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The *Neogondolella constricta* (Mosher and Clark, 1965) group in the Middle Triassic of North America: speciation and distribution

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Non-technical Summary.—Conodont microfossils extracted from limestone at "Fossil Hill" in central Nevada about 60 years ago were the first of Middle Triassic age (ca. 243 My) discovered in North America. These canoe-shaped elements were named *Neogondolella constricta*, a species that subsequently has been reported worldwide. However, the scope of this species has remained uncertain because it was based on comparatively small early growth stages characterized by features lost during growth. Abundant specimens of the *N. constricta* group recovered from the original type locality form the basis for documenting changes in morphology during their accretionary growth and provide better definition of the species. This facilitates discrimination of similar species, 10 of which are distinguished in Nevada, including four new taxa; most of these are also identified in British Columbia. Successive associations through the Fossil Hill strata include elements with similar platform shapes but different relative lengths, the younger species being longer. This succession is calibrated with established ammonoid fossil zones and contributes to a parallel conodont biozonation. Eurasian occurrences of the *Neogondolella constricta* group are assessed and their correlation with the Nevadan scheme summarized.

Abstract.—*Neogondolella constricta* (Mosher and Clark, 1965) from the Prida Formation at Fossil Hill in central Nevada was the first conodont described from Middle Triassic strata in North America. The species has since been widely reported from elsewhere despite uncertainties about its taxonomic scope and that of similar related taxa. Poor definition of these taxa has spawned a diverse nomenclature and inhibited use of the group in biozonation. Starting with a growth series of topotype *N. constricta*, we reassess allied contemporaneous taxa from North America. In Nevada, 11 conodont taxa are identified: *N. constricta*, *N. aldae* Kozur, Krainer, and Mostler, 1994b, *N. cornuta* Budurov and Stefanov, 1972, *N.* ex gr. *mesotriassica* (Kozur and Mostler, 1982), *N. postcornuta* (Kovács, 1994), *N. posterolonga* Kozur, Krainer, and Mostler, 1994b, *N. quasiconstricta* n. sp., *N. quasicornuta* n. sp., and three subspecies of *N. excentrica* Budurov and Stefanov, 1972. Successive associations of taxa display symmetry transition in posterior platform configuration. Subdivision of the upper Anisian–lower Ladinian is provided by dominant *N. constricta* plus relatively uncommon *N. quasiconstricta* n. sp. and *N. excentrica primitiva* n. subsp. in the Rotelliformis ammonoid zone. This is followed in the Meeki through the Subasperum zones by dominant *N. cornuta*, associated *N. posterolonga*, plus relatively uncommon *N. quasicornuta* n. sp., and a variety of asymmetric elements: the Meeki Zone includes *N.* aff. *N. cornuta*; the Occidentalis Zone adds *N. e. excentrica*; and finally, *N. e. sigmoidalis* n. subsp. appears in the Subasperum Zone. In British Columbia, the three subspecies of *N. excentrica* are recognized in, respectively, the Deleeni, Chischa, and Matutinum (and younger) ammonoid zones.

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Introduction

The first conodont species described from Middle Triassic strata in North America was *Neogondolella constricta* (Mosher and Clark, 1965) from the classic outcrop of the Prida Formation at Fossil Hill in the Humboldt Range of central Nevada (Fig. 1). This species has subsequently been widely reported from elsewhere, yet the taxonomic scope of the species, and many similar taxa assembled here as *N.* ex gr. *constricta*, remain poorly known and variably interpreted. This partly arises from the nature of the holotype, which is a relatively small, early growth stage for which an ontogenetic series has never been documented. The characteristic 'constricted' morphology of the posterior platform in *N. constricta* is common in early growth stages of many contemporaneous neogondolellins (Kozur et al., 1994b), which also often lack modern descriptions. Poor definition of many related taxa has spawned a diverse nomenclature and inhibited a robust biozonation for the upper Anisian and lower Ladinian strata where *N.* ex gr. *constricta* are often the dominant taxa.

In addition to the biostratigraphic utility of the group, it is noteworthy that *Neogondolella constricta* serves as the type species for *Pridaella* Budurov and Sudar, 1989, a genus proposed to

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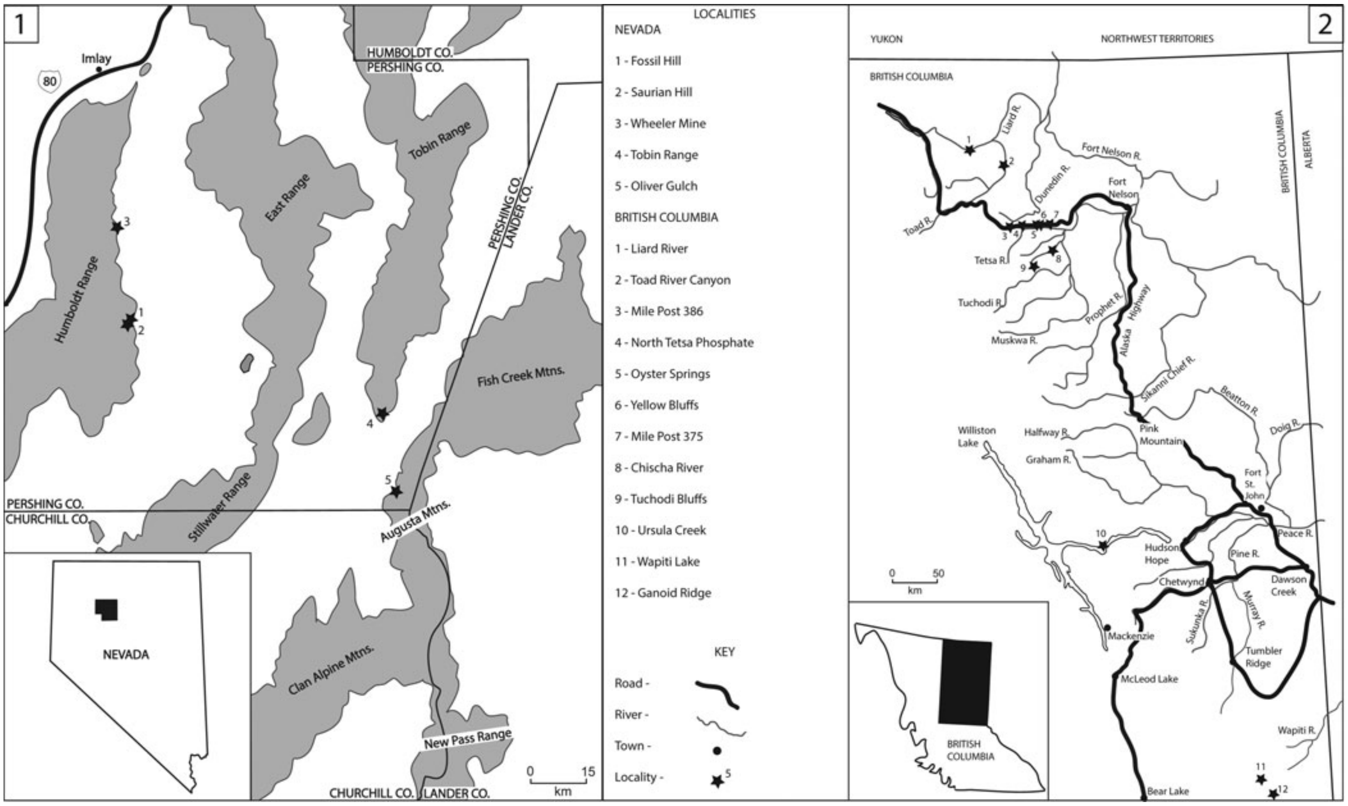

Figure 1. Maps of (**1**) Nevada and (**2**) British Columbia showing locations of sections and sites from which upper Anisian–lower Ladinian conodont collections are reported here.

accommodate this group of allied forms. The authors of that genus offered no rationale for this proposal other than to imply that the multielement apparatus of those species differed in non-specified ways from that of the type species of *Neogondolella*, *N. mombergensis* Tatge, 1956, from the Germanic Basin. The natural conodont assemblage from Monte San Giorgio, Switzerland, proposed as that of *Neogondolella* (Rieber, 1980; Orchard and Rieber, 1999; Goudemand et al., 2011, fig. 2B, C) corresponds, in fact, to *N.* ex gr. *constricta* (see Orchard, 2005, fig. 10) from the Humboldt Range of Nevada, which would serve as an apparatus template for *Pridaella* should that of *N. mombergensis* be demonstrably different. The recent conclusion of Chen et al. (2018) that *N. haslachensis* (Tatge, 1956), an endemic Germanic associate of *N. mombergensis*, has a nonbifid S3 element unlike the *constricta* group, suggests a potential justification for this nomenclatural change. However, the apparatus of *N. mombergensis* remains undescribed.

In this work, we present growth stages of topotype *Neogondolella constricta* from the upper Anisian Rotelliformis ammonoid Zone at Fossil Hill and reassess allied taxa from the Middle Triassic of Nevada and British Columbia (B.C.). We also compare these taxa with similar conodont faunas first described from Europe fifty years ago that were central to the formulation of European conodont zonation; the extent to which these can be applied in North America is controversial. We aim to stabilize species concepts, establish stratigraphic ranges in North America, and facilitate comparison with similar taxa reported from Eurasia.

Previous work

The Prida Formation at Fossil Hill (and nearby Saurian Hill) in Nevada is an important paleontological site that, apart from its pioneering conodont research, has been the focus for ammonoid studies for over a century (Smith, 1914; Silberling, 1962; Silberling and Nichols, 1982; Monnet and Bucher, 2005a, b). Notably, it provides the standard American ammonoid biochronology for the upper Anisian–lower Ladinian, which comprise the (Anisian) Rotelliformis, Meeki, Occidentalis, and (Ladinian) Subasperum ammonoid zones (Silberling and Tozer, 1968), as well as constituent subzones (Fig. 2). Conodont studies at Fossil Hill began with Mosher and Clark (1965), who introduced *Neogondolella constricta*. This was followed by major and very different taxonomic revisions by Nicora and Kovács (1984) and Ritter (1989). The application of nomenclature developed in Europe was challenged by Kozur et al. (1994b), who introduced new *Neogondolella* taxa for some of the Nevadan fauna based on published illustrations. More recent summaries of the conodont succession across the Anisian–Ladinian boundary (ALB) at Fossil and Saurian hills were presented by Bucher and Orchard (1995) and Orchard (2010), but differentiation of the *N. constricta* group was not attempted.

Contemporaneous Canadian sections where both ammonoids and conodonts are known were the subject of studies by Mosher (1973), Orchard and Tozer (1997), and Golding (2014). In B.C., *Neogondolella* ex gr. *constricta* are represented in many disjunct sections of the Toad and Liard formations, and

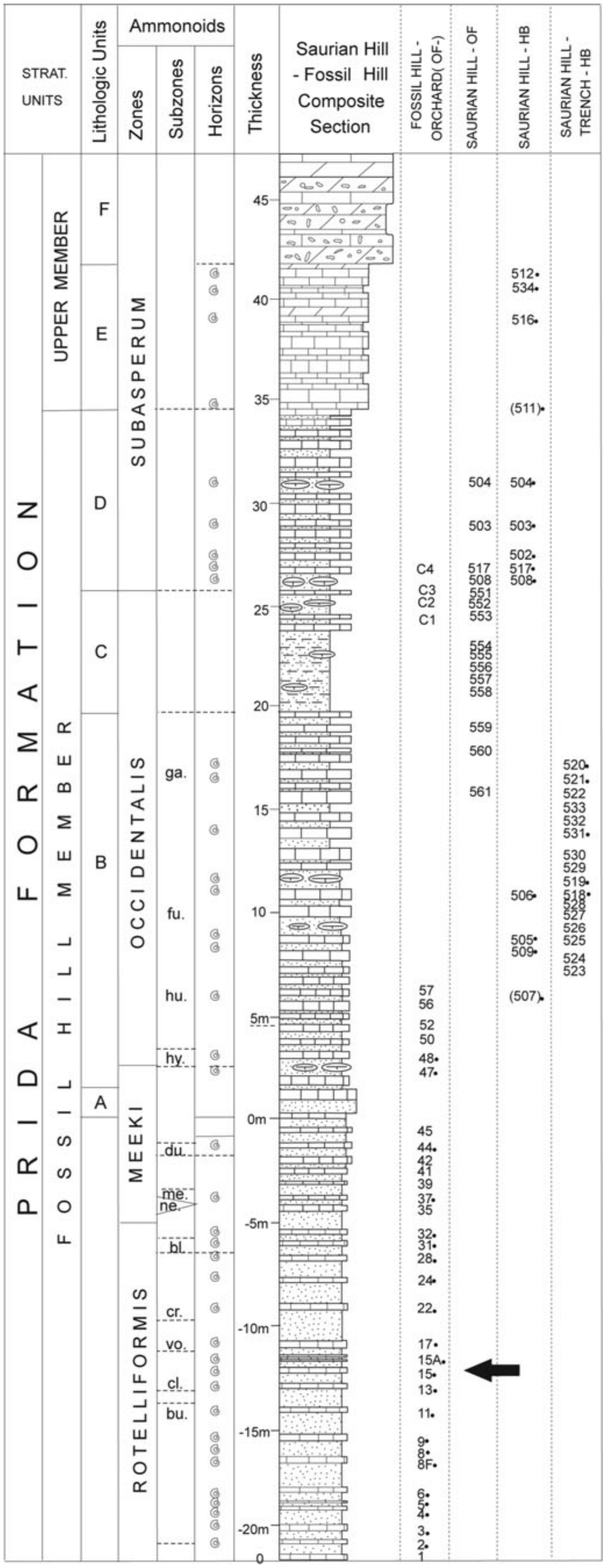

Figure 2. Composite stratigraphic section for Fossil and Saurian hills, Nevada, showing ammonoid horizons and zonal divisions (after Silberling and Nichols, 1982) and the relative positions of conodont samples collected by M.J. Orchard (OF) and H. Bucher (HB). Sample numbers with dots are ammonoid-bearing samples. Subzones are abbreviated within the Rotelliformis Zone: bu. = burckhardti, cl. = clarkei, vo. = vogdesi, cr. = cricki, bl. = blakei; subzones are abbreviated within the Meeki Zone: ne. = nevadanus, me. = meeki, du. = dunni; and subzones are abbreviated within the Occidentalis Zone (positions uncertain): hy. = hyatti, hu. = humboldtensis, fu. = furlongi, ga. = gabbi. Subzones below the blakei Subzone have been revised as a single vogdesi Subzone (Monnet and Bucher, 2005a). The original position of the type *Neogondolella constricta* is indicated by the large arrow.

the Vega Member of the Sulphur Mountain Formation. These strata include ammonoids of the Deleeni, Meeki, and Chischa zones in the upper Anisian, and of the Matutinum, Poseidon, and Meginae zones in the lower Ladinian (Tozer, 1994). The most recent ammonoid-based correlation of these B.C. ammonoid zones and those from Nevada was presented by Ji and Bucher (2018).

Neogondolella ex gr. *constricta* also occurs elsewhere in western and northern Canada (e.g., Orchard, 1991, 2006; Orchard et al., 2001; Henderson et al., 2018). Neither these nor recent descriptions of new Anisian conodonts from B.C. (Golding and Orchard, 2016, 2018) have featured analysis of the *Neogondolella constricta* group.

In Europe, much of the pioneering Middle Triassic conodont work was undertaken in Bulgaria (Budurov and Stefanov, 1972, 1973), from where several key species were first described. As was the norm at the time, published images of these early types are of poor resolution, which inhibits comparison. Contemporaneous Muschelkalk faunas were described from the relatively restricted Germanic Basin (Tatge, 1956; Trammer, 1975; Zawidzka, 1975; Rafek, 1976), while those representing the larger Tethyan oceanic region were described from Austria (Kozur and Mostler, 1982), Italy (Nicora and Brack, 1995), Greece (Krystyn, 1983), and Hungary (Kovács et al., 1990; Kovács, 1994). On the southern margin of Tethys, the Sephardic Province represented an additional faunal realm (Hirsch, 1994) with unique attributes.

Knowledge of the stratigraphic and geographic distribution of Balkan, Germanic, and Tethyan neogondolellin conodont taxa in North America should improve zonation and illuminate paths of migration within and between Europe and eastern Panthalassa. In recent decades, many studies from China, particularly from Guizhou Province, have reported *Neogondolella constricta* and allied forms (Wu et al., 2008; Lehrmann et al., 2015), which broadens their correlation potential further.

The evolving taxonomy

Identity of *Neogondolella constricta* group members has been hampered by taxonomic and nomenclatural uncertainty. Juvenile growth stages of several species may be indistinguishable because species-diagnostic features only become apparent with later growth. In their original report of the Fossil Hill conodonts, Mosher and Clark (1965) described a poorly diversified conodont succession dominated by segminiplanate (neogondolellin) platform conodonts that they assigned to three species of the genus *Gondolella*: *G. constricta* n. sp., *G. mombergensis*, and *G. navicula* Huckriede, 1958. In the same year, Bender and Stoppel (1965) introduced the genus *Neogondolella* with *G. mombergensis* as the type species for Triassic taxa resembling *Gondolella*, a genus now confined to the Pennsylvanian. In this paper, the original binomial names of species are used first, and thereafter current generic nomenclature is applied.

The original Fossil Hill species reported by Mosher and Clark (1965), Kovács and Nicora (1984), and Ritter (1989) included the Germanic *Neogondolella mombergensis*. Kovács and Nicora (1984) recognized two subspecies that they assigned to *N. m. mombergensis* and *N. m. longa* Budurov and Stefanov, 1973, the latter based on a Balkan taxon. Ritter's (1989) univariate and multivariate morphometric analyses of 18 successive *Neogondolella* Pa element populations from Fossil Hill concluded that the speciation criteria used by Kovács and Nicora (1984) were arbitrary and unsuitable for discrimination of zones. Rather, Ritter (1989) assigned all the conodonts to a single, morphologically diverse species, for which he regarded *N. mombergensis* as the priority name. However, as noted by Orchard (in Bucher and Orchard, 1995) and illustrated by Orchard and Rieber (1999, fig. 1), *N. mombergensis* is a distinctive species that differs from all those so far identified in North America.

A second species originally reported from Fossil Hill by Mosher and Clark (1965) was *Gondolella navicula*, but this is now recognized as a Late Triassic *Norigondolella* species (Kozur, 1990b) with a differing apparatus (Orchard, 2005). Hence, *N. constricta* retains nomenclatural seniority for the common elements of the upper Anisian fauna at Fossil Hill.

In Europe, early work in Bulgaria by Budurov and Stefanov (1972, 1973, 1975a) introduced new upper Anisian–lower Ladinian neogondolellin conodont species that provided a standard for comparison. A decade later, Nicora and Kovács (1984) concluded that two of those Balkan species, *N. cornuta* Budurov and Stefanov, 1972, and *N. balkanica* Budurov and Stefanov, 1975a, were in fact later growth stages, and therefore junior synonyms of *N. constricta*. Further revisions of the *constricta* group taxa were undertaken by Budurov and Stefanov (1984), Kovács et al. (1980, 1990), Kozur and Mostler (1982), Kovács (1994), and Kozur et al. (1994b). Kovács et al. (1990) formalized the 'growth stages' of *N. constricta* first as morphotypes α and β, and later (Kovács, 1994) as the subspecies *N. constricta cornuta* (= morphotype α) and *N. c. balkanica* (= β); a third morphotype (from Hungary) identified as morphotype γ was later named *N. c. postcornuta* (Kovács, 1994). In contrast, Kozur et al. (1994b) argued that (1) the Balkan species *N. cornuta* and *N. balkanica* were not conspecific with *N. constricta*; (2) the newly named *N. c. postcornuta* was an example of the previously described *Gondolella* (= *N.*) *mesotriassica* Kozur and Mostler, 1982; and (3) Nevadan elements formerly assigned to *N. mombergensis* represented a new species, *N. aldae* (with two subspecies). Kozur et al. (1994b) argued that none of the European taxa previously recorded at Fossil Hill occurred there.

Stratigraphic utility

Middle Triassic neogondolellin species, many of which are allied with *N. constricta*, have featured in biostratigraphic zonations under various guises. Neither Mosher and Clark (1965) nor Ritter (1989) recognized a difference in the stratigraphic range of the dominant species at Fossil Hill, although Sweet et al. (1971) differentiated an upper Anisian *constricta* Zone and a Ladinian *mombergensis* Zone in their standard Triassic zonation. Kovács and Nicora (1984) maintained these two ill-defined zones and noted that the contact between them was coincident with the base of the Occidentalis ammonoid Zone; they found no change in conodonts between the Occidentalis and Subasperum zones in Nevada. Studies by the first author (Bucher and Orchard, 1995; Orchard, 2010) have documented more diverse faunas that include species of *Paragondolella*, *Budurovignathus*, and probable new genera that collectively provide an improved biozonation for the interval, but the *constricta* group is far more common.

Middle Triassic Muschelkalk conodont faunas from the Germanic Basin were divided into seven zones by Kozur (1968b) but many of the constituent taxa appear confined to that basin. In Bulgaria, a Balkan Anisian conodont zonation featured successive range zones of *Paragondolella bulgarica* Budurov and Stefanov, 1975a, *Ozarkodina* (= *Nicorella*) *kockeli* Tatge, 1956, *P. excelsa* Mosher, 1968, *Neogondolella cornuta*, *N. excentrica* Budurov and Stefanov, 1972, and *N. bakalovi* Budurov and Stefanov, 1972 (Budurov and Stefanov, 1975b, 1983; Budurov, 1980; Budurov and Trifonova, 1994, 1995; Budurov and Vaptsarova, 1994; Budurov et al., 1995). This Balkan succession is not obviously applicable in Nevada, and neither is that of Kozur (1980) who summarized his earlier work and that of Mosher (1968) to propose a "standard zonation" for the interval that featured successive conodont zones of *N. constricta*, *N. pseudolonga* Kovács, Kozur, and Mietto, 1980, and *N. transita* Kozur and Mostler, 1971. Later, Kozur (1990a) presented a revised zonal scheme for Tethys that included three successive assemblage zones of *N. constricta*, *G.* (= *N.*) *praetrammeri* Kozur and Mostler, 1982, plus *N. mesotriassica*, and *N. transita*.

To some extent these various zonations can be aligned (see Nicora, 1993), but differing taxonomic concepts, resultant nomenclature, and geographic provenance hinder correlation. Similarly, the absence in North America of Tethyan *Gladigondolella* spp. and '*Neogondolella*' *trammeri* Kozur in Kozur and Mock, 1972, group; the Germanic endemics *N. mombergensis*, *N. haslachensis*, and *Gondolatus* spp.; and the Sephardic *Pseudofurnishius* restricts their global use. In contrast, some *N.* ex gr. *constricta* are not geographically restricted.

The most recent accounts of conodonts from the ALB sections in Hungary and Italy arose during deliberations concerning the choice of the global stratigraphic section and point (GSSP) for the stage boundary (Kovács, 1994; Nicora and Brack, 1995; Brack and Nicora, 1998). Accounts of the Bagolino GSSP section, Italy, document occurrences of 11 members of the *Neogondolella constricta* group, including taxa regarded here as synonyms and others unknown in North America. Later, although no taxonomic discussions were presented, the summaries provided by Muttoni et al. (2004) differentiated only six members, whereas Brack et al. (2005) included just five. Notably, these works do not record all the same taxa. A synthetic summary of the published *constricta* group conodont occurrences in Europe is given in Figure 3.

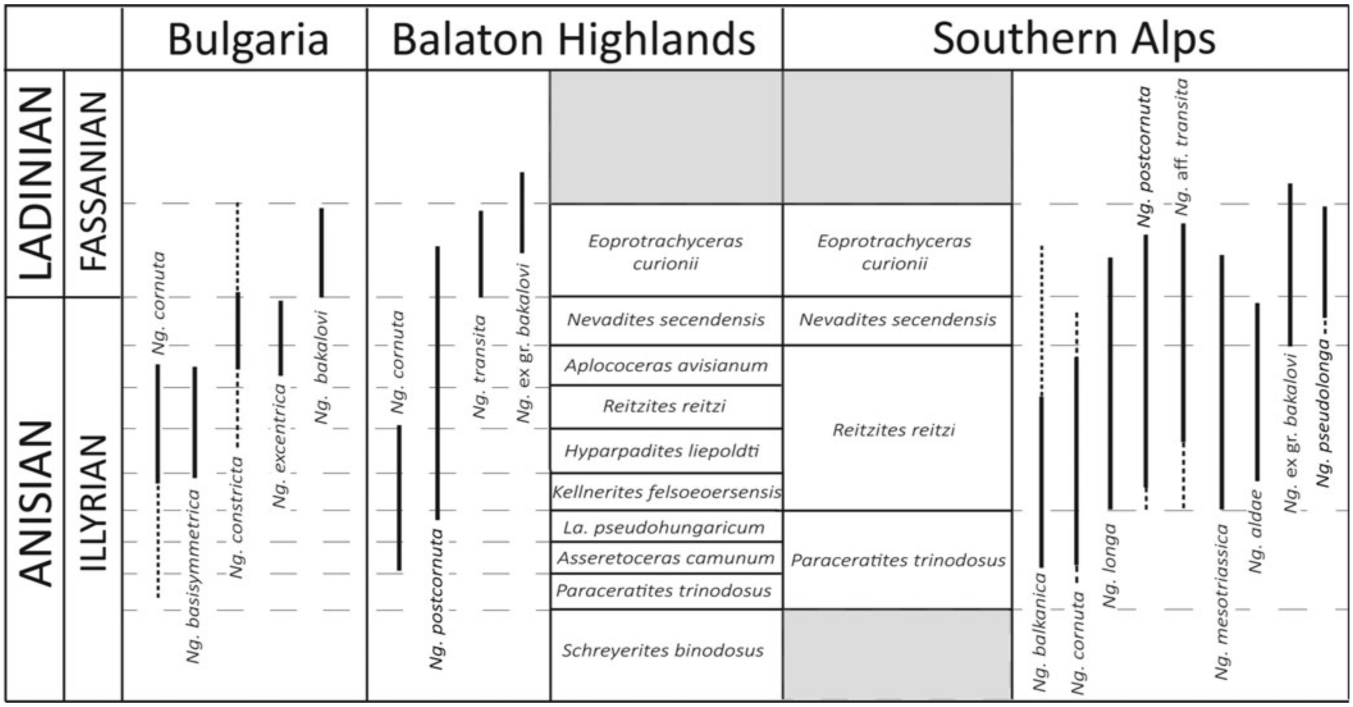

Figure 3. European ammonoid zones and the ranges of *Neogondolella constricta* group members within the late Anisian–early Ladinian based on the literature. Those of Southern Alps of Italy after Kozur et al. (1994b), Nicora and Brack (1995), Brack et al. (2005), and Muttoni et al. (2004); the Balaton Highlands, Hungary after Kovács (1994) and Vörös et al. (1996); and from Bulgaria after Budurov and Stefanov (1972). Elements allied with *N. transita* are probable examples of *N. excentrica* of this work. Synonymies of *N. balkanica* and *N. pseudolonga* are discussed in the text.

Materials

The foundations for this paper are numerous and often abundant collections of conodonts recovered from North American strata that have provided an ammonoid biochronology for the late Anisian and early Ladinian (Tozer, 1967, 1994; Silberling and Tozer, 1968; Monnet and Bucher, 2005a, b) (Figs. 4, 5). Nearly all of the 100+ conodont collections recovered are dominated by the *Neogondolella constricta* group.

In 1992, the Fossil Hill section and the nearby Saurian Hill section were sampled for conodonts in conjunction with H. Bucher, who guided the first author through the sections of the Prida Formation in which ammonoid faunas of the Rotelliformis, Meeki, Occidentalis, and Subasperum zones were identified. Additional matrix samples were taken from ammonoid collections, including bed-by-bed samples from an excavated trench exposure at Saurian Hill. Successions of 35 conodont collections from Fossil Hill and 37 from Saurian Hill were recovered (Table 1), in addition to others from nearby Wheeler Mine in the northern Humboldt Range. Some contemporaneous ammonoid-bearing samples were also collected from the Tobin Range (Rotelliformis and Meeki zones) (Fig. 1; Table 2). In total, about 80 samples from Nevada were processed and nearly all produced large conodont fauna.

Small Middle Triassic conodont samples from Canadian ammonoid matrices were originally provided by E.T. Tozer to Mosher (1973). Later, the first author collected bulk samples during 1983 field work with E.T. Tozer in the Toad–Liard River area. Follow-up fieldwork along the Alaska Highway by the present authors in 2011 yielded supplementary collections from locations that underpin parts of the standard Canadian ammonoid biochronology (Tozer, 1967, 1994). Upper Anisian and lower Ladinian strata yielded conodonts from nine sections that collectively spanned Deleeni through Meginae ammonoid zones, with representation of all but the Meeki Zone (Table 2). In addition, matrix samples were obtained from archival ammonoid collections representing the Deleeni Zone on Chischa River, the Matutinum Zone at Wapiti Lake, and the type localities of the Deleeni (Alaska Highway, milepost 375) and Poseidon (Tuchodi Bluffs) zones. Additional suites of contemporaneous samples were collected from sections of the Whistler and Llama formations near Wapiti Lake (1997–1998), and from the Toad Formation exposed at Ursula Creek on Williston Lake (1992, 1999, 2001) (Fig. 1).

Repository and institutional abbreviation.—Illustrated material is deposited in the National Type Collections of the Geological Survey of Canada and bear 6-digit type numbers prefixed with "GSC". Supporting collections bear the following GSC curation numbers: C-300201–300236 (Fossil Hill); C-201563–201566, C-201581–201594, C-201572, C-209954, C-209955, C-300240–300252, C-301228 (Saurian Hill).

Results and discussion

Many of these recovered collections contain hundreds of conodont elements, or part elements, including good representation of the multielement ramiform components (Orchard, 2005, fig. 10). The P_1 platform elements representing the *Neogondolella*

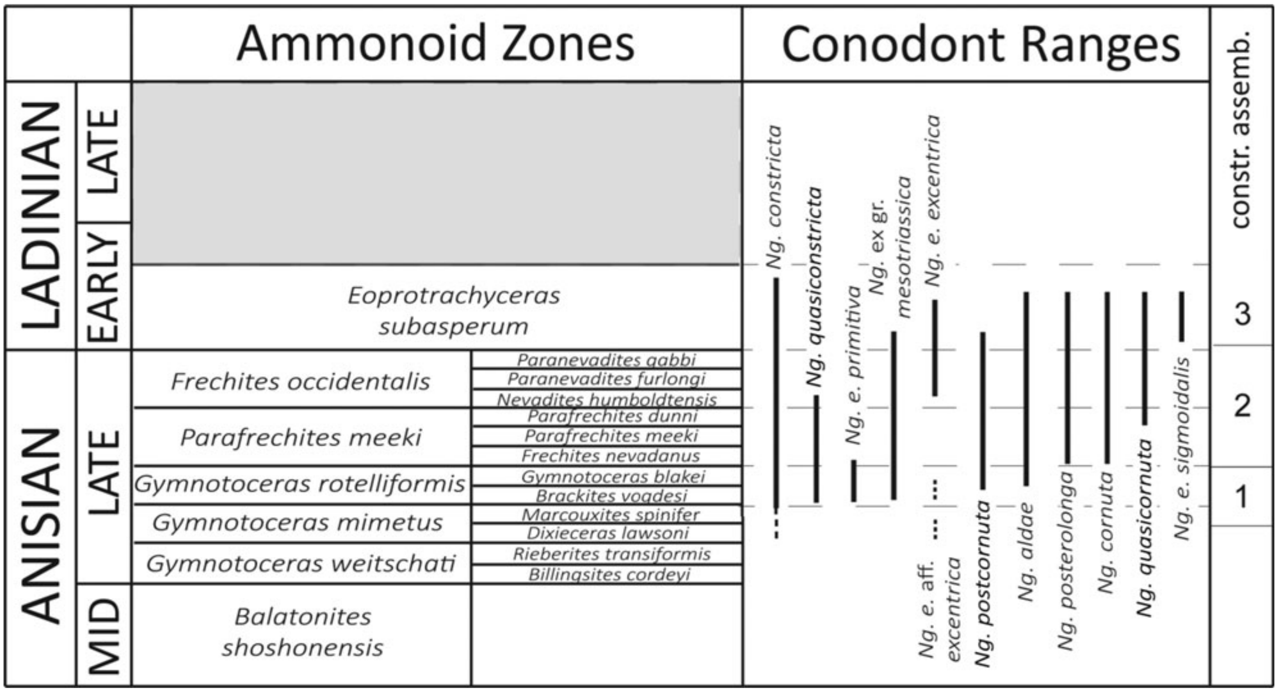

Figure 4. Summary of observed ranges of *Neogondolella constricta* group members with respect to the late Anisian–early Ladinian Nevadan ammonoid zones and subzones at Fossil and Saurian hills. Ammonoid zonation after Silberling and Tozer (1968), Silberling and Nichols (1982), and Monnet and Bucher (2005a, b). Three intervals of *N. constricta* group assemblages are shown on the right. New taxa identified in this work are *Neogondolella quasiconstricta* n. sp., *Neogondolella excentrica primitiva* n. subsp., *Neogondolella quasicornuta* n. sp., and *Neogondolella excentrica sigmoidalis* n. subsp.

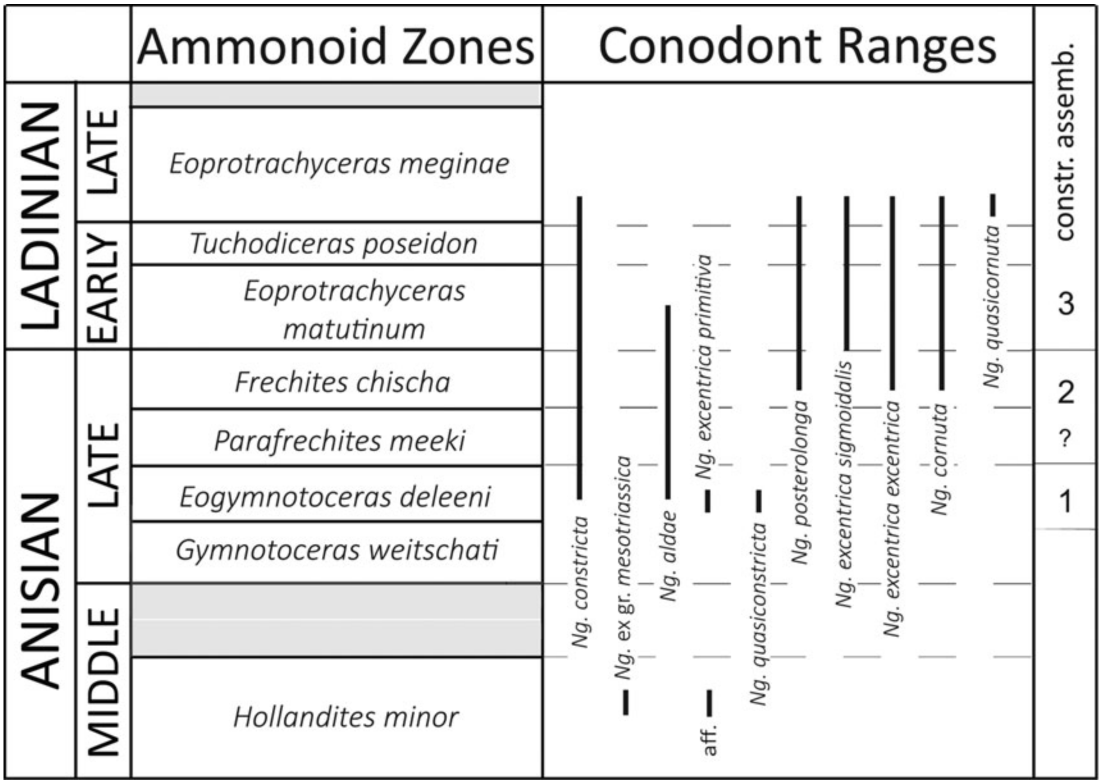

Figure 5. Summary of observed ranges of *Neogondolella constricta* group members with respect to the late Anisian–early Ladinian ammonoid zones in British Columbia (see Table 2). Ammonoid zonation after Tozer (1994), and Monnet and Bucher (2005b). Three intervals of *N. constricta* group assemblages are shown on the right. New taxa identified in this work are *Neogondolella excentrica primitiva* n. subsp., *Neogondolella quasiconstricta* n. sp., *Neogondolella excentrica sigmoidalis* n. subsp., and *Neogondolella quasicornuta* n. sp.; aff. = *Neogondolella excentrica* aff. *primitiva* n. subsp.

Table 1. Occurrences of *Neogondolella constricta* group members at Fossil Hill (above) and Saurian Hill (below), Nevada. Ammonoid zones are indicated above the sample numbers, which are in bold when the collections contain at least 100 *constricta* group elements. See text for relative abundances of species.

Fossil Hill

Ammonoid Zones	Rotelliformis																		Meeki								Occidentalis					?		Sub.	
FOSSIL HILL – FH	1	2	3	4	5	**6**	**8**	**9**	**11**	**13**	**15**	**15A**	**17**	**22**	**24**	**28**	**31**	**32**	**35**	**37**	39	41	**42**	**44**	45	**47**	**48**	**50**	52	**56**	57	C1	C2	C3	**C4**
N. constricta	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	–	–	–	–	X
N. aldae	–	–	–	–	–	–	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	–	–	–	–	X	–	X	–	X	–	–	–	–	X
N. cornuta	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	X	X	X	X	X	X	X	X	X	X	X	–	–	X	X	X
N. aff. *N. cornuta*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	X	–	X	X	X	X	X	X	X	X	–	–	–	–	X
N. excentrica primitiva n. subsp.	–	–	–	–	X	X	X	X	X	X	X	–	X	X	X	X	X	X	X	–	–	–	–	–	–	X	–	–	–	–	–	–	–	–	–
N. ex. aff. *excentrica*	–	–	–	–	–	–	–	–	–	X		X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
N. ex. excentrica	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	X	X	–	X	–	–	X	X	X
N. ex. sigmoidalis n. subsp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
N. mesotriassica	–	–	–	–	–	–	X	–	–	X	X	X	X	–	–	X	–	–	–	–	–	–	–	–	–	–	X	X	–	–	–	–	–	–	–
N. postcornuta	–	–	–	–	–	X	X	–	–	–	X	–	X	X	–	X	X	X	X	–	X	X	–	X	–	X	–	X	–	X	–	–	–	–	–
N. posterolonga	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	X	–	X	–	–	X	–	X	–	X	–	–	X	X	X
N. quasiconstricta n. sp.	–	–	–	–	–	X	X	–	X	–	X	–	X	X	X	–	X	–	–	–	–	–	–	–	–	X	X	X	–	–	–	–	–	–	–
N. quasicornuta n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	–	–	–	X	X	X	–	–	–	–	–	X	X

Saurian Hill

Ammonoid Zones	Occidentalis																					?								Subasperum							
SAURIAN HILL – SH	**524**	**505**	**525**	**526**	**527**	**528**	**506**	**518**	**519**	**529**	**530**	**531**	**532**	533	538	522	**521**	**520**	560	561	559	558	557	556	555	554	553	552	551	**508**	**517**	502	503	**504**	**516**	534	512
N. constricta	X	X	X	X	X	X	X	X	X	X	X	–	X	X	–	X	X	X	–	–	–	–	–	–	–	–	–	–	–	–	X	X	X	X	X	X	X
N. aldae	–	–	–	–	X	X	–	X	–	–	X	X	–	–	–	–	X	–	–	–	–	–	–	–	–	–	–	–	–	X	X	–	–	X	X	X	X
N. cornuta	X	X	X	X	X	X	X	X	X	X	X	X	X	X	–	X	X	X	–	–	X	–	–	–	–	–	–	–	–	X	X	X	X	X	X	X	X
N. aff. *N. cornuta*	X	X	X	X	X	X	X	X	X	X	X	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	X	X	–	X	–	–	X
N. excentrica primitiva n. subsp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
N. ex. aff. *excentrica*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
N. ex. excentrica	X	X	X	X	X	X	–	–	X	X	–	–	–	–	–	–	X	X	–	–	–	–	–	–	–	–	–	–	–	X	X	X	X	X	X	X	X
N. ex. sigmoidalis n. subsp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	X	X	X	X	X	X
N. mesotriassica	X	–	X	–	–	–	–	X	X	X	–	–	–	–	–	–	–	X	–	–	–	–	–	–	–	–	–	–	–	–	X	–	–	X	–	–	–
N. postcornuta	–	X	X	X	–	–	–	X	X	X	–	X	X	–	–	–	–	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	–	–	–
N. posterolonga	–	X	X	–	–	–	–	X	X	X	X	X	X	–	–	–	X	X	–	–	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
N. quasiconstricta n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
N. quasicornuta n. sp.	X	X	–	X	X	X	X	X	X	X	X	–	–	–	–	–	X	X	–	–	–	–	–	–	–	–	–	–	–	–	X	X	X	X	X	X	X

constricta group dominate most collections. Among them, the 'conservative' *N. constricta* and *N. cornuta* along with many less-specific early growth stages predominate, with the latter species largely replacing the former early in the Meeki Zone. Concurrently, *N. posterolonga* became increasingly common into the Ladinian. Far less common are eight other taxa: *N. aldae*, *N. excentrica primitiva* new subspecies, *N. e. excentrica*, *N. e. sigmoidalis* new subspecies, *N.* ex gr. *mesotriassica*, *N. postcornuta*, *N. quasicornuta* new species, and *N. quasiconstricta* new species. To date, 10 taxa have been recognized in the less-diverse faunas recovered from Canadian locations (Table 2).

The reconstructed growth series of topotype *Neogondolella constricta* from beds containing Rotelliformis Zone ammonoids at Fossil Hill, Nevada, reveals growth progression from early growth stage elements with a constricted posterior platform (as in the holotype) through progressively broader elements that have a narrowly and then broadly rounded posterior platform. An inclined terminal denticle lies posterior of the cusp and becomes increasingly prominent as growth proceeds: it may lie at the posterior end of the platform, or a narrow posterior platform brim may be developed.

The ontogenetic and other variation in platform configuration shown within topotype *N. constricta* populations are here considered to embrace diagnostic features of the Balkan species *N. cornuta* and *N. balkanica* (as was also determined by Nicora and Kovács, 1984), and of the later differentiated *N. tardocornuta* Budurov and Stefanov, 1984. The growth and variation seen in *N. constricta* are essentially the same as those observed in the more elongate species that succeeds it, for which *N. cornuta* is regarded as the appropriate name. The two Nevadan species display similar posterior morphogenesis but can be distinguished by their platform shape and length: breadth ratio. Based on the relative platform dimensions of the holotypes, we suggest that both *N. balkanica* and *N. tardocornuta* are junior synonyms of *N. constricta*, and that the Alpine *N. pseudolonga* is an early growth stage of *N. cornuta* or perhaps *N. posterolonga*. Restudy of these European species from their type localities, as has been done here for *N. constricta*, will be necessary to confirm these suggested synonymies.

The two subspecies of *Neogondolella aldae* introduced by Kozur et al. (1994b), *N. a. aldae* and *N. a. posterolonga*, are raised to species level. These species, which retain the juvenile feature of a narrow posterior platform, are reported from the upper Anisian and lower Ladinian in both the USA and Canada, and from European localities (see below). These species were formerly confused with the Germanic *Neogondolella mombergensis* and Balkan *N. longa*, neither of which are certainly known from North America.

Later growth stages of both *Neogondolella constricta* and *N. cornuta* have essentially rounded, symmetrical posterior platforms of uniform width, but they commonly co-occur with elements of similar relative length that have either asymmetric or expanded and truncated posterior platforms. Hence, in Nevada, *N. constricta* is associated with the asymmetric *N. excentrica primitiva* n. subsp. and the quadrate *N. quasiconstricta* n. sp. in the Rotelliformis Zone, and later *N. cornuta* co-occurs with *N. quasicornuta* n. sp. and the asymmetric *N. e. excentrica* in the Occidentalis Zone. Most of the intervening Meeki Zone contains the asymmetric *N. e.* aff. *cornuta*, which may have an accessory posterior denticle but lacks a secondary posterior process. In the Ladinian Subasperum Zone, rare *N. e. sigmoidalis* n. subsp. occurs (Fig. 4), often with *N. posterolonga*.

These associations exhibit symmetry transition in their posterior platform configuration that is like that shown by the Pelsonian triad *Paragondolella bulgarica*, *P. hanbulogi* Sudar and Budurov, 1979, and *P. bifurcata* Budurov and Stefanov, 1972. As a backdrop to this pattern, two major trends are recognized within the *constricta* group. The first is an elongation and relative narrowing of the platform, which is quite abrupt early in the Meeki Zone; the second is the elaboration of the posterior platform to produce a longer, more differentiated secondary process and extended keel in *N. excentrica*, starting with *N.* aff. *N. cornuta*.

In B.C., these taxa are less common, but *N. constricta* and *N. e. primitiva* n. subsp. occur in the Deleeni Zone; *N. cornuta* occurs with *N. e. excentrica* in the uppermost Anisian Chischa Zone; and *N. e. sigmoidalis* n. subsp. occurs in association with *N. posterolonga* in the Ladinian Matutinum and Poseidon zones, and maybe into the Meginae Zone based on its occurrence with the ammonoid *Silenticeras bamberi* Fauna, which is known to be bracketed between the Poseidon and Meginae III zones (Tozer, 1994, p. 33). No conodonts are known from the Meeki Zone in B.C., but an appearance of *N. cornuta* earlier than *N. e. excentrica* (*N. transita* of previous authors) would align with Nevadan and European sections (Figs. 3, 4). The interval with *N. e. sigmoidalis* n. subsp. may be equivalent in age (and perhaps in content) to the Tethyan *transita* Zone (Kozur, 1990a) and the Balkan *bakalovi* Zone.

One outcome of this study is that *Neogondolella constricta* sensu stricto is resurrected as an upper Anisian species that demonstrably appears prior to *N. cornuta* in Nevada and B.C. and thus identifies an interval that predates a *cornuta* Zone. A *constricta* Zone has not been widely used in Europe recently, but a *cornuta* Zone has been regarded as immediately succeeding a *Paragondolella excelsa* Zone in the much older Trinodosus Zone. Occurrences of *N. cornuta* at these levels may be based on similar elements with a prominent posterior denticle, which has been regarded as diagnostic for that species.

The "standard zonation" for the ALB interval proposed by Kozur (1980) features the successive conodont zones of *N. constricta*, *N. pseudolonga*, and *N. transita*. This succession compares moderately well with the Nevadan succession because *N. pseudolonga* may represent an early growth stage of the contemporaneous *N. cornuta* or *N. posterolonga*, and *N. transita* may include elements here assigned to *N. excentrica sigmoidalis* n. subsp.

The Tethyan zonal scheme of Kozur (1990a), with successive assemblage zones of *N. constricta*, *N. praetrammeri* – *N. mesotriassica*, and *N. transita* has less applicability in North America because the *trammeri* group does not occur, and the scope of *N. mesotriassica* is unclear.

The main conodont events recognized in the Balaton Highland, Hungary by Kovács (1993a, b; Fig. 3) also have limited expression in Nevada where the first event, the appearance of *N. postcornuta*, is not readily discernible due to its rarity, and the second event, the appearance of '*N.*' *trammeri*, is not known. A third event in Hungary (Kovács, 1993a, b) features

Table 2. Occurrences of the *Neogondolella constricta* group members from spot samples in other mostly late Anisian–early Ladinian localities in British Columbian and Nevada. GSC curation numbers are given for these collections.

Section	Lat./Long. of Section	GSC Cur. No.	Field No.	Formation	Age (Zone)	*Neogondolella* ex gr. *constricta*
British Columbia						
West Toad River	59°11′16″N, 124°41′39″W	O-99560– 99562	83-MJO-203A–C	Toad	Upper Anisian (*E. deleeni*)	*N. constricta*
		C-103867	83-MJO-Bone	Toad	Upper Anisian (*E. deleeni*)	*N. constricta*; *N. aldae;* *N.* aff. *N. cornuta*
East Toad River	59°11′30″N, 124°41′50″W	O-99566	83/205B	Toad	Upper Anisian (*E. deleeni*)	*N. constricta*; *N. aldae*
		O-99592	83/215F	Toad	Middle Anisian (*H. minor*+)	*N.* ex gr. *mesotriassica*
Mile Post 375 West	58°39′16″N, 124°14′48″W	C-201925	92-AH25	Toad	Upper Anisian (*E. deleeni*)	*N. constricta*
		C-201926	92-AH26	Toad	Middle Anisian (*H. minor*)	*N. excentrica* aff. *primitiva*
Yellow Bluffs	58°39′14″N, 124°15′50″W	C-201902	92/AH2	Toad	Upper Anisian (*E. deleeni*)	*N. constricta*; *N. aldae* *N. excentrica primitiva*
		C-304063	92-AH27 = Tydel	Toad	Upper Anisian (*E. deleeni*) type locality	*N. constricta*
		C-201921 C-201973	92/AH21a 92/AH21b	Toad	Upper Anisian (*F. chischa*)	*N. constricta*; *N. aldae*; *N. posterolonga*; *N. excentrica* aff. *sigmoidalis*
Oyster Springs	58°39′20.9″N, 124° 15′ 50″ W	V-002629	OS-C2	Toad	Upper Anisian (*F. chischa*)	*N. posterolonga*; *N. excentrica sigmoidalis*
North Tetsa Phosphate	58°40′04″N, 124°25′55″W	C-210919	92-AH19	Toad	Middle–Upper Anisian	*N. constricta*; *N. quasiconstricta*
Mile Post 386	58°39′00″N, 124°39′00″W	C-101072	82/AH1	Liard	Lower Ladinian (*bamberi* fauna)	*N. constricta*; *N. cornuta*; *N. posterolonga*; *N. excentrica sigmoidalis*
		C-101076	92-AH5	Liard	Lower Ladinian (*bamberi* fauna)	*N. constricta*; *N. posterolonga*
		C-210908 C-210909	92-AH8 92-AH9	Liard	Lower Ladinian (*bamberi* fauna)	*N. constricta*; *N. aldae*; *N. posterolonga*; *N. cornuta*; *N.* aff. *N. cornuta*; *N. excentrica excentrica*
		C-201903	92-AH3	Liard	Lower Ladinian (*bamberi* fauna)	*N. aldae*; *N. posterolonga*; *N. cornuta*; *N.* aff. *N. cornuta*; *N. excentrica excentrica*; *N. excentrica* aff. *sigmoidalis*
East Chischa River	58°32′52″N, 123° 58′ 52″ W	O-74724	74724	Toad	Upper Anisian (*E. deleeni*)	*N. constricta*
South Chischa River	58°33′14″N, 123°53′17″W	O-74731	74731	Toad	Upper Anisian (*E. deleeni*)	*N. constricta*; *N. aldae*?; *N. posterolonga*?
Tuchodi Bluff	58°22′11″N, 124°18′20″W	O-68286	68286	Liard	Lower Ladinian (*T. poseidon*)	*N. cornuta;* *N. posterolonga*; *N. excentrica sigmoidalis*
Ursula Creek	55°59′55″N, 123°09′18″W	C-305970	01/URC9	Toad	Upper Anisian–Lower Ladinian	*N. constricta*; *N. posterolonga*
Ganoid Ridge	54°32′04″N, 120°43′53″W	C-303533	97/WapA6	Llama	Lower Ladinian (*T. poseidon*?)	*N. constricta*; *N. posterolonga*; *N. excentrica sigmoidalis*
		C-303536	97-Wap-A9	Llama	Lower Ladinian (*T. poseidon*?)	*N. constricta*; *N. cornuta*?; *N. posterolonga*
		C-303544	97/WapB18	Llama	Upper Anisian (*F. chischa*)	*N. constricta*; *N. cornuta;* *N. posterolonga*;
		C-303543	97-Wap-B17	Llama	Upper Anisian (above *F. chischa*)	*N. cornuta*; *N. excentrica excentrica*
Wapiti Lake, NW	54°41′30″N, 120° 59′ 45″ W	O-83862	83862	Llama	Lower Ladinian (*E. matutinum*)	*N. aldae*; *N. posterolonga*; *N. excentrica* aff. *sigmoidalis*
Nevada						
Fossil Hill	40°16′03″N, 118°05′27″W	C-176334	HB139	Prida	Upper Anisian (*F. occidentalis*)	*N. constricta*; *N. aldae*; *N. mesotriassica*; *N. postcornuta*; *N. posterolonga*
		C-159817	HB238	Prida	Upper Anisian (*F. occidentalis*)	*N. constricta*; *N. cornuta*; *N. posterolonga*; *N. excentrica excentrica*; *N. excentrica primitiva*
Oliver Gulch	40°02′42″N, 117°33′34″W	C-301229	HB583	Prida	Middle Anisian (*B. shoshonensis*)	*N. constricta*; *N. cornuta*; *N. posterolonga*; *N. excentrica excentrica*
		C-176111	HB584	Prida	Middle Anisian (*B. shoshonensis*)	*N. constricta*; *N. aldae*?; *N. posterolonga?*
		C-301230	HB585	Prida	Middle Anisian (*B. shoshonensis*)	*N. constricta*; *N. posterolonga*?
		C-301231	HB598	Prida	Middle Anisian (*B. shoshonensis*)	*N. constricta*; *N. quasiconstricta*
Wheeler Mine	40°25′06″N, 118°08′40″W	C-176316	HB20	Prida	Lower Ladinian (*E. subasperum*)	*N. constricta*; *N. cornuta*; *N. postcornuta*; *N. posterolonga*; *N. quasicornuta*

Table 2. Continued.

Section	Lat./Long. of Section	GSC Cur. No.	Field No.	Formation	Age (Zone)	*Neogondolella* ex gr. *constricta*
Tobin Range	40°22′37″N, 117°31′33″W	C-159817	HB237	Prida	Upper Anisian (*P. meeki*)	*N. constricta*; *N. cornuta*; *N. postcornuta*; *N. posterolonga*
		C-159818	HB239	Prida	Upper Anisian (*G. rotelliformis*)	*N. constricta*; *N. aldae*; *N. cornuta*?; *N. posterolonga*; *N. excentrica primitiva*
		C-176819	HB240	Prida	Upper Anisian (*G. rotelliformis*)	*N. constricta*; *N. aldae*; *N. cornuta*?; *N. excentrica primitiva*; *N. postcornuta*; *N. quasiconstricta*
		C-159820	HB241	Prida	Upper Anisian (*G. rotelliformis*)	*N. constricta*; *N. excentrica primitiva*; *N. postcornuta*; *N. quasiconstricta*
		C-159821	HB243	Prida	Upper Anisian (*G. rotelliformis*/*P. meeki*)	*N. constricta*; *N. postcornuta*
		C-159822	HB245	Prida	Upper Anisian (*G. rotelliformis*/*P. meeki*)	*N. constricta*; *N. aldae*?; *N. posterolonga*; *N. excentrica primitiva*

the appearance of *N. transita* near the base of the Curionii Zone, which may also be comparable with the appearance of *N. e. sigmoidalis* n. subsp.

The conodont succession at the ALB GSSP at Bagolino (Fig. 3) in the southern Alps of Italy is unclear because different species have been recorded by Nicora and Brack (1995), Muttoni et al. (2004), and Brack et al. (2005). The present account represents a North American taxonomic yardstick for comparison through which the identity and morphological scope of these European species may be better understood.

Conclusions

A study of upper Anisian and early Ladinian conodonts from classic Middle Triassic sites in Nevada and B.C. focused on related taxa united as the *Neogondolella constricta* group. These are by far the most common components of the North American faunas as well as having a worldwide distribution. Their potential to contribute to a temporal framework for the interval has not been fully realized due to conflicting taxonomic interpretations. This is rooted in the choice of an early growth stage as the holotype of *N. constricta*, an original description that lacks an ontogenetic component, and poorly defined group members. This work provides an improved definition for the central species based on abundant growth stages of topotype material, and critically reviews previous records of the species group.

The distinction of *Neogondolella constricta* from *N. cornuta*, and the suggested synonymy of several other taxa (*N. balkanica*, *N. tardocornuta*, *N. pseudolonga*), is here newly based on relative platform dimensions rather than differences in posterior platform–cusp configuration (nature of terminal denticle, presence of platform brim), which varies during growth and is regarded as intraspecific. The nature and distribution of the allied species *N. aldae* and *N. posterolonga*, based on Nevadan material, is documented from both North America and Europe, whereas the European-based taxa *N. bakalovi*, *N. longa*, *N. mesotriassica*, and *N. postcornuta*, are comparatively rare or absent in the present faunas.

Less common elements of the upper Anisian *constricta* group conodont faunas are those that show elaboration of the posterior platform through a change in symmetry and the development of accessory denticles. Among posteriorly curved platforms that have been previously assigned to *Neogondolella excentrica* and *N. transita*, three subspecies are differentiated, two of which are new: *N. e. primitiva* n. subsp. and *N. e. sigmoidalis* n. subsp. Elements characterized by a broader, 'truncated', and denticulate posterior platform are assigned to *N. quasiconstricta* n. sp. and *N. quasicornuta* n. sp., taxa that are morphological analogues of the older *Paragondolella bifurcata* and the Germanic *Gondolella* (= *N.*) *prava* Kozur, 1968a.

In North America, the species *N. constricta* and *N. cornuta* are associated with comparable elements showing the extended posterior symmetries: (1) *N. constricta* + *N. excentrica primitiva* n. subsp. + *N. quasiconstricta* n. sp.; and (2) *N. cornuta* + *N. e. excentrica* + *N. quasicornuta* n. sp. (Fig. 4). Calibrated with the Nevadan ammonoid zonation, the first conodont assemblage (1) occurs alone in the Rotelliformis Zone and is joined and overwhelmed by the second association (2) by the Occidentalis

Zone. In the intervening Meeki Zone, *cornuta*-like elements have an accessory posterior denticle but no extended process. A different association (3) is characterized by *N. posterolonga* and *N. e. sigmoidalis* n. subsp. and occurs in the Ladinian Subsaperum Zone.

These intervals can also be recognized in B.C.: the *constricta* association in the Deleeni Zone; the *cornuta* association in the Chischa Zone; and the *posterolonga* fauna in the Matutinum, Poseidon, and ?Meginae (*bamberi* fauna) zones (Fig. 5). The ranges of less common species of the *constricta* group are variable but generally long ranging through the interval under study. Nevadan faunas are also more diverse than those from B.C., as may be expected from their lower paleolatitude. Many of the North American *constricta* group representatives also occur in Europe and farther afield.

Correlation with *Neogondolella* ex gr. *constricta* elements in Europe and their succession is unclear due to differing taxonomic criteria employed for species differentiation. Nevertheless, a similar pattern can be discerned within the various zonal schemes proposed in Europe, although some elements do not occur in North America, namely the Germanic *N. mombergensis* – *Ng. haslachensis* lineage, and the Tethyan "*N.*" ex gr. *trammeri* and *Gladigondolella* spp. Re-assessment of European faunas, especially those described here as *N. excentrica* subspp., may support the proposed North American succession.

Systematic paleontology

Taxonomic scope.—The *Neogondolella constricta* group includes segminiplanate platform-bearing species known or suspected to be characterized by an early growth stage with a narrow, constricted posterior platform, and a relatively low blade–carina. Included among these are species that are only known as later growth stages that resemble other *constricta* group members. The group is centered on the holotype of *N. constricta* from the Prida Formation of Nevada, a juvenile element from the upper Anisian Rotelliformis Zone. Very similar juvenile elements occur throughout the upper Anisian and lower Ladinian strata worldwide, but they mature into a variety of different species.

Differentiation of members of the *constricta* group must generally rely on morphological features of adult elements. The following previously described taxa (with original genus name) are discussed here: *Neogondolella aldae* Kozur, Krainer and Mostler, 1994b; *Neogondolella bakalovi* Budurov and Stefanov, 1972; *Neogondolella balkanica* Budurov and Stefanov, 1975a; *Gondolella constricta* Mosher and Clark, 1965; *Neogondolella cornuta* Budurov and Stefanov, 1972; *Neogondolella excentrica* Budurov and Stefanov, 1972; *Neogondolella longa* Budurov and Stefanov, 1973; *Gondolella mesotriassica* Kozur and Mostler, 1982; *Gondolella postcornuta* Kovács, 1994; *Neogondolella posterolonga* Kozur, Krainer and Mostler, 1994b; *Gondolella pseudolonga* Kovács, Kozur, and Mietto, 1980; *Neogondolella tardocornuta* Budurov and Stefanov, 1984; and *Gondolella transita* Kozur and Mostler, 1971.

Class Conodonta Pander, 1856
Order Ozarkodinidae Dzik, 1976
Family Gondolellidae Lindström, 1970

Subfamily Neogondolellinae Hirsch, 1994
Genus *Neogondolella* Bender and Stoppel, 1965

Type species.—*Gondolella mombergensis* Tatge, 1956 (Ta 1956/5) from the upper Muschelkalk, Schmidtdiel Quarry, Momberg, near Marburg, Germany.

Neogondolella constricta (Mosher and Clark, 1965)
Figures 6, 7

p*	1965	*Gondolella constricta* Mosher and Clark, p. 560, pl. 65, figs. 11, 18, 21, 24, 25 (only).
p	1965	*Gondolella mombergensis* Tatge; Mosher and Clark, p. 560, pl. 65, figs. ?20, 28 (only).
?	1975a	*Neogondolella balkanica* Budurov and Stefanov, p. 792–794, pl. 1, figs. 24–31.
p	1976	*Neogondolella constricta*; Rafek, pl. IV, fig. 24 (only).
p	1976	*Neogondolella* cf. *longa* Budurov and Stefanov; Rafek, pl. I, figs. 34, 35 (only).
	1980	*Gondolella constricta*; Kovács and Kozur, pl. 3, fig. 4a–c.
	1981	*Neogondolella cornuta*; Mietto and Petroni, p. 552–553, pl. 57, figs. 5a, b.
	1981	*Neogondolella longa*; Mietto and Petroni, p. 553–554, pl. 57, figs. 8a–c.
non	1982	*Neogondolella constricta*; Papšová and Pevný, Pl. XX, figs. 7–12.
?	1984	*Neogondolella tardocornuta* Budurov and Stefanov, p. 605–607, pl. 1, figs. 15–20.
	1984	*Neogondolella cornuta*; Farabegoli et al., figs. a1–3, b1–3.
p	1986	*Gondolella constricta*; Kovács, pl. IV, fig. 4a–d; pl. V, figs. 5a–d, 6a–d; pl. VI, figs. 3a, b, 4a, b; pl. X, figs. 4a–c, 5a–c, 6a–c (only).
non	1986	*Gondolella constricta*; Dürkoop et al., pl. 21, figs. 1a–c, 2a, b.
non	1990	*Neogondolella constricta*; Ding and Huang, pl. 1, figs. 2, 3.
	1992	*Neogondolella constricta*; Koca et al., pl. 1, figs. 11a–c, 13.
	1992	*Neogondolella* cf. *cornuta*; Koca et al., pl. 1, figs. 15a–c.
	1992	*Neogondolella constricta*; Chhabra and Kumar, pl. 3, figs. 2, 3a, b, 4a–c, 6a, b.
	1994b	*Neogondolella constricta*; Kozur et al., p. 172–174, pl. 4, figs. 12–15, 17, 20.
non	1996	*Neogondolella constricta*; Polak et al., pl. 12, figs. 1–5.
?	1997	*Neogondolella constricta*; Buryi, pl. 1, fig. 15.
non	1997	*Gondolella constricta*; Pevný and Salaj, p. 101–102, pl. IX, figs. 14, 15; pl. X, figs. 1, 2; ?pl. XI, figs. 2, 3.
	1997	*Gondolella balkanica*; Pevný and Salaj, p. 103, pl. XI, figs. 6–8; pl. XV, figs. 5–8.
	1999	*Neogondolella* ex gr. *constricta*; Orchard and Rieber, pl. 4., figs. 1–12 (multielement).
p	2006	*Neogondolella* ex gr. *constricta*; Orchard, pl. 5., figs. 9, 10 (only).

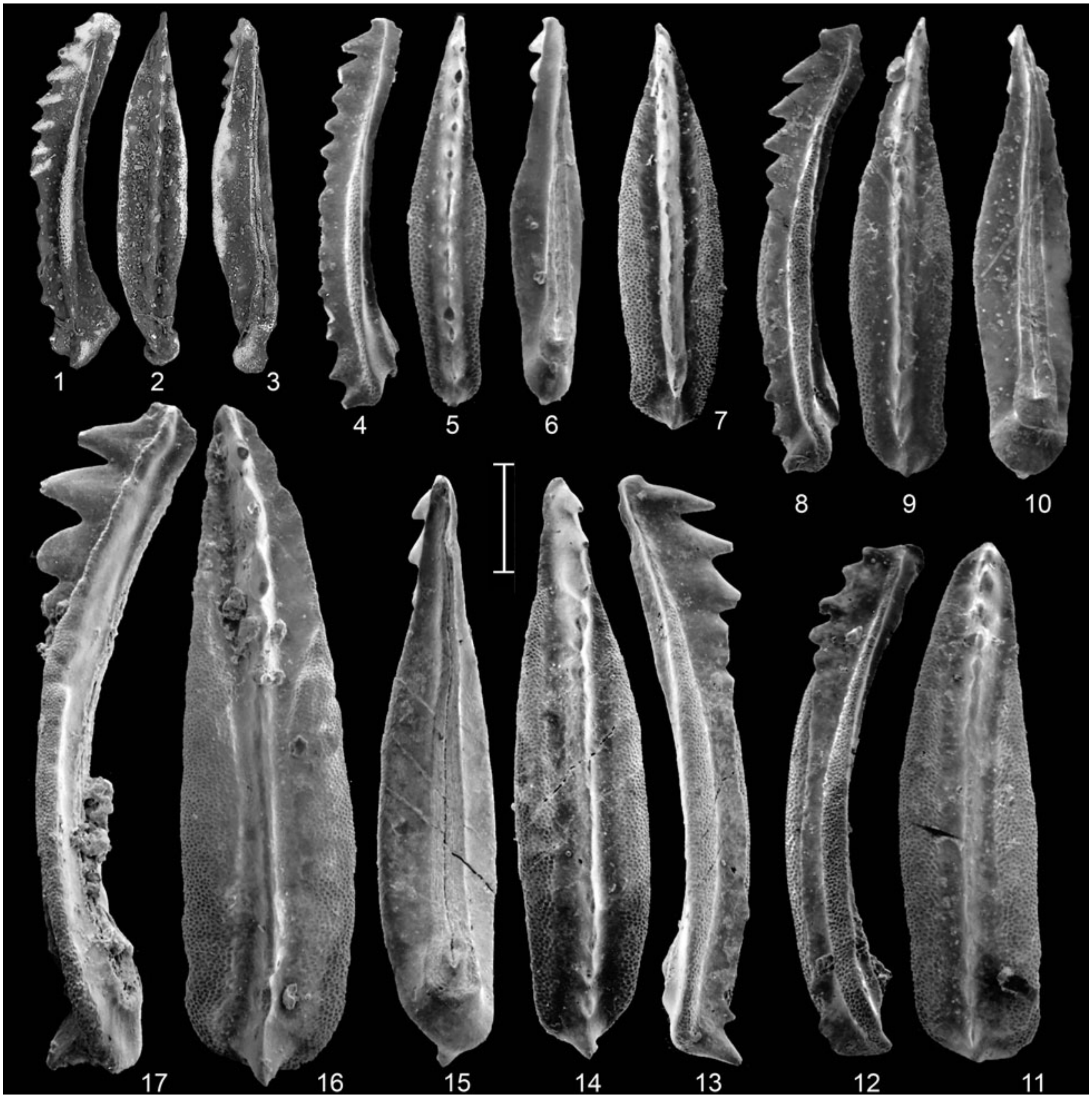

Figure 6. *Neogondolella constricta* (Mosher and Clark) from the Rotelliformis Zone, Fossil Hill, Nevada. (**1–3**) USNM 145189, refigured holotype, clarkei Subzone; (**4–6**) GSC 141848, FH15, clarkei Subzone; (**7**) GSC 141849, FH6, burckhardti Subzone; (**8–10**) GSC 141850, FH24, cricki Subzone; (**11, 12**) GSC 141851, FH8, burckhardti Subzone.; (**13–15**) GSC 141852, FH17, vogdesi Subzone; (**16, 17**) GSC 141853, FH22, cricki Subzone. Scale bar = 200 μm.

non 2006 *Neogondolella constricta*; Sun et al., pl. 1, figs. 21–24.
non 2006 *Neogondolella constricta*; Dong and Wang, pl. 41, figs. 10, 18.
non 2008 *Neogondolella constricta*; Wu et al., pl. II, figs. 12–15.
p 2008 *Neogondolella mombergensis* (Clark and Mosher) (sic); Wu et al., pl. II, figs. 4, 5, 18, 22.
p 2008 *Neogondolella navicula* (Clark and Mosher) (sic); Wu et al., pl. I, figs. 2, 3, 7, 10.
non 2009 *Neogondolella constricta*; Zhang et al., figs. 3. 13, 16.
2010 *Neogondolella constricta*; Orchard, fig. 9. 14, 15.
2014 *Neogondolella* ex gr. *constricta* morphotype gamma; Golding, fig. 2.24, parts 1–6.
2014 *Neogondolella* ex gr. *constricta* morphotype delta; Golding, fig. 2.25, parts 1–6.
non 2014 *Neogondolella constricta*; Sun et al., 2014, fig. 3h, k–m.
2015 *Neogondolella* ex gr. *constricta*; Lehrmann et al., fig. 6.9, 6.10.
non 2017 *Neogondolella constricta*; Bo et al., fig. 4.1–4.4.
2019 *Neogondolella constricta*; Zhang et al., fig. 7.13a–c.

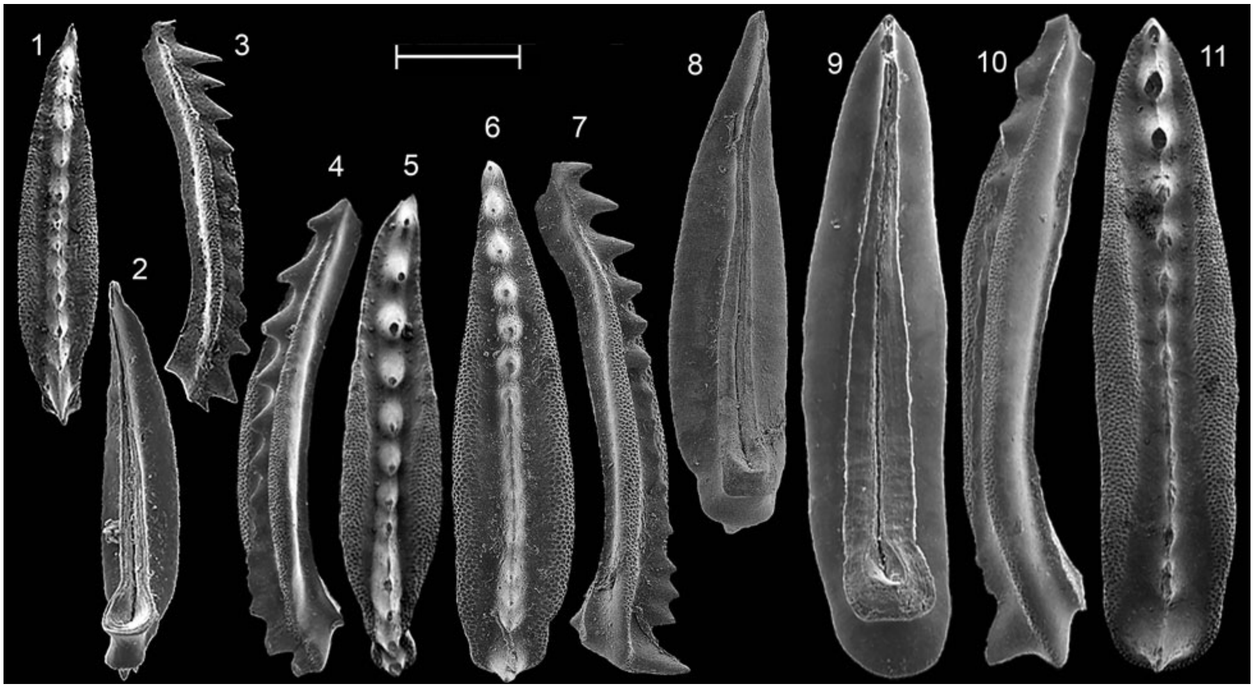

Figure 7. *Neogondolella constricta* (Mosher and Clark) from B.C. (**1–3**) GSC 141854, sample 83/205B, Toad Formation, Toad River Canyon, Deleeni Zone; (**4, 5**) GSC 141855, and (**9–11**) GSC 141856, both sample 92/AH2, Yellow Bluffs, Alaska Highway, Deleeni Zone; (**6–8**) GSC 141857, sample 97/WapA6, Llama Formation, Cirque B, Ganoid Ridge, bracketed between the Poseidon and Meginae zones. Scale bar = 200 μm.

non	2019	*Neogondolella constricta*; Xie et al., fig. 3.2, 3.3, 3.7.
non	2021	*Neogondolella* ex gr. *constricta* (Mosher and Clark); Golding, p. 584, pl. 3., figs. 29–35.
non	2021	*Neogondolella constricta*; Qin et al., pl. 8., figs. 8–13.

Holotype.—USNM 145189 (Mosher and Clark, 1965, pl. 65, figs. 21, 24, 25). Re-illustrated in Figure 6.1–6.3. From sample FH3, clarkei Subzone of the Rotelliformis Zone, upper Anisian, Prida Formation, Fossil Hill, Nevada; deposited in the US National Museum of Natural History.

Diagnosis.—The relatively short and arched segminiplanate P_1 element has at first a slender, biconvex platform that broadens with growth and maintains a typical length breadth ratio of ~4:1. A posterior platform constriction present in juveniles disappears during growth as the posterior platform expands and becomes as broad as the median platform. The rounded posterior margin of later growth stages may include a narrow brim around a large, upright to slightly reclined terminal denticle that generally becomes larger than the cusp during growth, which is typically the penultimate carina denticle. During growth, the anterior blade denticles become increasingly elevated relative to those of the median carina, which become increasingly fused. On the underside, a symmetrical basal loop of uniform width surrounds the subterminal pit.

Occurrence.—*Neogondolella constricta* occurs in Nevada throughout the Fossil Hill Member of the Prida Formation at Fossil Hill, where it is abundant (many hundreds of specimens) in the Rotelliformis Zone, but much less so through the Meeki and Occidentalis zones, and into the Subasperum Zone. Elsewhere in Nevada, the species is known from the Wheeler Mine area, and in the Tobin Range. In B.C., it is particularly common in the Deleeni Zone, including in the type locality of that zone and additional locations nearby. Elsewhere in B.C. it ranges through the Poseidon Zone (Table 2).

Neogondolella constricta has a global reach: upper Muschelkalk, northern Germany (Rafek, 1976); Campogrosso section, NE Italy (Mietto and Petroni, 1981); middle Bivera Formation, southern Alps, northern Italy (Farabegoli et al., 1984); Alsóhegy, N. Hungary (Kovács and Kozur, 1980); NE Rudabánya Mountains, Hungary (Kovács, 1986); eastern Turkey (Koca et al., 1992); Kalapani Limestone, northern India (Chhabra and Kumar, 1992); western Carpathians, Slovakia (Pevný and Salaj, 1997); chert of Tsentralnaya Mts, Sikhote–Alin (Buryi, 1997); subsurface Polish lowlands (Narkiewicz, 1999); Jones Lake Formation, distal allochthon, south-central Yukon Territory (Orchard, 2006); Xinyuan Formation, Guandao, Nanpanjiang Basin, South China (Lehrmann et al., 2015); Kamura Formation, Kamura, central Kyushu Island, Japan (Zhang et al., 2019). In China, several reports of *N. constricta* are discounted (see synonymy) or are insufficiently illustrated (Wang and Wang, 1976; Wang et al., 2005), but the species does occur in the Qingyan Formation in Guizhou Province (Wu et al., 2008). Those reported from Bithynian strata at Deşli Caira, Romania (Golding, 2021) are now excluded from this species.

Description.—The holotype is a comparatively small, elongate element with a platform that extends throughout the length of the element but narrows at a posterior constriction near the cusp and expands around the final denticle. The axial blade–

carina is composed of ∼15 relatively low, closely spaced denticles, the anterior ones of which are slightly larger, higher, and more discrete than those of the median carina. The cusp is the penultimate denticle and is twice the size of the adjacent posteriormost denticle. Later growth stages show the posterior platform constriction progressively overgrown to produce at first a tapered posterior outline and then a broad, rounded posterior outline equal in breadth to that of the median part. Concurrently, the anterior denticles of the fixed blade become relatively higher, those of the median carina become increasingly fused into a low ridge, and the posteriormost denticle enlarges and dominates the posterior margin; a narrow posterior platform brim often develops. Very large elements may have some subdued anterior platform crenulation.

Comparisons.—Adult specimens of *Neogondolella constricta* differ from those of *N. cornuta* in their comparatively shorter and broader platform (4–4.5:1 compared with 5–5.5:1), an outline that is commonly biconvex rather than subrectangular, and in their less conspicuous posterior carina and cusp. Both *N. aldae* and *N. posterolonga* differ from *N. constricta* by possessing platforms that are wider in the anterior and much narrower in the posterior.

Remarks.—The distinctive posterior denticle (not the cusp) of *Neogondolella cornuta* is often larger than that in *N. constricta*, but later growth stages of both species can display a prominent and reclined terminal denticle, which has been regarded as diagnostic for *N. cornuta*. Variation in this feature led to separation of both *N. balkanica* (upright denticle with a platform brim) and *N. tardocornuta* (upright denticle without a brim) in the Balkans. Nicora and Kovács (1984) previously suggested that *N. balkanica* was synonymous with *N. constricta*, while *N. tardocornuta* was originally combined in *N. balkanica* by its authors (Budurov and Stefanov, 1975). The holotypes of both Balkan species have platform proportions (∼4:1) comparable to that of *N. constricta*, and variability of the posterior margin in the Nevadan material is such that those species are provisionally included in synonymy here. As pointed out by Kozur et al. (1994b), the types of all these species originated in different parts of the late Anisian–early Ladinian, but this does not exclude a long range for *N. constricta.*

Neogondolella aldae Kozur, Krainer and Mostler, 1994b
Figure 8

p 1965 *Gondolella navicula* Huckriede; Mosher and Clark, p. 560–561, pl. 66, figs. 10, 17, 18, 21 (only).
p 1984 *Gondolella mombergensis longa* (Budurov and Stefanov, 1973); Nicora and Kovács, p. 150, pl. 10, figs. 2, 4, 9 (only).
* 1994b *Neogondolella aldae* Kozur, Krainer, and Mostler, p. 179–181.
* 1994b *Neogondolella aldae aldae* Kozur, Krainer, and Mostler, p. 181–182 (see synonymy).
p 2008 *Neogondolella mombergensis* (Mosher and Clark) (sic); Wu et al., pl. II, fig. 9.
p 2014 *Neogondolella* ex gr. *transita*, morphotype beta; Golding, fig. 2.29, parts 1–3.
2014 *Neogondolella constricta* morphotype beta; Golding, fig. 2.23, parts 1–9.

Holotype.—The specimen, figured by Nicora and Kovács (1984, pl. 10, fig. 9) as *Gondolella mombergensis longa* Budurov and Stefanov. From sample N49 in the middle Prida Formation, *Nevadites humboldtensis* Smith, 1914, beds of the lower Occidentalis Zone at Fossil Hill, Humboldt Range, Nevada.

Occurrence.—Mosher and Clark (1965) illustrated elements from the Meeki Zone in Nevada, and Kozur et al. (1994b) gave a range of lower Meeki and Occidentalis zones. In the present study, the species was found to occur first in the middle of the Rotelliformis Zone and as high as the Subasperum Zone. *Neogondolella aldae* is one of the more common species of the *constricta* group in the Humboldt Range, being found in small numbers in about half the studied samples. Elsewhere in Nevada, the species is known from the Tobin Range. In Canada, the species occurs in the Deleeni and Chischa zones at Yellow Bluffs, in the Deleeni Zone of Toad River Canyon, in the Matutinum Zone at Wapiti Lake, and as high as the Meginae Zone along the Alaska Highway at milepost 386 (Table 2).

In Europe, *Neogondolella aldae* occurs in the Reitzi Zone and Nevadites Zone of the Alps and Bulgaria (Kozur et al., 1994b) but it has not featured in many studies. A specimen illustrated by Wu et al. (2008) from the Qingyan Formation in Guizhou, China, appears to represent this species.

Description.—The platform of this arched segminiplanate element is widest around midlength, with biconvex margins in the anterior two-thirds to three-quarters, and subparallel margins in the remainder of the distinctly narrower posterior platform. Large specimens show increasing lateral growth in the posterior part, which remains narrower than the anterior platform. Overall, the typical length:breadth ratio is about 4:1. The narrowly rounded to subquadrate posterior margin of adult elements may include a very narrow platform brim around a large, moderately reclined terminal denticle, which is separated from the smaller cusp immediately in front of it; both these denticles commonly lie in the posterior constricted part. To the anterior, denticles of the carina of mature elements are largely fused into a low ridge that rises to the posterior and extends to the anterior relatively elevated fixed blade, which is commonly composed of 4 discrete denticles. On the underside of the largest specimens, the pit is anteriorly shifted within the basal scar that extends behind it.

Comparisons.—Unlike *Neogondolella constricta* and *N. cornuta*, the posterior platform constriction present in juveniles of *N. aldae* does not disappear during growth as the posterior platform remains narrow. *Neogondolella posterolonga* differs in its longer and more slender platform. The older *N. shoshonensis* Nicora, 1976, has a similar platform outline but is narrower with a higher posterior carina.

Figure 8. *Neogondolella aldae* Kozur, Krainer, and Mostler from (**1–10**) the Toad Formation in B.C. and (**11–19**) the Prida Formation in Nevada. (**1–3**) GSC 141858, sample 92/AH21, Yellow Bluffs, Alaska Highway, Chischa Zone; (**4, 5**) GSC 141859, sample 92/AH2, Toad Formation, Yellow Bluffs, Alaska Highway, Deleeni Zone; (**6–8**) GSC 141860, sample 83/205B, Toad River Canyon, Deleeni Zone; (**9, 10**) GSC 141861, sample 83/ MJO-Bone. Toad River Canyon, ?Deleeni Zone; (**11, 12**) GSC 141862, sample FH47, Meeki–Occidentalis zonal boundary; (**13–15**) GSC 141863, sample SH516, Subasperum Zone; (**16, 17**) GSC 141864, sample SH531, Occidentalis Zone; (**18, 19**) GSC 141865, sample SH517, Subasperum Zone. Scale bar = 200 μm.

Remarks.—The original description of *Neogondolella aldae* (Kozur et al., 1994b) included reference to its distinct terminal "cusp" that was not fused with the posterior platform margin, unlike in *N. cornuta*. As discussed, previously, such fusion is variable and a more reliable character to distinguish the two species is their platform shape. Note that the true cusp in the adults of the *constricta* group is the penultimate denticle of the carina and not the larger terminal denticle.

Some Nevadan specimens previously illustrated by Nicora and Kovács (1984) and included in *Neogondolella aldae* by Kozur et al. (1994b) do not exhibit the constricted posterior platform present in the holotype; these are excluded from the present species.

Neogondolella cornuta Budurov and Stefanov, 1972
Figure 9.1–9.6, 9.9–9.15

p 1965 *Gondolella constricta* Mosher and Clark, p. 560, pl. 65, fig. 22 (only).

p 1965 *Gondolella mombergensis* Tatge; Mosher and Clark, p. 560, pl. 65, fig. 29 (only).

Figure 9. (**1–6, 9–15**) *Neogondolella cornuta* Budurov and Stefanov from the Prida Formation, Nevada, Occidentalis Zone; (**11–15**) the Llama Formation, B.C., Chischa Zone. (**1, 2**) GSC 141866, sample FH56; (**3, 4**) GSC 141867, sample SH524; (**5, 6**) GSC 132583, sample SH524; (**9, 10**) GSC 141869, sample SH527; (**11–13**) GSC 141870; (**14, 15**) GSC 141871, both from sample 97/WapB18, Cirque B, Ganoid Ridge. (**7, 8**) *Neogondolella* aff. *N. cornuta* Budurov and Stefanov; GSC 141872, sample SH524. Scale bar = 200 μm (**1–13**), 250 μm (**14, 15**).

p	1965	*Gondolella navicula* Huckriede; Mosher and Clark, p. 560–561, pl. 66, figs. 19, 20 (only).
*	1972	*Neogondolella cornuta* Budurov and Stefanov, p. 839–840, pl. 3, figs. 9–15, 20–22.
	1975	*Gondolella cornuta*; Trammer, pl. 22, figs. 8a, b, 9a, b.
?	1980	*Gondolella pseudolonga* Kovács, Kozur and Mietto, p. 218–219, pl. 1, figs. 1–4.
	1984	*Gondolella cornuta*; Vrielynck, p. 187–189, pl. 3, figs. 4a–c.
p	1984	*Gondolella pseudolonga*; Vrielynck, p. 194–195, pl. 3, figs. 2a–c (only)
	1986	*Neogondolella constricta* (Mosher and Clark); Orchard, pl. 5.4, fig. 8 (only).
non	1986	*Gondolella cornuta*; Dürkoop et al., pl. 17, fig. 5a, b; pl. 20, figs. 13a–c, 15a, b.
	1991	*Neogondolella cornuta*; Uroševič and Sudar, pl. 1, fig. 13.
?	1995	*Neogondolella cornuta*; Ramovš and Goričan, pl. 8, fig. 4.
	1997	*Gondolella cornuta*; Pevný and Salaj, pl. XII, figs. 3, 11.
?	1999	*Neogondolella cornuta* > *N. mesotriassica*; Narkiewicz, pl. 3, figs. 3, 4.
	2005	*Neogondolella* ex gr. *constricta*; Orchard, fig. 10A–I (multielement).
non	2005	*Neogondolella cornuta*; Wang et al., pl. II, fig. 20.
non	2006	*Neogondolella constricta cornuta*; Dong and Wang, pl. 41, fig. 3.
	2006	*Neogondolella* ex gr. *constricta*; Orchard, pl. 4, fig. 15.
	2008	*Neogondolella* ex gr. *constricta*; Nakrem et al., fig. 5.18–5.20.
	2010	*Neogondolella cornuta*; Orchard, fig. 9.12, 9.13.
non	2014	*Neogondolella constricta cornuta*; Sun et al., fig. 3.g?, i, j.
?	2016	*Neogondolella constricta cornuta*; Sun et al., fig. 3.5.
non	2019	*Neogondolella constricta cornuta*; Xie et al., fig. 3.12.
non	2021	*Neogondolella cornuta*; Qin et al., pl. 3, figs. 3, 4; pl. 7, fig. 4; pl. 9, figs. 9–11.
	2022	*Neogondolella cornuta*; Karádi et al., fig. 9D.
	2022	*Neogondolella pseudolonga*; Karádi et al., fig. 9C.

Holotype.—Budurov and Stefanov, 1972, pl. 3, figs. 20–22, Bu 1045/1, from middle–upper Illyrian strata, III γ = *cornuta* conodont zone; Golo–Bârdo mountains south of Pernik, Bulgaria. Budurov's collections (Bu) are in the Geologisches Institut, Sofia, Bulgaria.

Occurrence.—In Nevada, *Neogondolella cornuta* appears in the Meeki Zone, is abundant (many hundred specimens) through the Occidentalis Zone and is less common in the Subasperum Zone. It also occurs at Wheeler Mine and in the Tobin Range. In B.C., it is known from the Chischa and Poseidon zones at Wapiti Lake, and with the *bamberi* ammonoid fauna at milepost 386, Alaska Highway (Table 2).

In addition to the Bulgarian types that characterize the Illyrian (Budurov and Trifonova, 1995), *Neogondolella cornuta* is recorded in southwestern Holy Cross Mountains, Poland (Trammer, 1975); Carnic Alps–Dolomites, NE Italy (Vrielynck, 1984); Stuhini Group, Stikine terrane, northern B.C. (Orchard, 1986, 1991); eastern Serbia (Uroševič and Sudar, 1991); central Slovenia (Ramovš and Goričan, 1995); western Carpathians, Slovakia (Pevný and Salaj, 1997); ?subsurface Polish lowlands (Narkiewicz, 1999); Table Mountain Formation, Sylvester Allochthon, northern B.C. (Orchard, 2006); Botneheia Formation, Milne Edwardsfjellet, Svalbard (Nakrem et al., 2008), and the Transdanubian Range, Hungary (Karádi et al., 2022). In China, a probable juvenile growth stage of this species was illustrated by Sun et al. (2016) from the Upper Guanling Formation in Guizhou Province, but other reports are suspect (see synonymy).

Description.—A relatively elongate, arched segminiplanate P_1 element with a comparatively long and slender subrectangular platform with subparallel platform margins and a typical length:breadth ratio of ~5–5.5:1. Submature elements show the characteristic biconvex anterior platform and constricted posterior that disappears during growth as the posterior platform broadens. A prominent, slightly to strongly reclined and terminal denticle ("horn") is characteristic of mature elements but this may be overtaken by the cusp in the largest specimens, wherein a narrow platform brim may be developed on the broad, rounded posterior margin. During growth, the anterior blade denticles become slightly elevated relative to those of the median carina, which may be wholly fused. The lowest part of the carina is at element midlength, beyond which the posterior fused carina is often relatively elevated in front of the large posterior denticles. On the underside, the pit is anteriorly shifted within the basal loop, which extends a short distance to the posterior with a rounded or subquadrate outline.

Comparisons.—*Neogondolella cornuta* was regarded as a later growth stage and therefore a synonym of *N. constricta* by Nicora and Kovács (1984), but in the present work the taxon is interpreted as its direct descendant. Small specimens of the two species may be indistinguishable, but the relatively long platform and longer posterior keel characteristic of *N. cornuta* become more common features in the *constricta* group populations through the upper Anisian. Posterior platform configuration may appear similar in the two species, but greater weight is given here to the relative platform length and outline.

Neogondolella aldae differs from *N. cornuta* in outline, with the relatively broad anterior and reduced posterior platform of the former contrasting with the sub-parallel margins of the latter. The platform of *N. posterolonga* is like that of early growth stages of *N. cornuta* and may have arisen through neotony. According to Kovács (1994), the most diagnostic feature for distinguishing *N. cornuta* from its successor species *N. postcornuta* is the penultimate denticle of the carina in specimens of moderate size: this is a conspicuous cusp in the former, ancestral species but is not evident in *N. postcornuta*, which also has the terminal denticle fused to the platform.

Remarks.—*Gondolella pseudolonga*, which is based on a submature growth stage from Italy (Kovács et al., 1980), has denticulation characteristic of relatively early growth stages of *Neogondolella* ex gr. *constricta*. The character of adult *N. pseudolonga* is conjectural, but the platform length to breadth ratio of its holotype is 5:1, which corresponds to that of both *N. cornuta* and *N. posterolonga*. *Neogondolella pseudolonga* may be a junior synonym of *N. cornuta*, although Kozur et al. (1994b, p. 174) regarded it as an earlier growth stage and synonym of *N. longa* from the *excentrica* Zone of western Bulgaria. However, the holotype of *N. longa* has a length: breadth ratio of ~6:1 and is narrower than the present species, although its variability is unknown.

Neogondolella cornuta ladinica Kozur et al., 1994b, is based on elements with an extended basal scar on an upturned basal posterior margin, a feature that becomes more common through the range of the species in Austria, finally replacing the nominate subspecies. Differentiation of such forms has not proven possible in the North American material.

Neogondolella aff. *N. cornuta* Budurov and Stefanov, 1972
Figure 9.7, 9.8.

Remarks.—These elements resemble *Neogondolella cornuta* in all respects other than they have a posteriormost denticle that is offset from the main carinal axis. They are distinctly longer than *Neogondolella excentrica primitiva* n. subsp., but show a similar, generally rudimentary posterior elaboration. In *N. e. excentrica*, a posterior secondary process and keel are developed, which are absent in *N.* aff. *N. cornuta*. About 85 elements with this morphology occur, always with *N. cornuta*; this is a little more common than *N. e. excentrica*.

Neogondolella excentrica Budurov and Stefanov, 1972

*1972 *Neogondolella excentrica* Budurov and Stefanov, p. 840–841, pl. 4, figs. 9–28.

Holotype.—Bu 1707/1, from lα = *excentrica* conodont-Zone 1, Golo–Bârdo mountains south of Pernik, Bulgaria. Budurov's collections (Bu) are in the Geologisches Institut, Sofia, Bulgaria.

Description.—The P_1 elements assembled here are elongate segminiplanate conodonts in which a posterior platform constriction occurs in front of a variably inturned posterior platform that may bear up to 3 additional nodes posterior of the inconspicuous cusp. On the underside, one side of an asymmetrical basal scar extends as a posterior keel. In adult specimens, the anterior blade and posterior carina denticles are higher and more discrete than those of the more fused median carina.

Remarks.—Many populations of the *Neogondolella constricta* group from Nevada and B.C. include posteriorly asymmetric elements with a variably inturned posterior platform process above a posterior keel. In a few specimens, there is no deflection of the posterior platform, although an extended keel is well developed, implying transition from other members of the *constricta* group. Most of these forms previously have been assigned to either *N. excentrica* or to *N. transita*. Kozur et al. (1994b) regarded these two species as synonyms, with the subsymmetrical platform of *N. transita* being connected with the strongly curved platforms of *N. excentrica* through a morphological continuum. Budurov and Stefanov (1972) included a variety of platform symmetries in their species, but none resembles the holotype of *N. transita* (platform ratio 4:1; straight axis; large, triangular cusp; upturned, pointed posterior platform tip; aff. *N. suhodolica* Budurov and Stefanov, 1973). As noted by Kovács (1984), a comparative study of populations of each taxon in their respective type areas is needed to resolve the scope of each. In this work, we subdivide *N. excentrica* into three subspecies, two of which are new. These differ in their relative platform dimensions and posterior platform configuration. Records of *N. transita* in Hungary and Italy are shown as *N.* ex gr. *excentrica* in Figure 5.

Neogondolella excentrica excentrica Budurov and Stepanov, 1972
Figure 10.1?, 10.2–10.7

1965 *Polygnathus tethydis* Huckriede; Mosher and Clark, p. 563, pl. 66, fig. 13.
* 1972 *Neogondolella excentrica* Budurov and Stefanov, p. 840–841, pl. 4, figs. 9–28.
p 1975 *Gondolella excentrica* (Budurov and Stefanov); Trammer, pl. 25, figs. 4a–c (only).
p 1975 *Gondolella excentrica*; Zawidzka, pl. 42, figs. 5a, b (only).
1975 *Gondolella navicula* Huckriede; Zawidzka, pl. 40, figs. 4a, b.
1976 *Neogondolella transita* Kozur and Mostler; Rafek, pl. IV, figs. 31–33.
1976 *Neogondolella excentrica*; Nicora, p. 639–640, pl. 84, figs. 3–5.
1979 *Neogondolella excentrica*; Mietto and Petroni, p. 9, pl. I, figs. 5a–c.
1981 *Gondolella transita*; Mietto and Petroni, p. 555–556, pl. 57, figs. 9a–c.
? 1981 *Gondolella basisymmetrica huckriedei* (Budurov and Stefanov); Mietto and Petroni, p. 555–556, pl. 57, figs. 2a, b.
1983 *Neogondolella excentrica*; Kolar-Jurkovšek, p. 341–342, pl. 12, figs. 1a–d.
1984 *Gondolella lindstroemi* (Budurov and Stefanov); Vrielynck, p. 192–193, pl. 3, figs. 5a–c.
? 1991 *Gondolella transita* (Kozur and Mostler, 1971); Urošević and Sudar, pl. 1, fig. 16.
2000 *Neogondolella excentrica*; Márquez-Aliaga et al., fig. 6.11.

Diagnosis.—As for species plus this slender morphotype has a length:breadth ratio in adult specimens of ≥5:1; commonly subparallel platform margins; an asymmetric posterior margin bearing a tapered, often pointed and offset posterior platform; and a slightly to strongly extended postero-lateral basal keel. The posterior platform is typically inturned and may bear several denticles forming a secondary carina.

Occurrence.—About 60 specimens of *Neogondolella excentrica excentrica* occur in collections from the

Figure 10. (**1**) *Neogondolella excentrica* aff. *excentrica* Budurov and Stefanov from Prida Formation, Fossil Hill, Nevada. GSC 141873, sample FH13, Rotelliformis Zone/clarkei Subzone. (**2–7**) *Neogondolella excentrica excentrica* Budurov and Stefanov from (**2**) Llama Formation, B.C. and (**3–7**) Prida Formation, Saurian Hill, Nevada. (**2**) GSC 141874, sample WAP-B17, Cirque B, Ganoid Ridge, Chischa Zone; (**3–5**) GSC 141875, sample SH529; (**6, 7**) GSC 141876, sample SH529, both Occidentalis Zone. (**8–15**) *Neogondolella excentrica sigmoidalis* n. subsp. from (**8–12**) sample SH512, Prida Formation, Nevada, Subasperum Zone, and (**13–15**) Llama Formation, B.C. (**8–10**) GSC 141877, holotype; (**11, 12**) GSC 141878; (**13–15**) GSC 141879, sample 97/WapA6, Cirque B, Ganoid Ridge, Wapiti Lake area, bracketed between Poseidon and Meginae zones. Scale bar = 200 μm.

Occidentalis and lower Subasperum zones in Nevada; the posterior fragment illustrated by Mosher and Clark (1965) came from the Protrachyceras Beds. Nicora (1976) also illustrated the species from Fossil Hill. Rare specimens of *N. e.* aff. *excentrica* occur in the Rotelliformis Zone. The subspecies occurs also in Chischa Zone on Ganoid Ridge, and as high as the *bamberi* Fauna along the Alaska Highway in B.C.

In Europe, Kozur et al. (1994b) noted specimens like these occurred in the Nevadites Zone and lower Curionii Zone. Examples of this subspecies are reported from southwestern Holy

Cross Mountains, Poland (Trammer, 1975); Upper Muschelkalk, northern Germany (Rafek, 1976); ?San Ulderico section, NE Italy (Mietto and Petroni, 1979); Campogrosso section, NE Italy (Mietto and Petroni, 1981); Idrske Krnice, Slovenia (Kolar-Jurkovšek, 1983); Carnic Alps-Dolomites, NE Italy (Vrielynck, 1984); Eastern Serbia (Uroševič and Sudar, 1991); NE Spain (Márquez-Aliaga et al., 2000).

Remarks.—This subspecies corresponds to the holotype of the species and other elements originally illustrated by Budurov and Stefanov (1972), most of which have an inturned posterior platform. The posterior platform is variably developed in Nevadan material, but the presence of a distinct secondary lobe or process is regarded as diagnostic. Although typically offset posteriorly, relatively straight elements occur rarely in the Nevadan material. Mature specimens of *N. e. excentrica* have long rectangular platforms comparable to that of associated *N. cornuta*. Two much smaller elements with a strongly deflected posterior platform (Fig. 10.1) occur earlier than typical specimens and are given an aff. designation.

Neogondolella excentrica primitiva new subspecies
Figure 11.1–11.11, 11.12?–11.14?

? 1976 *Neogondolella prava* (Kozur); Rafek, pl. IV, figs. 28, 29.
1976 *Neogondolella excentrica*; Nicora, p. 639–640, pl. 84, figs. 1a, b, 2a, b.
? 1980 *Gondolella transita* Kozur and Mirăuța, taf. 1, figs. 1a–d.
? 1982 *Gondolella* cf. *transita* Kozur and Mostler; Bagnoli, p. 7, pl. 1, figs. 4a, b.
1991 *Neogondolella excentrica* Budurov and Stepanov; Uroševič and Sudar, pl. 1, fig. 15.
? 1994b *Neogondolella* sp. aff. *N. transita* (Kozur and Mostler); Kozur et al., pl. 3, figs. 21, 24.
p 2008 *Neogondolella constricta* (Mosher and Clark); Wu et al., pl. II, figs. 12, 15.
p? 2008 *Neogondolella mombergensis* (Mosher and Clark) (sic); Wu et al., pl. I, fig. 13.
p? 2014 *Neogondolella* ex gr. *constricta*, morphotype epsilon; Golding, fig. 2.26, parts 1–3.
2014 *Neogondolella excentrica*; Sun et al., fig. 4e.

Holotype.—GSC 141882 (Fig. 11.5–11.7), from the Fossil Hill Member of the Prida Formation, burckhardti Subzone of the Rotelliformis Zone (sample FH-6), Fossil Hill, Nevada.

Diagnosis.—This is a relatively short subspecies of *N. excentrica* with a length: breadth 4.5: 1; a short, obliquely directed, posteriorly rounded postero-lateral platform lobe; a relatively low blade/carina in front of the 1 or 2 larger offset terminal denticles; and a weakly extended, asymmetrical basal scar posterior of the pit on the lower side.

Occurrence.—In Nevada, about 35 elements are assigned to *Neogondolella excentrica primitiva* n. subsp., mostly from the Rotelliformis Zone, with rare elements occurring in the Meeki Zone at Fossil Hill and in the Tobin Range. Nicora (1976) also illustrated the subspecies from the Star Canyon section in Nevada. In B.C., the subspecies occurs in the Deleeni Zone at Yellow Bluffs. A specimen assigned to *N. e.* aff. *primitiva* n. subsp. occurs in the middle Anisian Minor Zone along the Alaska Highway (Fig. 11.12–11.14).

Kozur et al. (1994b) noted forms similar to this subspecies occurring in the *Reitziites reitzi* Zone in Austria, and additional records may occur in the Upper Muschelkalk of northern Germany (Rafek, 1976); in the northern Apuseni Mountains in Romania; in Punta Bianca, NW Italy (Bagnoli, 1982); eastern Serbia (Uroševič and Sudar, 1991); in the Qingyan Formation in Guizhou Province (Wu et al., 2008); and the Upper Guanling Formation in Guizhou Province, China (Sun et al., 2014).

Etymology.—From Latin *prīmitīvus,* signifying the first representative of the species.

Comparisons.—These elements share relative platform dimensions with *Neogondolella constricta* but differ from that species in their asymmetric posterior platforms. They differ from the nominate subspecies in its comparatively shorter length, lower posterior carina height, shorter basal scar, and the rounded posterior platform lobe. The latter margin is like that of *N. e. sigmoidalis* n. subsp., but both the entire element and the posterior basal keel of *Neogondolella excentrica primitiva* n. subsp. is much shorter. Kozur et al. (1994b) assigned similar forms to *N.* sp. aff. *transita*, although only a posterior fragment was illustrated. An older specimen assigned to *N. e.* aff. *primitiva* n. subsp. differs from these elements in possessing a slightly higher blade–carina.

Remarks.—The asymmetric posterior platform of *Neogondolella excentrica primitiva* n. subsp. is generally manifest as a deflected rounded lobe that may appear as a secondary process, as in the holotype, or simply as a posterior-lateral expansion with an incurved posterior carina. Commonly there is an additional offset posteriormost denticle like that seen in younger and longer elements assigned to *Neogondolella* aff. *N. cornuta*.

Neogondolella excentrica sigmoidalis new subspecies
Figure 10.8–10.15

1976 *Neogondolella excentrica* Budurov and Stefanov; Rafek, pl. II, figs. 1–3.
1992 *Neogondolella excentrica*; Chhabra and Kumar, pl. 3, figs. 8a–c, 9a–c.
p 1994a *Neogondolella* cf. *aequidentata* Kozur et al., pl. 3, fig. 2a–c.
p 1994 *Gondolella transita*; Kovács, p. 487, taf. 3, figs. 1, 3 (only).
p 2004 *Neogondolella bakalovi* Budurov and Stefanov; Muttoni et al., pl. 1, figs. 5a–c.
p 2014 *Neogondolella* ex gr. *transita* morphotype alpha; Golding, fig. 2.28, parts 1–9.

Holotype.—GSC 141877 (Fig. 10.8–10.10), from the upper member of the Prida Formation, upper Subasperum Zone (sample 512), Saurian Hill, Nevada.

Figure 11. (**1–11**) *Neogondolella excentrica primitiva* n. subsp. (**1–7, 9–11**), from Prida Formation, Nevada. (**1, 2**) GSC 141880, sample FH8, Rotelliformis Zone/burckhardti Subzone; (**3, 4**) GSC 141881, sample FH44, Meeki Zone/dunni Subzone; (**5–7**) GSC 141882, holotype, FH6, Rotelliformis Zone/burckhardti Subzone; (**8**) GSC 141883, sample 92AH-2, Deleeni Zone; (**9–11**) GSC 141884, sample FH48, Occidentalis Zone; (**12–14**) *Neogondolella excentrica* aff. *primitiva* n. subsp. GSC 141885, sample AH26, Minor Zone. Scale bar = 200 μm.

Diagnosis.—A subspecies of *Neogondolella excentrica* with an elongate, weakly arched platform of largely uniform width and a length:breadth ratio of 5.5:1. In upper view, the posteriormost one-fifth of the platform has a sigmoidal outline, is inturned, and terminates in a rounded posterior margin. A low blade/carina has relatively discrete anterior denticles, partly fused medial carina, and several large and discrete denticles posterior of the cusp. The basal scar extends beneath the posterior inturned platform far posterior of the pit.

Occurrence.—This relatively uncommon subspecies is represented by about 12 elements from the Subasperum Zone at Saurian Hill in Nevada, and the Matutinum and Poseidon zones at Wapiti Lake, Oyster Springs, and Tuchodi Bluffs in B.C. Specimens from the Chischa Zone have less-developed keels, whereas typical specimens occur with ammonoids of the *bamberi* Fauna.

Other records are those of the ?Upper Muschelkalk of northern Germany (Rafek, 1976); the Curionii Zone at Felsőörs in Hungary (Kovács, 1994) and in the Belvedere section in the Italian Dolomites (Muttoni et al., 2004); the Carnic Alps in Austria (Kozur et al., 1994a); and the Kalapani Limestone, northern India (Chhabra and Kumar, 1992).

Etymology.—From the Greek word *sigmoeidḗs*, shaped like the letter sigma.

Remarks.—The long, slender platform and extended keel differentiates *Neogondolella e. sigmoidalis* n. subsp. from *Neogondolella e. primitiva* n. subsp., while the rounded posterior platform distinguishes it from *N. e. excentrica*. The specimen illustrated by Kozur et al. (1994a) differs from typical *N. aequidentata* Kozur, Krainer, and Lutz, 1994a, in its asymmetry and lower, less arched carina.

In lower Ladinian samples from B.C., elements of *Neogondolella posterolonga* occur in which posterior platform asymmetry occurs without an extended keel on the underside. These appear to be transitional to *Neogondolella e. sigmoidalis* n. subsp., which shares the same relative platform dimensions. This mirrors the intermediate nature of *N.* aff. *N. cornuta* between *N. cornuta* and *N. e. excentrica*, and the variants included in *N. e. primitiva* n. subsp.

Neogondolella ex gr. *mesotriassica* (Kozur and Mostler, 1982)
Figure 12

p* 1982 *Gondolella mesotriassica* Kozur and Mostler, p. 293–294, pl. 1, figs. ?2, 3, 4.
p 1994b *Neogondolella mesotriassica*; Kozur et al., pl. 4, figs. 7–9 (only).
2014 *Neogonolella constricta longa* Budurov and Stafanov; Sun et al., fig. 4d.

Holotype.—Kozur and Mostler, pl. 1, fig. 4, sample BM 44/75, from within the Reiflingen limestones at Buchberg, near Göstling, lower Austria.

Occurrence.—Slightly different specimens assigned to this group occur sporadically through the upper Anisian in Nevada, largely in the Rotelliformis Zone, but also in younger strata. In B.C., the occurrence of this species is bracketed by the Minor and Deleeni zones on Toad River. The characteristic form starts at the base of the Reitzi Zone in Austria (Kozur et al., 1994b). A similar element was illustrated from the Upper Guanling Formation in Guizhou Province, China (Sun et al., 2014).

Description.—The segminiplanate P_1 elements are arched, with a subrectangular platform with a squared-off or truncated posterior margin that may have a v-shaped notch visible in upper view. The platform is slightly broader at midlength and tapers in both directions before often broadening at the posterior end. The blade denticles are more discrete than the largely fused median carina, and together they impart an arcuate upper profile to the element. The carina ends in a small terminal denticle that is separated from those to the anterior, including the cusp. Additional denticles commonly are developed on the posterior platform margin. The basal pit is subterminal in the keel, with an asymmetrical basal loop that reflects the lateral expansion of the posterior end.

Remarks.—The holotype of *Neogondolella mesotriassica* has a v-shaped notch on the posterior margin, but it has neither a truncated posterior platform, nor accessory posterior denticles, as cited in the original diagnosis. The terminal denticle of the holotype is discrete and quite unlike those of the two paratypes, which have the final denticle fused with the posterior platform margin. The latter feature led Kovács et al. (1990, p. 171) to suggest that one paratype was an example of the gamma morphotype of *N. constricta*, later named *N. postcornuta* (Kovács, 1994). On the contrary, Kozur et al. (1994b) regarded most examples of the latter species as

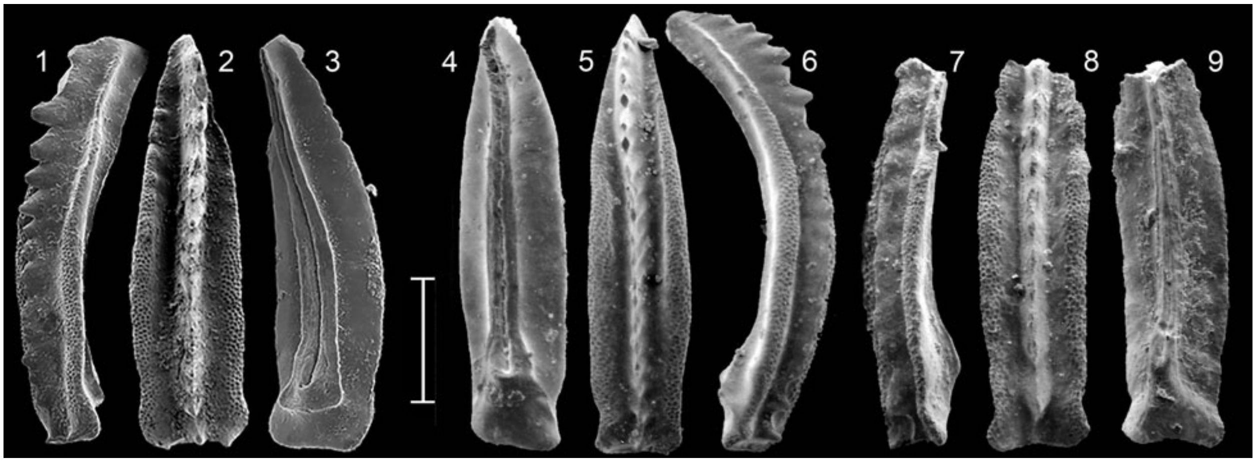

Figure 12. *Neogondolella* ex gr. *mesotriassica* (Kozur and Mostler) from (**1–3**) Toad Formation, B.C. and (**4–9**) Prida Formation, Nevada. (**1–3**) GSC 141898, sample 83/215F, Toad River Canyon, Minor–Deleeni zonal boundary; (**4–6**) GSC 141899, sample FH13, Rotelliformis Zone/clarkei Subzone; (**7–9**) GSC 141900, sample FH48, Occidentalis Zone/hyatti Subzone. Scale bar = 200 μm.

examples of *N. mesotriassica*, but did not provide a formal taxonomic revision. Both species are retained here based on the divergent morphology of the holotypes.

These elements resemble *Paragondolella bifurcata*, which is also characterized by a squared-off posterior margin and accessory denticles, but that species differs in its high carina and blade. *Neogondolella quasiconstricta* n. sp. has similar features but is much broader posteriorly.

Uncommon examples of *Neogondolella mesotriassica* from both Nevada and B.C. differ in detail but are united by the narrow, truncated, and denticulate character of the posterior margin. The morphology of the holotype and the diversity in the current material suggest further revision will be necessary within this group. The three examples illustrated are from progressively younger horizons and appear to lengthen and show anterior pit migration, which is the same trend recognized in other members of the *constricta* group.

Neogondolella postcornuta (Kovács, 1994)
Figure 13

1975	*Gondolella longa*; Trammer, pl. 23, figs. 2a, b, 3a, b.
p 1990	*Gondolella constricta* morphotype γ Kovács et al., p. 188, pl. 1, fig. 4a–c; pl. 3, fig. 5.
* 1994	*Gondolella constricta postcornuta* Kovács, p. 484, pl. 1, figs. 4, 5; pl. 2, figs. 2–5; pl. 6, fig. 4 (see synonymy).

Holotype.—Kovács, p. 484, pl. 1, fig. 4a–d, catalogue number T-6451, sample No. 4, Öskü road-side section, Balaton Highland, Hungary, reposited in the Museum of the Hungarian Geological Survey (Kovács et al., 1990, fig. 10). Lower Curionii Zone, Vászoly Limestone Member of the Buchenstein Formation.

Occurrence.—Similar specimens occur throughout upper Anisian and into Ladinian strata at Fossil Hill, Nevada, but their occurrence is sporadic because they are not always distinguishable from some growth stages of *N. cornuta*. The species has not been recognized in B.C.

In the Balaton Highland, Hungary, *Neogondolella postcornuta* occurs from the uppermost part of the meriani B horizon to the lower Curionii Zone. The first primitive representatives of the species occur in the uppermost bed of the meriani B horizon, whereas common typical ones occur in the liepoldti horizon (Kovács, 1994). A very similar element to the largest illustrated here was figured from southwestern Holy Cross Mountains, Poland (Trammer, 1975). Similar transitional forms occur in the upper Curionii Zone in the Vászoly and Felsőörs sections (Kovács, 1994).

Description.—The segminiplanate P_1 element is relatively narrow, elongate, and slightly arched with a posteriorly inclined main denticle completely fused with the posterior platform end. The platform is narrowly biconvex for the most part but narrows in its posterior part. The cusp is inconspicuous in the low carina that passes anteriorly into higher and less fused denticles. The small basal pit is subterminal in position.

Comparisons.—According to Kovács (1994), *Neogondolella postcornuta* differs from intermediate-sized elements of its

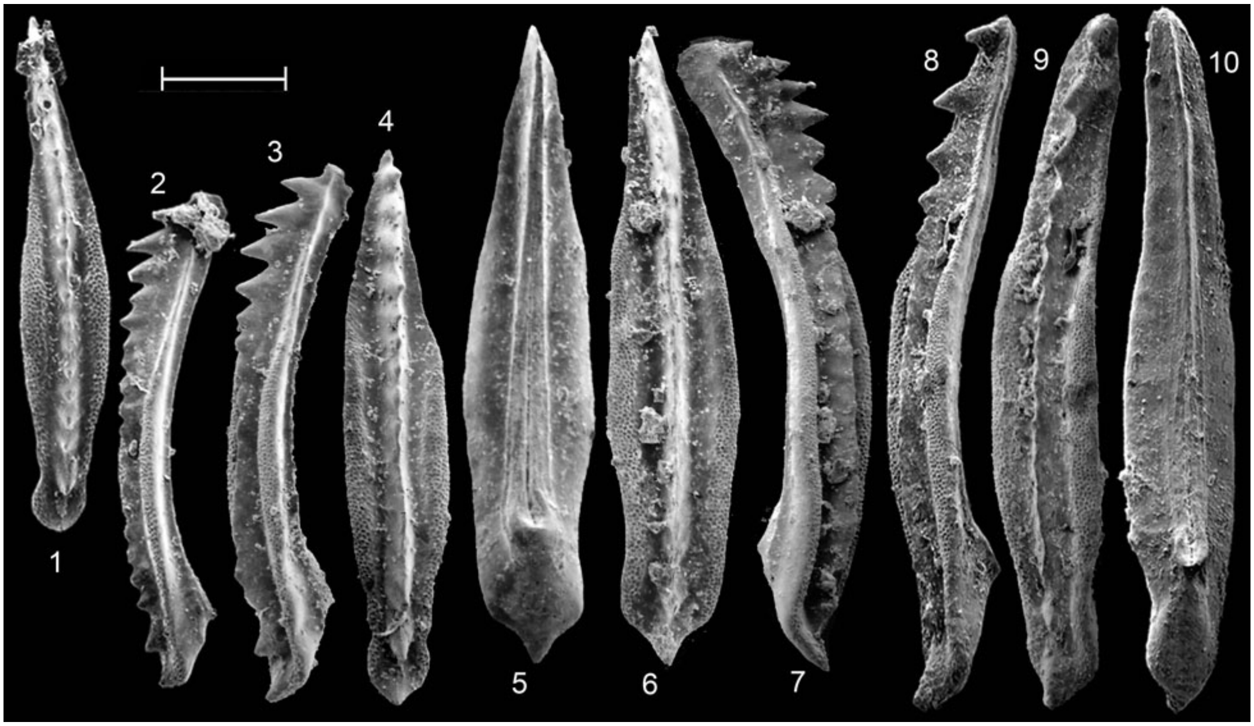

Figure 13. *Neogondolella postcornuta* (Kovács) from Prida Formation, Fossil Hill, Nevada. (**1, 2**) GSC 141901, sample FH35, Meeki Zone/nevadanus Subzone; (**3, 4**) GSC 141902, sample FH47, Meeki–Occidentalis zonal boundary; (**5–7**) GSC 141903, sample FH8, Rotelliformis Zone/burckhardti Subzone; (**8–10**) GSC 141904, sample FH50, Occidentalis Zone. Scale bar = 200 μm.

forebear *Neogondolella cornuta* by the lack of a conspicuous cusp anterior of the last denticle of the carina, and by the complete fusion of the terminal denticle to the platform end. However, Kovács (1994) stressed that these distinguishing characteristics applied chiefly to elements of intermediate size, and both early juvenile and hyperadult growth stages were less distinctive. The Nevadan specimens of this species do not exhibit the subparallel lateral platform margins and truncated posterior margin seen in *N. cornuta*.

As discussed by Kovács (1994), *N. postcornuta* gives rise to *N. bakalovi*, a Balkan species characterized by a strongly extended posterior platform. Although rare specimens from Nevada show a similar feature, typical elements of the latter species are not recorded in North America. Specimens of *N. posterolonga* have a similar platform shape but are narrower, longer, and lack the fused posterior denticle.

Remarks.—Elements exhibiting the characteristic posterior configuration of *Neogondolella postcornuta* occur sporadically through the range of *N. cornuta*, and it is difficult to separate many smaller specimens in which a terminal denticle is located on the platform margin. Chen et al. (2015) provided a broad review of Middle Triassic conodonts and suggested *N. postcornuta* was in fact a junior synonym of *N. pseudolonga*. As discussed previously, *N. pseudolonga* is here regarded as a probable synonym of *N. cornuta* or *N. posterolonga*. This emphasizes the difficulty of interpreting different growth stages of these allied species.

Neogondolella posterolonga Kozur, Krainer, and Mostler, 1994b
Figure 14

p 1976	*Neogondolella navicula* (Huckriede); Rafek, Pl. III, fig. 7 (only).
? 1982	*Gondolella pseudolonga* Kovács, Nicora, and Mietto; Bagnoli, p. 6, pl. 1, figs. 5a, b.
p 1984	*Gondolella constricta* Mosher and Clark; Nicora and Kovács, p. 144–148, pl. 8, fig. 3.
p 1984	*Gondolella mombergensis mombergensis* Huckriede; Nicora and Kovács, p. 149–150, pl. 9, figs. ?7, ?10.
p 1984	*Gondolella mombergensis longa* (Budurov and Stefanov); Nicora and Kovács, p. 150, pl. 10, figs. 6, 7.
* 1994b	*Neogondolella aldae posterolonga* Kozur et al., p. 182–183.
1995	*Neogondolella constricta*; Ramovš and Goričan, pl. 9, fig. 3a, b.
1997	*Gondolella constricta*; Pevný and Salaj, pl. XI, figs. 2, 3.
? 2001	*Neogondolella* ex gr. *constricta*; Orchard et al., pl. 1, fig. 18.
? 2004	*Neogondolella* ex gr. *constricta*; Sano and Orchard, fig. 6.13, 6.14.
p 2014	*Neogondolella transita* morphotype beta; Golding, fig. 2.29, parts 4–6.
p 2021	*Neogondolella* ex gr. *constricta*; Golding and Orchard, p. 29, pl. 15, figs. 1–4.

Holotype.—The specimen figured by Nicora and Kovács (1984, pl. 10, fig. 7) as *N. mombergensis longa*, from sample N50, in the middle Prida Formation, lower Occidentalis Zone age at Fossil Hill, Humboldt Range, Nevada.

Occurrence.—Typical representatives of *Neogondolella posterolonga* appear in the Meeki Zone and form a larger component of the faunas in the Occidentalis and Subasperum zones in Nevada. Kozur et al. (1994b) recorded first occurrences in the upper Meeki Zone, but some early growth stages of *constricta* group elements from the Rotelliformis Zone are similar. Elsewhere in Nevada, the species is known from Wheeler Mine, and in the Tobin Range. In B.C., examples occur in the Chischa Zone at Yellow Bluff; the Matutinum Zone at Wapiti Lake; the Poseidon Zone at Ganoid Ridge and Tuchodi Bluff; and the Meginae Zone along the Alaska Highway at milepost 386 (Table 2).

The specimen from Hungary comes from the Curionii Zone (Kovács, 1994). The species is also recorded in the southwestern Holy Cross Mountains, Poland (Trammer, 1975); Upper Muschelkalk, northern Germany (Rafek, 1976); ?Punta Bianca, NW Italy (Bagnoli, 1982); central Slovenia (Ramovš and Goričan, 1995); western Carpathians, Slovakia (Pevný and Salaj, 1997); and ?Necoslie Breccia, Cache Creek terrane, Nechako (Orchard et al., 2001; Sano and Orchard, 2004; Golding and Orchard, 2021).

Description.—The platform of this arched segminiplanate element is slender, widest anterior of unit mid-length, and relatively long and narrow for the posterior one-fourth to one-third of its length. Typical length:breadth ratios are 5.0–5.5:1. The blade carina is like other *constricta* group taxa, with more discrete anterior denticles, a lower, largely fused medial carina in later growth stages, and higher, more discrete posterior denticles, including an often-enlarged cusp and a prominent weakly to strongly inclined terminal denticle around which a very narrow platform brim may be developed. On the underside, there is a short, often irregular posterior extension of the basal loop.

Remarks.—Kozur et al. (1994b) originally included *Neogondolella posterolonga* as a subspecies of *N. aldae*, but it is here elevated to a species. In contrast to the latter, *N. posterolonga* has a much longer and narrower, less biconvex platform. In *N. constricta* and *N. cornuta*, the constriction disappears during later growth whereas in the present species the posterior platform is noticeably narrower. In this sense, the species is considered to retain a juvenile morphology in adult specimens.

Neogondolella posterolonga has been confused with *N. longa*, but that species is longer, narrower (length:breadth ratio ~6:1), and of more uniform width and with more discrete denticles. *Neogondolella pseudolonga* was regarded as an early growth stage of *N. longa* by Kozur et al. (1994b) but it may be related to the present species or to *N. cornuta*. Both *N. postcornuta* and *N. bakalovi* may have a similar platform shape, but they have a terminal denticle fused with the platform margin.

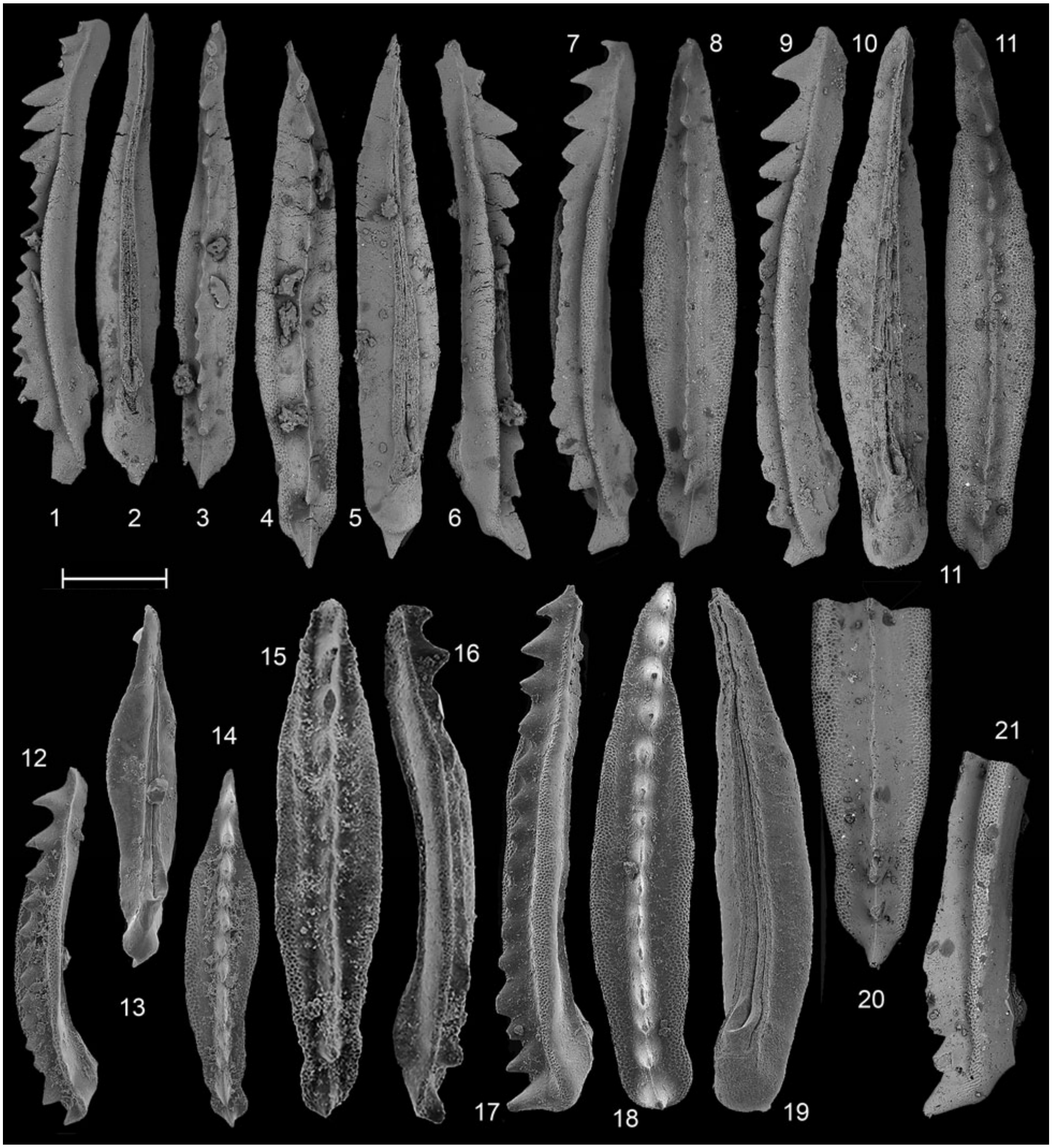

Figure 14. *Neogondolella posterolonga* Kozur, Krainer and Mostler from (**1–11**) Prida Formation, Nevada, Subasperum Zone, and (**12–21**) from B.C. (**1–3**) GSC 141890; (**4–6**) GSC 141891, both from sample SH520; (**7, 8**) GSC 141892; (**9–11**) GSC 141893, both from Subasperum Zone SH534; (**12–14**) GSC 141894, sample 97/WapA6, Llama Formation, Poseidon? Zone; (**15, 16**) GSC 141895, sample 82/AH1, Liard Formation, near milepost 386, Alaska Highway, 2 m below Meginae Zone; (**17–19**) GSC 141896, from sample GSC cur. No. O-83862, Llama Formation, Wapiti Lake, Matutinum Zone; (**20, 21**) GSC 141897, sample 01/URC9, Toad Formation, Ursula Creek, Williston Lake, 95 m above the Permian–Triassic Boundary. Scale bar = 200 µm.

Neogondolella quasiconstricta new species
Figure 15.1–15.7

p 1980 *Gondolella prava* Kozur; Szabo et al., pl. 59, fig. 12 (only)

? 1980 *Neogondolella bifurcata* Budurov and Stefanov; Pisa et al., p. 817, pl. 80, figs. 5a, b, 6a–c, 7a, b.

1982 ‘*Gondolella*’ *bifurcata* (Budurov and Stefanov); Sudar, pl. II, fig. 6; pl. III, fig. 1.

? 1984 ‘*Gondolella*’ *bifurcata*; Farabegoli et al., fig. 5.d1–d3, e1, e2.

1990 *Neogondolella bifurcata bifurcata*; Kovács et al., pl. 1, fig. 2.

?p 2003 ‘*Gondolella’ bifurcata*; Kovács, pl. C-IV, figs. 3–5; C-VII, figs. 1, 2 (only).

Figure 15. (**1–7**) *Neogondolella quasiconstricta* n. sp. from Prida Formation, Nevada. (**1–3**) GSC 141905, sample FH6, Rotelliformis Zone/burckhardti Subzone; (**4–6**) GSC 141906, holotype, sample FH17, Rotelliformis Zone/vogdesi Subzone; (**7**) GSC 141907, sample FH24, Rotelliformis Zone/cricki Subzone. (**8–15**) *Neogondolella quasicornuta* n. sp. from Prida Formation, Nevada and (**9, 10**) Liard Formation, B.C. (**8**) GSC 141908, sample SH524, Occidentalis Zone; (**9, 10**) GSC 141909, sample 92-AH-3, Alaska Highway, *bamberi* Fauna; (**11, 12**) GSC 141910, sample SH504, Subasperum Zone; (**13–15**) GSC 141911, holotype, sample SH519, Occidentalis Zone. Scale bar = 200 μm.

?p 2005 *Paragondolella bifurcata*; Kovács and Rálisch-Felgenhauer, pl. XIV, fig. 2a–e; pl. XVI, fig. 1a–c.

? 2008 *Neogondolella bifurcate* (sic); Wu et al., pl. I, figs. 4–6, 11, 12, 18, 19.

? 2014 *Neogondolella constricta* morphotype zeta; Golding, fig. 2.23, parts 1–6.

Holotype.—GSC 141906 (Fig. 15.4–15.6), from the Fossil Hill Member of the Prida Formation, vogdesi Subzone of the Rotelliformis Zone (sample FH17), Fossil Hill, Nevada.

Diagnosis.—The platform of the comparatively large P_1 element has a length:breadth ratio of 3.5–4:1, an expanded postero-lateral margin, and commonly accessory denticles on one or both sides of the prominent terminal denticle. The blade carina is low throughout, with more discrete blade denticles passing into a largely fused median carina. The pit is subterminal within the triangular keel.

Occurrence.—*Neogondolella quasiconstricta* n. sp. occurs principally in the Rotelliformis Zone in Nevada, always in association with, but as a minor component of abundant *Neogondolella constricta* collections. Younger occurrences are far less common. Elsewhere in Nevada, the species is known from the Tobin Range, and in Canada it occurs in the late Anisian of North Tetsa Phosphate section on the Alaska Highway. About 25 elements were assigned to this species.

The species is also recognized from the base of the Reitzi Zone in Felsőörs, Hungary (Szabo et al., 1980; Kovács, 2003); Han–Bulog Limestone, SE Bosnia (Sudar, 1982); ?middle Bivera Formation, southern Alps, northern Italy (Farabegoli et al., 1984), and southern Alps (Pisa et al., 1980). Some elements from the the Qingyan Formation in Guizhou Province, China (Wu et al., 2008) could be representatives of this species, although crucial lateral views were not provided.

Description.—The large segminiplanate P_1 element has a platform with a length:breadth ratio of 3.5–4:1 and an expanded posterior end with a subtriangular outline; the median platform is generally narrower but may be biconvex. The blade–carina is low throughout, with 4–5 discrete anterior blade denticles rising above the downturned anterior platform, and a largely fused median carina. The terminal posterior denticle is prominent and is commonly accompanied by discrete accessory denticles on one or both sides of it. The pit is subterminal within the basal scar that expands progressively to the posterior where the triangular outline mirrors that of the platform.

Etymology.—Combination of the Latin *quasi-* as if, and *constricta*, the often-co-occurring species that shares the same platform length:breadth ratio.

Comparisons.—*Neogondolella quasiconstricta* n. sp. is similar to, and has often been combined with *Paragondolella bifurcata*, which differs in having a distinctly high blade and carina, as is characteristic of the genus and the associated Pelsonian species, *P. bulgarica* and *P. hanbulogi*. *Gondolella fueloepi pseudobifurcata* Kovács, 1994, from the *costatus* horizon of the Reitzi Zone resembles *Neogondolella quasiconstricta* n. sp. but it has a distinctive posterior platform brim.

Remarks.—Typical specimens of *P. bifurcata* illustrating the diagnostic blade–carina feature were figured by Budurov (1980) and Qin et al. (2021). On the contrary, many specimens assigned to *P. bifurcata* have a low carina (see synonymy), and although this may result from allometric growth (Chen et al., 2016), there are no high-bladed elements with this platform configuration in the Nevadan material.

Muschelkalk neogondolellins with a single secondary carina developed as nodes posterior of the cusp were assigned to *Gondolella mombergensis prava* by Kozur (1968a, b), and that designation was adopted by Szabo et al. (1980). Subsequently these forms have generally been assigned to *Paragondolella bifurcata* (e.g., Kovács, 2003), however the holotype of *Neogondolella prava* (Kozur, 1968a, pl. 1, fig. 2a, b) is clearly allied with its Germanic associate *N. mombergensis*, as shown by similar arched platforms, blade–carina configuration, and geniculate anterior platform (see refigured holotype in Orchard and Rieber, 1998, fig. 1). Rafek (1976, fig. 4) illustrated a variety of *N. prava* morphotypes from the upper Muschelkalk, which correspond to neither *P. bifurcata* nor *N. quasiconstricta* n. sp.

Neogondolella quasiconstricta n. sp. often occurs with both *Neogondolella constricta* and *N. excentrica primitiva* n. subsp., with which it shares relative platform dimensions and a relatively low blade–carina. The three species differ in their posterior configurations, as do the Pelsonian triad of species mentioned above.

Neogondolella quasicornuta new species
Figure 15.8–15.15

? 1979 *Neogondolella mombergensis prava* (Kozur); Mietto and Petroni, p. 10, pl. II, fig. 6a, b.

p 1980 *Gondolella prava* Kozur; Szabo et al., pl. 59, fig. 13a, b (only).

1983 *Neogondolella bifurcata* (Budurov and Stefanov); Kolar-Jurkovšek, p. 336–337, pl. 7, fig. 1a–c (only).

?p 2003 ‘*Gondolella*’ *bifurcata*; Kovács, pl. C-IV, fig. 6a, b (only).

Holotype.—GSC 141911 (Fig. 15.13–15.15), from the Fossil Hill Member of the Prida Formation, Occidentalis Zone (sample SH519), Saurian Hill, Nevada.

Diagnosis.—The P_1 platform element is comparatively long and narrow with a length:breadth ratio of 5–6:1, and subparallel lateral margins that broaden near the posterior end. The blade–carina is low throughout, higher in the anterior, fused in the central part, and slightly elevated in the posterior one-third. A prominent terminal denticle is commonly flanked by accessory denticles. The pit is slightly shifted anterior in the keel, which extends beneath the postero-lateral platform expansion posterior of the pit.

Occurrence.—*Neogondolella quasicornuta* n. sp. is uncommon from high in the Meeki Zone through the low Occidentalis Zone and into the Subasperum Zone at Fossil Hill, and in the latter zone at Wheeler Mine, Nevada. About 50 elements are represented within the abundant collections of *Neogondolella cornuta* from Nevada. The species is not yet identified in B.C.

In Europe, similar elements are known from ?San Ulderico section, NE Italy (Mietto and Petroni, 1979) (no upper view); ? Balaton Highland, Hungary (Szabo et al., 1980; Kovács, 2003) (no lower view); and Idrske Krnice, Slovenia (Kolar-Jurkovšek, 1983).

Description.—The elongate segminiplanate P_1 elements of this species have a length:breadth ratio of 5–6:1. The lateral platform margins are subparallel for much of the element length before broadening near the posterior end. The generally low blade–carina resembles that seen in *Neogondolella cornuta* with more discrete anterior blade denticles, a fused median carina, and slightly elevated, less-fused posterior carinal denticles. A very prominent terminal denticle is accompanied by one or more accessory denticles on the posterior margin. The pit is slightly shifted anterior in the keel, which extends beneath the postero-lateral platform expansion.

Etymology.—Combination of the Latin *quasi-* as if, and *cornuta*, the species that co-occurs and shares its platform length:breadth ratio.

Remarks.—*Neogondolella quasicornuta* n. sp. shares relative platform dimensions with both *N. cornuta* and *N. excentrica excentrica*, with which it often co-occurs. As in the much shorter *N. quasiconstricta* n. sp., the three associated species differ in their posterior platform configurations. The specimen from Balaton Highland is relatively longer than any others illustrated from Hungary, but no lower view is shown.

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Declaration of competing interests

The authors declare none.

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