uppermost Changshing Limestone.



Diagnosis: The Pa element has a subrectangular platform in which one margin is slightly to strongly indented; bifurcated or deflected posterior carinas are commonly developed in large specimens.

Remarks. Orchard et al. (1994) and Mei (1996) have described this species and compared it with *Neogondolella deflecta*. The latter species, based on an apparently corroded specimen from the upper Changhsing Limestone, has a wedge-shaped, uniformly tapered platform and deflected posterior carina. *Neogondolella dicerocarinata* Wang and Wang has a similar platform shape to *N. deflecta* but has a bifid posterior carina. Specimens included in *N. tulongensis* may show carinal features similar to both of these Permian species, but they generally have subrectangular platforms and often one or both platform margins are sinuous. Elaborations of the posterior carina (deflections, bifurcations, accessory nodes) are seen in late growth stages of several Permian and Triassic *Neogondolella* species and such features seen in posterior platform fragments should not be regarded as necessarily diagnostic for a particular species. Although the holotype of *N. tulongensis* is a large, 'gerontic' specimen, the current interpretation of the species includes smaller growth stages. Three morphotypes of *N. tulongensis* are differentiated in the Spiti material.

alpha morphotype nov.

Pl. 3, fig. 11-17

- 1984 *Gondolella carinata* - Matsuda, pp. 119-122, pl. 1, fig. 3 (only).
 1984 *Neogondolella carinata* - Hatleberg & Clark, pl. 4, figs. 16, 20.
 1994 *Neogondolella tulongensis* - Orchard et al., p. 835, pl. 2, fig. 1, 4.
 1995 *Gondolella tulongensis* - Garzanti et al., pl. 1, fig. 2, 3 (only).
 ?1995 *Clarkina dicerocarinata* - Wang, pl. 1, fig. 12.
 1996 *Clarkina tulongensis* - Mei, p. 145, pl. 18.1, fig. 1, 2?, 3?, 4, 5.

Diagnosis: This morphotype is characterized by a relatively symmetrical subrectangular platform. Late growth stages may have a secondary or bifid posterior carina.

Remarks: Some specimens of alpha morphotype possess enlarged and partly fused carinal nodes (Pl. 3, figs. 15-16).

Occurrence: *Otoceras latilobatum* Zone, Selong; *Otoceras woodwardi* and *Ophiceras tibeticum* zones, Guling, Lingti, Lalung, Muth; Bed 5, unnamed interval, Guling; bed 63 (Khunamuh Fm., E2), Guryul Ravine (Matsuda, 1984); ?transition bed 26, Meishan (Wang, 1995); basal limestone of Thinigaon Formation, Thakkhola (Hatleberg & Clark, 1984).

beta morphotype nov.

Pl. 3, fig. 2, 5-10

- 1984 *Gondolella carinata* - Matsuda, pp. 119-122, pl. 1, fig. 1, 2 (only).
 1994 *Neogondolella tulongensis* - Orchard et al., p. 835, pl. 2, fig. 1-4.
 1995 *Gondolella aff. taylorae* - Garzanti et al., pl. 1, fig. 8 (only).
 1995 *Gondolella aff. tulongensis* - Garzanti et al., pl. 2, fig. 8.
 1996 *Neogondolella planata* - Belka & Wiedmann, pl. 2, fig. 5.

Diagnosis: A morphotype of variable length to breadth ratio with a markedly indented inner platform margin, and a prominent cusp +/- adjacent carinal denticle.

Remarks: Younger representatives of this morphotype have a higher, more prominent posterior carina.

Occurrence: *Otoceras latilobatum* Zone, Selong; *Otoceras woodwardi* and *Ophiceras tibeticum* zones, Guling, Lingti, Lalung, Muth; bed 57 (Khunamuh Fm., E2), Guryul Ravine (Matsuda, 1984); Tamba Kurkur Formation, Thini (Belka & Wiedmann, 1996).

gamma morphotype nov.

Pl. 3, fig. 1, 3, 4

- 1981b *Gondolella deflecta* - Bhatt et al., p. 201, pl. 2, fig. 6, 7.
 1981b *Gondolella cf. deflecta* - Bhatt et al., p. 201, pl. 2, fig. 4, 5, 10, 11.
 1984 *Gondolella carinata* - Matsuda, pp. 119-122, pl. 2, fig. 4, 5 (only).
 ?1995 *Clarkina deflecta* - Wang, pl. 1, fig. 6, 7 (only).

Diagnosis: A morphotype with a commonly fused carina that is laterally deflected at the posterior end of the platform.

Remarks: Specimens included here are generally large and have either parallel or sinuous platform margins. Some specimens have pronounced fusion of the carinal nodes.

Occurrence: *Otoceras latilobatum* Zone, Selong; *Otoceras woodwardi* and *Ophiceras tibeticum* zones, Guling, Lingti, Lalung, Muth; bed 64 (Khunamuh Fm., E3), Guryul Ravine, (Matsuda, 1984); ?transition bed 26, Meishan (Wang, 1995).

Neogondolella zhejiangensis (Mei, 1996)

Pl. 1, figs. 16, 22-25

- ?1984 *Gondolella carinata* - Matsuda, pp. 119-122, pl. 2, fig. 1 (only).
 1994 *Neogondolella aff. taylorae* Orchard et al., p. 833, pl. 2, fig. 17-19.
 1995 *Clarkina changxingensis* - Wang, pl. 1, fig. 1, 5, 9.
 1995 *Clarkina deflecta* - Wang, pl. 1, fig. 8 (only).
 1995 *Gondolella tulongensis* - Garzanti et al., pl. 2, fig. 2? (only).
 1996 *Clarkina zhejiangensis* Mei, p. 145, pl. 18.2, fig. 16, 17.
 1996 *Neogondolella orchardi* Mei, p. 144, pl. 18, fig. 12 (only).

Diagnosis: The Pa element has an elongate oval platform, broadest medially or with subparallel lateral margins, a rounded posterior margin and a low blade which passes into a carina composed of discrete nodes. A small subterminal cusp is surrounded by a narrow posterior brim which may bear an accessory posterior denticle.

Remarks: Mei (1996) established this species based on specimens referred to *Clarkina changxingensis* by Wang (1994, 1995) that closely resemble those elements compared to *N. taylorae* by Orchard et al. (1994). *Neogondolella zhejiangensis* is intermediate between *N. orchardi* and *N. taylorae* in terms of platform breadth and posterior outline but the species does not have the prominent, discrete cusp of *N. taylorae*.

Occurrence: *Otoceras latilobatum* Zone, Selong; *Otoceras woodwardi* Zone, Guling, Lingti, and Lalung; ?bed 57 (Khunamuh Fm., E2), Guryul Ravine, (Matsuda, 1984); transition beds 26, 27a, b, c, d, Meishan (Wang, 1994, 1995).

Neogondolella sp. A

Pl. 4, fig. 5, 6

- 1995 *Gondolella carinata* - Garzanti et al., pl. 2, fig. 9 (only).

Remarks: The relatively uncommon Pa element has an oblong platform and commonly a sinuous inner margin, a narrowly rounded posterior margin, and a moderately high, even crested carina terminating in an unremarkable cusp surrounded by a narrow platform brim. This platform shape is intermediate between *N. planata* and *N. tulongensis*, but the carina is markedly and uniformly higher. *N. kazi* is broader, has fused carinal nodes, and a prominent cusp.

Occurrence: *Otoceras woodwardi* Zone, Muth and Guling.

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Locality Registry.

The following GSC locality numbers have been assigned to conodont collections discussed in the text and housed in the collections of the Geological Survey of Canada.

Selong: L50=C-301262, M50=C-301263, U50=C-301264.

Meishan: 12(=»24")=C-158625.

Guling: 1=C-302286, 2=C-302287, 3=C-302288, 4=C-302289, 5=C-302290.

Lingti: 3=C-303706, 4=C-303707, 5=C-303708, 6=C-303709, 7=C-303710.

Lalung: 1=C-302291, 2=C-302292, 3=C-302293, 4=C-302294.

Muth: 1=C-303711.2=C-303712, 4=C-303713.