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Naked Species of *Gondolella* (Conodontophorida): Their Distribution, Taxonomy, and Evolutionary Significance

Peter H. von Bitter
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Naked Species of *Gondolella* (Conodontophorida): Their Distribution, Taxonomy, and Evolutionary Significance

Abstract

The oldest known species of *Gondolella* lacking a platform, indeed the oldest known species of *Gondolella* s.s., is *G. gymna*, from northwestern Illinois and Japan, of early Desmoinesian and Morrowan-Atokan age, respectively. The concept of "naked" gondolelliform conodonts was based on *Gondolella denuda* Ellison, a species that occurs in rocks of early Missourian age in Illinois, Missouri, Nebraska and, rarely, in Ohio. A new "naked" species of *Gondolella*, *G. postdenuda* sp. nov., occurs in and is characteristic of rocks of Virgilian age. It is common in the Queen Hill Shale of Kansas and Nebraska but also occurs less frequently in the Heebner Shale of Kansas, Oklahoma, and Nebraska, the lower Beil Limestone of Kansas, the Salem School Limestone of northcentral Texas, and the shale overlying the latter member. A second new "naked" species of *Gondolella*, *G. neospathodiformis* sp. nov., is known from only a single locality of the Heebner Shale in northern Oklahoma.

Gondolella gymna, *G. denuda*, and *G. postdenuda* sp. nov. each apparently possessed an apparatus of seven element types, six of which were paired. The ramiform elements belonging to each of these three (as well as those belonging to broad-platformed species) were apparently vicarious, or nearly so, and the ramiform elements of one cannot be distinguished from those of the other without difficulty and considerable uncertainty. *Gondolella neospathodiformis* sp. nov. is based on a blade-like platform element.

The most probable ancestor of "naked" (and other) species of *Gondolella* appears to be the *Spathognathodus bultyncki* group of Lower Carboniferous age. The descendants of the former are probably conodonts placed in the genus *Neospathodus* Mosher. The four "naked" species of *Gondolella* may have evolved during the Pennsylvanian in a direct ancestor-descendant relationship. Alternatively, the evolution of this group may have involved any of four or more phylogenetically more complex paths—paths that included regressive platform development and iterative mosaic evolution, as well as dimorphism.

Introduction

The conodont genus *Gondolella* was defined by Stauffer and Plummer (1932) on the basis of elements that were tongue-, canoe-, or gondola-shaped, that possessed a bar or base (= platform) that was slender to thick and broad, and that had an aboral flaring loop. All of the species included in this genus by its authors possessed broad platforms. In 1941 a narrow blade-like form, *Gondolella denuda* Ellison, was included in this genus. This was the first of the naked gondolellids known. The term "naked" is used by us much as it was by Ellison (1941), to describe those gondolellids whose Sp (or platform) elements lack a true, broad platform. In this paper we document the occurrence and biostratigraphic, taxonomic, and phylogenetic significance of *G. denuda* as well as of three additional naked species, two of which are new.

Stratigraphic and Geographic Distribution (Fig. 1)

The oldest known species of *Gondolella* lacking a broad platform is *Gondolella gymna* from the Seville Limestone of northwestern Illinois (Merrill and King, 1971) and from rocks of either similar or older age (Fig. 1) (depending on correlation source) in Japan (Koike, 1967). Slightly younger rocks in northwestern Illinois ("Seville" in Merrill, 1975) and western Missouri (Tiawah Member in Vernon Co., Missouri, and the shale in the Scammon Formation below the Tiawah Member in Henry Co., Missouri) contain *Gondolella laevis* Kosenko and Kozitskaya, a species that has a platform intermediate in width between *G. gymna* and younger broad-platformed Desmoinesian species. This species was interpreted by Merrill and King (1971) and Merrill (1975) to be an evolutionary intermediate between *G. gymna* and the fully platformed Desmoinesian gondolellid species such as *G. bella*.

Only two other, somewhat minor, occurrences of naked gondolellids are known from rocks of pre-Missourian age. *Gondolella* cf. *gymna* occurs sparingly with the broad-platformed *G. magna* in the Lonsdale Member of northwestern Illinois (Merrill, 1975: 54) and in the Holdenville Formation of Jackson Co., Missouri.

Missourian occurrences of naked species of *Gondolella* are confined to one species, *G. denuda* Ellison, from three nearly contemporaneous early Missourian occurrences, the Hushpuckney and Stark Shales of the Kansas City and Omaha areas, the Cramer Member of northern Illinois, and one specimen from the Lower Brush Creek Member of eastern Ohio. This last specimen was formerly interpreted to have been ancestral to (=*Prioniodina camerata sensu* Ellison, 1941), rather than conspecific with, *G. denuda*, and was omitted from the occurrences of species of *Gondolella* (Merrill, 1975:51). This is the first report of a species of *Gondolella* from the Appalachians. Species of *Gondolella* are known from many other units of Missourian age in the Midcontinent and Illinois, but those species, both older and younger, have broad platforms as do other species that occur with *G. denuda* in the Hushpuckney, Stark, and Cramer. No other species of *Gondolella* are known from

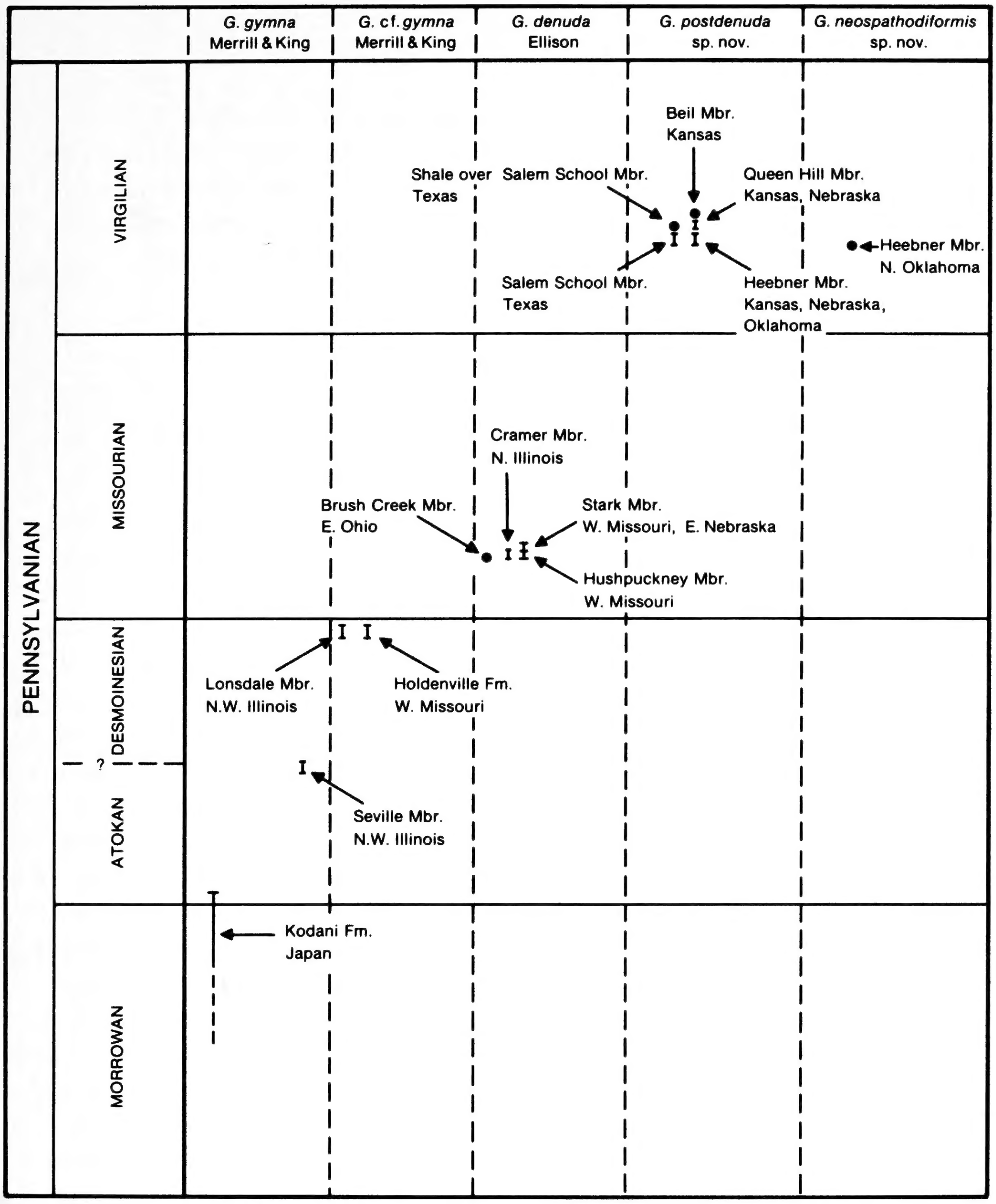


Fig. 1 Stratigraphic distribution of naked species of *Gondolella*.

the Appalachian region other than the single platform (or Sp) element from the Lower Brush Creek.

Virgilian naked gondolellids belong to two species, *Gondolella postdenuda* sp. nov. and *Gondolella neospathodiformis* sp. nov. The oldest Virgilian occurrence is in the Heebner Shale of Nebraska, Kansas, and Oklahoma, where both species are very rare. The slightly younger Queen Hill Shale of Nebraska and Kansas contains *Gondolella postdenuda* sp. nov. somewhat more abundantly and predictably, and contains broad-platformed species only very rarely (Ellison, 1941; Mendenhall, 1951). *Gondolella postdenuda* sp. nov. is also known from the lowest part of the Beil

Limestone at one locality in Kansas (as *G. denuda* in von Bitter, 1972) as well as from the Salem School Limestone and the shale directly overlying the latter in northern Texas (Fig. 1).

Gondolella postdenuda sp. nov. and *Gondolella neospathodiformis* sp. nov. are the youngest species of *Gondolella* of which we are aware (with the possible exception of Clark's 1972 report of specimens from the Upper Pennsylvanian and Lower Permian of Nevada that he called *G. bella*). The stratigraphic and geographic distribution of naked species of *Gondolella* is shown in Tables 1 and 2.

Environmental Distribution and Faunal Associates

The ecological requirements and biologic associates of species of *Gondolella* and the controversy surrounding their environmental setting (deep vs. shallow water) has been considered at length by Merrill and von Bitter (1976). With the possible exception of species of *Diplognathodus*, species of *Gondolella*, including the naked forms, are environmentally the most restricted of Pennsylvanian conodonts. Where found they commonly occur in profusion, but are absent from the greater part of the stratigraphic section. The most abundant and well-represented distribution in terms of the number and stratigraphic spacing of units bearing species of *Gondolella* occurs in the Kansas City Group (Missourian) of Kansas, Missouri, Nebraska, and Iowa.

Naked gondolellids, in common with those species bearing broad platforms, generally occur in rocks containing significant numbers of elements of species of *Idioprioniodus* (Merrill and von Bitter, 1976). *Gondolella* generally does not occur in samples with substantial numbers of elements of species of *Aethotaxis*, although exceptions to these generalizations are known. Some of the occurrences of *Gondolella gymna* in the Seville Limestone are in rocks containing as many or more elements of species of *Aethotaxis* than of *Idioprioniodus* (Merrill and King, 1971). Some of the occurrences of *G. denuda* in the Cramer Member (Table 2) are in conjunction with uncharacteristically large numbers of specimens assignable to species of *Aethotaxis*, *Cavusgnathus*, and *Ellisonia* as well as to those of *Idioprioniodus*. In the Queen Hill Shale and the base of the overlying Beil Limestone, *G. postdenuda* sp. nov. occurs without species of *Idioprioniodus*. The fact that von Bitter (1972) found only a few doubtful fragments of elements of species of *Idioprioniodus* as high stratigraphically as the Queen Hill, and Ellison (1941), von Bitter (1972), and Perlmutter (1975) failed to report any younger occurrences may be the result of disappearance (extinction?) rather than environmental exclusion. Although several apparently suitable stratigraphic units for both genera are present higher in the stratigraphic column, *Gondolella* and *Idioprioniodus* seem to disappear from the American Midcontinent at almost the same stratigraphic position. Species of the *Idiognathodus-Streptognathodus* plexus are reduced or eliminated above this horizon, although both *Gondolella* and *Idiognathodus* occur higher in the western United States (Clark, 1972).

As Tables 1 and 2 demonstrate, the majority of samples producing broad or naked species of *Gondolella* have been derived from thin, fissile, black, phosphatic shales, the tan phosphatic shales directly overlying them, and from transitional higher units,

Table 1 **Distribution of *Gondolella gymna* Merrill and King and *G.* cf. *gymna* Merrill and King in the Morrowan-Desmoinesian of North America and Japan**

Taxon	Location	Formation/ Member	Age	Sample	Sp	Oz	Lo	Hi	Ne	Syn	Tr	Indet.	Associated conodonts: *Gondolella* spp. with broad-platformed Sp element	Associated conodonts: *Idioprioniodus* spp.	Lithology
G. cf. *gymna*	NW Illinois	Lonsdale Mbr.	late Desmoinesian	2C	5	106	29	19	7	45	4	—	A	A	Soft light tan shale
				6B	—	1	—	—	—	—	—	—	A	A	Light grey crinoidal biomicrite
				7B	1	2	—	—	1	—	—	—	A	A	Rusty grey intramicrite
				7D	1	2	1	1	—	1	—	—	A	A	Rusty grey intramicrite
				7E	—	1	1	—	—	1	—	—	A	A	Rusty grey intramicrite
				8C	—	4	1	1	2	—	3	—	A	A	Soft light grey shale
				8D	11	204	46	31	7	65	16	—	A	A	Light grey algal biomicrite
				8E	4	4	2	2	—	—	—	—	A	A	Soft light grey shale
				11	—	1	—	1	—	—	—	—	A	A	White calcareous sandstone with fossil plants
				12B	1	9	2	—	—	—	—	—	A	A	Soft medium bluish grey clay shale
				13C	1	1	—	—	—	—	—	—	A	A	Soft medium bluish grey clay shale
				14B	—	1	—	—	—	—	—	—	A	A	Nodular brecciated grey micrite
	W Missouri	Holdenville Fm.	late Desmoinesian	1	1	—	1	1	1	—	—	—	R	C	Grey to blue grey soapy shale
G. gymna	NW Illinois	"Seville" Mbr.	early Desmoinesian	11D	—	14	3	7	1	—	—	2	C	C	Light grey sparse mixed biomicrite
				11E	2	2	—	1	—	—	—	—	C	C	Light grey sparse mixed biomicrite

Continued on page 6.

Table 1 continued

Taxon	Location	Formation/ Member	Age	Sample	Sp	Oz	Lo	Hi	Ne	Syn	Tr	Indet.	Associated conodonts: *Gondolella* spp. with broad-platformed Sp element	Associated conodonts: *Idioprioniodus* spp.	
G. gymna	N W Illinois	Seville Mbr.	late Atokan or early Desmoinesian	4B	14	2	—	—	1	16	10	27	—	C	Medium grey sparse mixed biomicrite
				8A	1	1	1	—	—	1	—	—	—	C	Brownish grey sparse spiculitic biomicrite
				8B	26	14	7	1	1	28	2	148	—	C	Medium grey fossiliferous calcareous shale
				10-I-h	1	1	1	—	—	1	1	5	—	C	Medium bluish grey fossiliferous micrite (10-I-h and 10-II-d)
				10-II-d	1	—	1	1	—	2	2	—	—	C	
				14A	2	1	1	7	3	8	8	—	—	C	Medium grey packed crinoidal biomicrite
				14B	20	4	2	4	3	7	—	—	—	C	Medium grey sparse mixed biomicrite
				14C	84	44	35	16	5	43	10	3	—	C	Dark grey sandy fossiliferous micrite
				16A	6	6	5	1	—	8	—	2	—	C	Dove grey sparse mixed biomicrite
				16D	62	30	6	20	—	13	3	—	—	C	Dark grey slightly calcareous shale
				20	4	2	—	1	—	1	2	1	—	C	Medium bluish grey sparse to packed mixed biomicrite
	Japan	Kodani Formation	late Morrowan to early Atokan	43	3[1]	1[2]							—	7[4]	See Koike (1967) for details regarding lithology, detailed stratigraphic position and depository. (43, 126 and 130)
				126	1[1]	—	Remaining ramiform elements not recognizable from plates of Koike (1967) (43, 126 and 130)						—	2[4]	
				130	3[1]	1[2]							—	1[4]	

131	3[1]	3[2]	Remaining ramiform elements not recognizable from plates of Koike (1967)	—	1[4]	See Koike (1967) for details regarding lithology, detailed stratigraphic position and depository.
132	9[1]	3[2]		—	4[4]	
133	4[1]	1[2]		6[3]	—	
134	1[1]	1[2]		6[3]	—	
17	2[1]	—		—	3[4]	
28	1[1]	—		—	1[4]	

A = Abundant; C = Common; R = Rare

[1] *Gondolella* ? sp. A of Koike (1967)

[2] *Lonchodina* sp. A of Koike (1967)

[3] von Bitter and Merrill (1977) placed these in *Neogondolella clarki* (Koike)

[4] *Lonchodina* spp. of Koike (1967) probably represent elements of *Idioprioniodus* spp.

Table 2 Distribution of *Gondolella denuda* Ellison, *G. postdenuda* sp. nov., and *G. neospathodiformis* sp. nov. in the Missourian and Virgilian of North America

Taxon	Location	Formation/ Member	Age	Sample	Sp	Oz	Lo	Hi	Ne	Syn	Tr	Indet.	Associated conodonts: *Gondolella* spp. with broad-platformed Sp element	Associated conodonts: *Idioprioniodus* spp.	Lithology
G. denuda	E Ohio	Lower Brush Creek	Missourian	39B	1	—	—	—	—	—	—	—	—	C	Tan calcareous shale with limestone nodules
	N Illinois	Cramer	Missourian	2A	139†		38	19	6	33	7	—	C	C*	Unsorted mixed biosparite
				2B	8	2	4	5	1	6	—	1	C	C*	
				2C	43†	—	1	11	6	6	—	—	C	C*	
	W Missouri	Hushpuckney	Missourian	4	2	9	1	1	3	3	1	—	C	A	Brown-tan phosphatic shale
				5	1	—	—	1	—	1	—	—	C	A	
				8	10	17	1	1	—	—	—	—	C	A	
	W Missouri	Stark	Missourian	1	11	3	1	—	—	—	—	6	C	C	Black phosphatic shale
	E Nebraska	Stark	Missourian	6B	36	1	18	10	4	6	2	—	—	C	Black phosphatic shale
				6C	23	2	14	6	6	16	2	—	—	C	Grey soft shale
G. postdenuda sp. nov.	S Kansas	Heebner	Virgilian	He-2-1	1	—	—	—	—	—	—	—	—	C	Earthy, black shale
				He-2-2A	1	—	—	—	—	—	—	—	—	C	Black, fissile shale
	S C Kansas			He-5-1	6	—	—	—	—	—	—	—	—	C	Yellowish-brown clayey to sandy shale
	N Oklahoma			He-7-1	1	—	—	—	—	—	—	—	—	R	Brown to olive clayey shale
	S Kansas			He-8-1	2	—	—	—	—	—	—	—	—	C	Greyish-black to olive soft clayey shale
	N E Kansas			He-10-1	1	—	—	—	—	—	—	—	—	C	Black, fissile phosphatic shale

	E Nebraska			He-14-1	4	3	3	1	12	4	1	—	R	A	Chocolate-brown to greenish yellow clayey shale
	E Kansas	Queen Hill	Virgilian	QH-1-1	2	2	+2	Ramiform elements other than Oz and Hi? (= Lo element) elements not differentiated by von Bitter (1972)					—	—	Black, fissile phosphatic shale
	E Kansas			QH-1-2	21	9	+4						—	—	Brown, earthy phosphatic shale
	S Kansas			QH-2-3	36	11	6	5	7	6	1	—	—	—	Brown, clayey phosphatic shale
	E Nebraska			QH-4-2	12	4	3	5	2	4	1	2	—	—	Brownish-grey phosphatic shale
				QH-4-3	12	2	—	5	2	2	—	—	—	—	Black, fissile phosphatic shale
	E Nebraska			2	5	1	—	—	—	1	1	—	R	—	Black phosphatic shale
	E Kansas	Beil	Virgilian	B-1-1	—	1	—	—	—	—	—	—	—	—	Bluish-grey bioclastic limestone
	N Texas	Brown marine Shale about 15′ ± above Salem School Mbr.	Virgilian	Sal-Sp-3	1	—	—	—	—	—	—	—	—	C	Brown friable marine shale
	N Texas	Salem School	Virgilian	Sal-1-2	—	1	—	—	—	—	—	—	—	—	Thin-bedded, shaley limestone
G. neospathodiformis sp. nov.	N Oklahoma	Heebner	Virgilian	He-7-1	17	—	—	—	—	—	—	—	—	R	Brown to olive clayey shale
				He-7 Recolln.	2	—	—	—	—	—	—	—	—	R	Brown to olive clayey shale
	N Oklahoma	Plattsmouth	Virgilian	P-6-1	1	—	—	—	—	—	—	—	—	R	Medium-bedded, grey limestone

A = Abundant; C = Common; R = Rare.

* Also common are *Aethotaxis*, *Cavusgnathus*, *Hindeodus* and *Ellisonia*. Great difficulty in separating Sp and Oz elements in some samples has led to their combination in samples Cramer 2A and 2C.

† Sp and Oz elements were not differentiated by Merrill (1975).

generally limestones. Exceptions are dark, shaly limestones such as the Seville, light-coloured shales such as Lower Brush Creek, and clean light-coloured limestones such as the Lonsdale and Cramer (Tables 1 and 2). Analysis of these exceptions should provide additional insight into the ecology of *Gondolella*.

Phylogenetic Methods and Philosophy

Conodonts are skeletal parts that performed unknown functions within the body of animals whose taxonomic affinities may never be discovered. Despite this, conodont workers have found conodonts to be readily distinguishable from the remains of other groups such as those of fish and worms. Conodonts of Ordovician to Triassic age, taken collectively, appear to belong to a rather uniform, coherent group, a group that did not contain structural and physiological differences of the magnitude found between, for example, mammals and dinosaurs. Although there is evolutionary convergence within this group, this convergence is not between the taxa of major taxonomic categories such as those referred to above but is, as stated, within a taxonomically restricted and uniform group. The observed convergence in conodonts generally expresses itself as the reappearance of a morphologic feature after a long interval of time—of the duration of a geologic period or more. This observation and the fact that we are dealing in this study with a much shorter interval of time allow us to conclude that morphologically closely similar, but distinct, conodont platform elements are not only vaguely related but form a direct or indirect evolutionary ancestor–descendant relationship. This conclusion may also be applied, with some caution, to the nonplatform elements.

Phylogenetic trees depend rather heavily on taxonomic decisions and it is necessary to outline what taxonomic characters have been used in the recognition of the various taxa. First and foremost when working with gondolellids is the requirement that the platform element possesses the definitive aboral loop. Naked gondolellids should, by definition, lack a broad platform on their Sp elements. If both these criteria are met and it has been established that we are dealing with naked gondolellids, then other criteria such as platform and denticle length, apparatus composition, fusion or lack of fusion of denticles, distribution of white matter, and the presence or absence of a lateral ridge are used to recognize different species of naked gondolellids.

The other aspect of great importance in the construction of phylogenetic trees is where, in time and space, a particular fossil has been found. Any phylogenetic tree must be compatible with the stratigraphic positions, and consequently the ages, of the fossils on which it is based. In outlining the five phylogenetic alternatives (Figs. 2–6) we have carefully considered the stratigraphic occurrences and ranges of the various taxa (Fig. 1).

The Phylogeny of Naked Species of Gondolella

Two possibly interrelated aspects must be considered when attempting to trace the phylogeny of this group of conodonts. The first is the evolutionary relationship the four naked species of *Gondolella* had to one another. Secondly, it is necessary to determine the evolutionary relationship of this group to the more common species of *Gondolella* that have broad platforms in their apparatuses.

Both aspects are difficult to evaluate, not only because of the presence of thick sequences lacking any species of *Gondolella*, but also because of the scarcity of convincing intermediate forms.

Considering the first question, the simplest phylogeny is shown in Fig. 2. It is based on the premise that morphological similarity implies or denotes relationship and that because the naked platforms of each of these four species are more similar to each other than they are to broad-platformed species of *Gondolella*, then they are in fact directly phylogenetically related.

The above is the simplest and most attractive phylogeny and may ultimately prove to be the one that comes closest to representing the evolutionary history of naked species of *Gondolella* during the Pennsylvanian. It does, however, suffer from a number of shortcomings.

(a) Sp elements of *Gondolella* cf. *gymna* from the Lonsdale Member and the Holdenville Shale are morphologically similar to those of *G. gymna*. Indeed, if these elements were found in the Seville Member they would be identified as the Sp elements of *G. gymna*; however, not only is the occurrence of *Gondolella* cf. *gymna* stratigraphically a considerable distance from that of *G. gymna*, but it also occurs with abundant broad-platformed gondolellids. This fact makes it uncertain to which apparatus the associated ramiform elements (Fig. 8) belong and creates the (to us unlikely) possibility that the *Gondolella* cf. *gymna* Sp element is really an Oz element of a broad-platformed species of *Gondolella*, one that resembles the Sp element of *G. gymna* owing to possible convergence.

(b) There is considerable stratigraphic distance separating the highest occurrence of *G. gymna* from the lowest occurrence of *G. denuda*. There are, in this interval, a number of stratigraphic levels such as the Hanover, the Mineral Wells, the Sniabar, and the Hertha in which broad-platformed species of *Gondolella* occur. Although one would expect evolutionary forms intermediate to *G. gymna* and *G. denuda* to occur in environments that are suitable for other species of *Gondolella*, this is, for unknown reasons, not the case.

(c) In considering the phylogenetic relationship between *G. denuda* and *G. postdenuda* sp. nov. one is struck by the close morphologic similarity between their platform elements as well as the similarity between their ramiform elements. There is, however, the same difficulty as in (b) in that there is a thick stratigraphic interval containing units such as the Quivira Shale, the Muncie Creek Shale, the Eudora Shale, and the LaSalle and Little Vermillion Limestones that contain abundant specimens of *Gondolella* with broad platforms but lack the evolutionary intermediate naked gondolellids that one would expect.

(d) *Gondolella neospathodiformis* sp. nov., if directly evolved from *G. postdenuda* sp. nov., represents a rather drastic shortening of the platform and enlargement of the main cusp. In addition, it is much smaller than are most specimens of *G. postdenuda* sp. nov. encountered and apparently lacked ramiform elements in its apparatus.

A second possible phylogeny is outlined in Fig. 3. It has been established (Merrill, 1975: fig. 12) that *Gondolella gymna*, a species bearing a naked platform, gave rise to

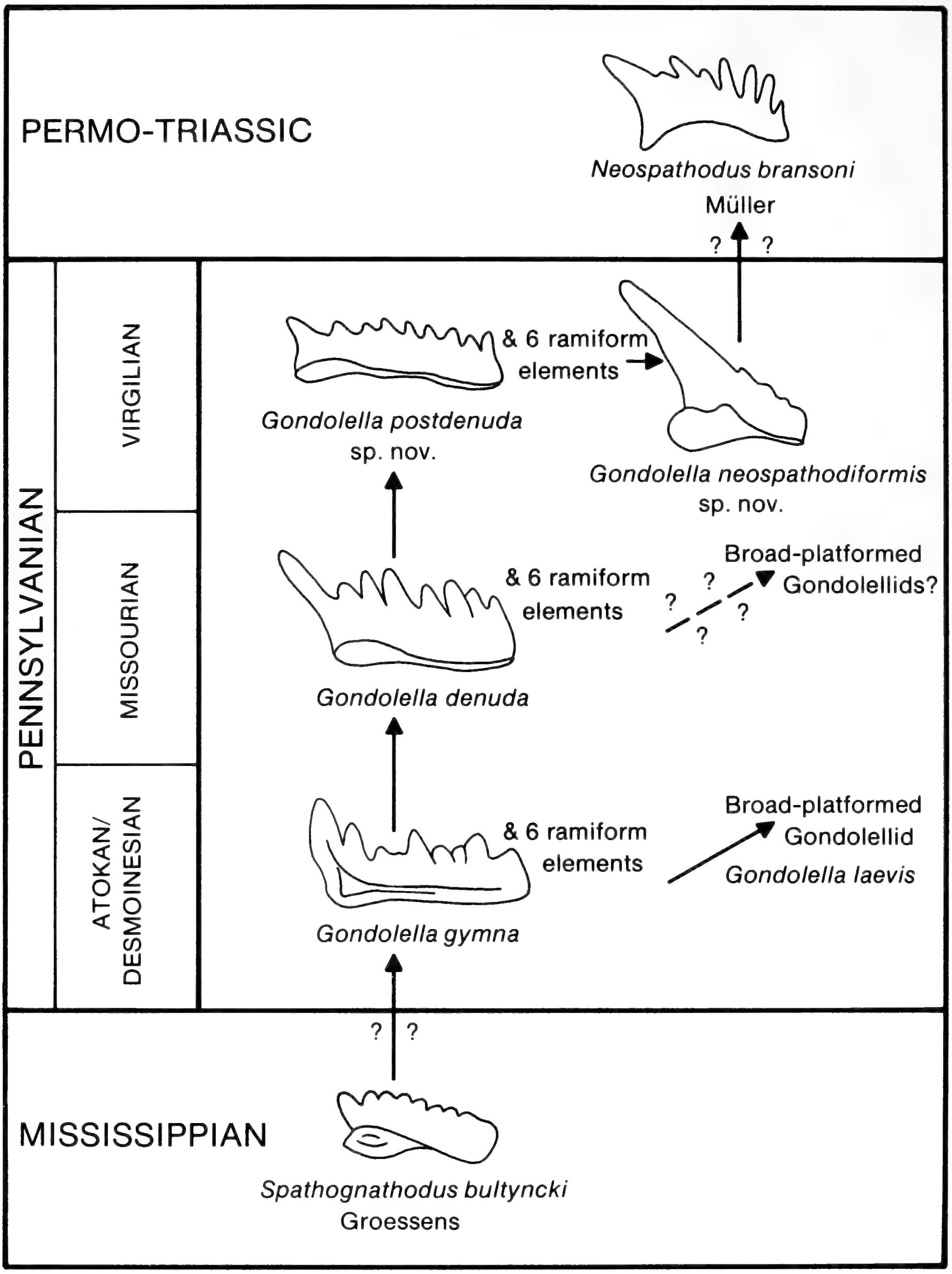


Fig. 2 Evolution of naked species of *Gondolella*, the simplest and most parsimonious phylogenetic solution.

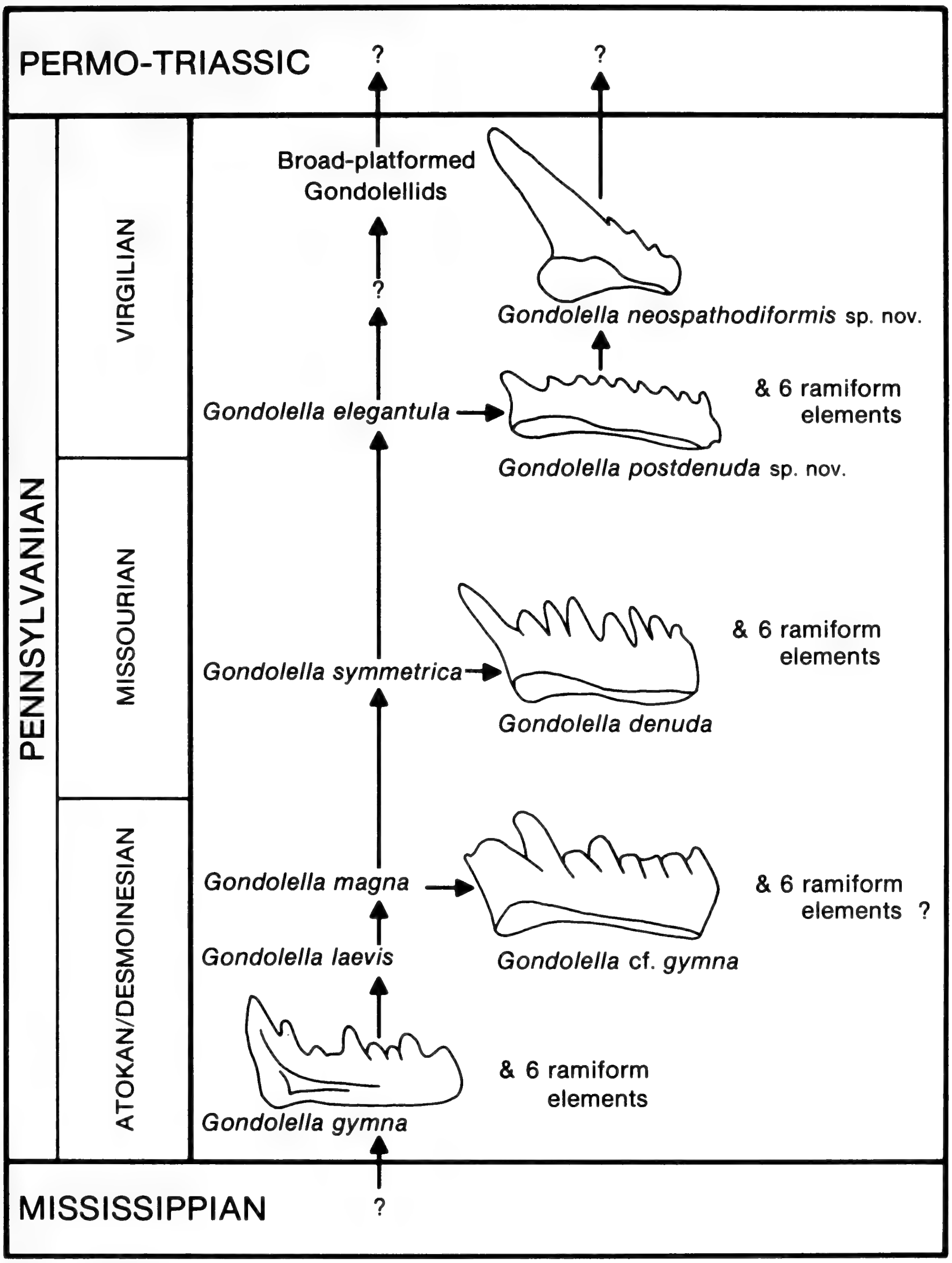


Fig. 3 Evolution of naked species of *Gondolella* from a stock of broad-platformed species by regressive platform development.

the more broad-platformed *G. laevis* as well as to younger Desmoinesian gondolellids. Although the phylogeny of younger broad-platformed species remains to be described the phylogeny of these broad-platformed species as at present understood is shown in Fig. 3. In this phylogeny there is no reason known to us why retrogressive ($\neq$ reverse) evolution (i.e., broad platform to naked platform) could not have taken place a number of times in the Desmoinesian (*G. magna* to *G.* cf. *gymna*), in the Missourian (*G. symmetrica* to *G. denuda*), and in the Virgilian (*G. elegantula*, a species similar to *G. sublanceolata*, to *G. postdenuda* sp. nov.). In this phylogeny, the development of *G. neospathodiformis* sp. nov. was probably from *G. postdenuda* sp. nov. by direct evolution.

Ellison (1942:121, pl. 21, figs. 1–4) illustrated transitional forms between *G. denuda* and *G. symmetrica* and interpreted the evolution as having proceeded in that direction. Our second suggested phylogeny is the reverse of that evolutionary pathway. Other transitions such as that illustrated by Ellison are not known, and until they are, this suggestion must be viewed as a weak phylogenetic contender.

A third phylogenetic possibility for this group, one first suggested by Ellison (1941), is that a naked gondolellid species gave rise to all broad-platformed species (Fig. 4). Ellison (1941) suggested that *G. denuda*, the naked Missourian species, was ancestral to all gondolellid species with broad platforms, a suggestion that unfortunately neglected to explain the geologically older species with broad platforms that both Ellison, and Stauffer and Plummer (1932), had found. The transition from *G. gymna* to *G. laevis* described by Merrill (1975) however, does represent one such transition. Unfortunately, despite the fact that Merrill (1975) suggested a continuous lineage of naked gondolellids that gave rise to species with broad platforms several times, we at present lack proof of other instances of such iterative mosaic evolution in species of *Gondolella* with broad platforms.

In the preceding we have been concerned with understanding and relating morphologic changes at different stratigraphic levels within the naked platform elements of a number of species of *Gondolella*. Ellison (1941) and Merrill and King (1971) noted morphologic transitions and intermediates between the conodont elements they called "*camerata*" and "*denuda*" and "*transitans*" and "*gymna*", respectively. von Bitter (1972) considered that such pairs represent normal symmetry transitions between Sp and Oz elements of *G. denuda* and *G. gymna*, respectively, an opinion we follow herein. Nevertheless, it remains a possibility that "*camerata*" and "*denuda*" as well as "*transitans*" and "*gymna*" do represent homologous elements that expanded from the normal Oz to naked (Sp) platforms to broad (Sp) platforms in some parts of the generic range of *Gondolella* and not during others (Fig. 5). In such a phylogeny the two pairs indicated would form the first two-thirds of such a series. This remains an alternative, one that constitutes a fourth phylogenetic possibility.

A fifth, and final, possibility (Fig. 6) explaining the distributions and morphologic intergradations that we observe in Pennsylvanian naked gondolellids is based on observations and ideas already touched upon: first, the morphologic plasticity exhibited by the Sp and Oz elements, i.e. they are morphologically similar; and second, the concept that the Sp and Oz elements may have been homologous elements that were part of a series consisting on one hand of Oz elements, and on the other of an intergrading series ranging from naked to broad platforms. In this postulated phylogeny two morphotypes, possibly sexual dimorphs (Jeppsson, 1972; Merrill and Merrill, 1974), existed concurrently (Fig. 6) throughout most of the

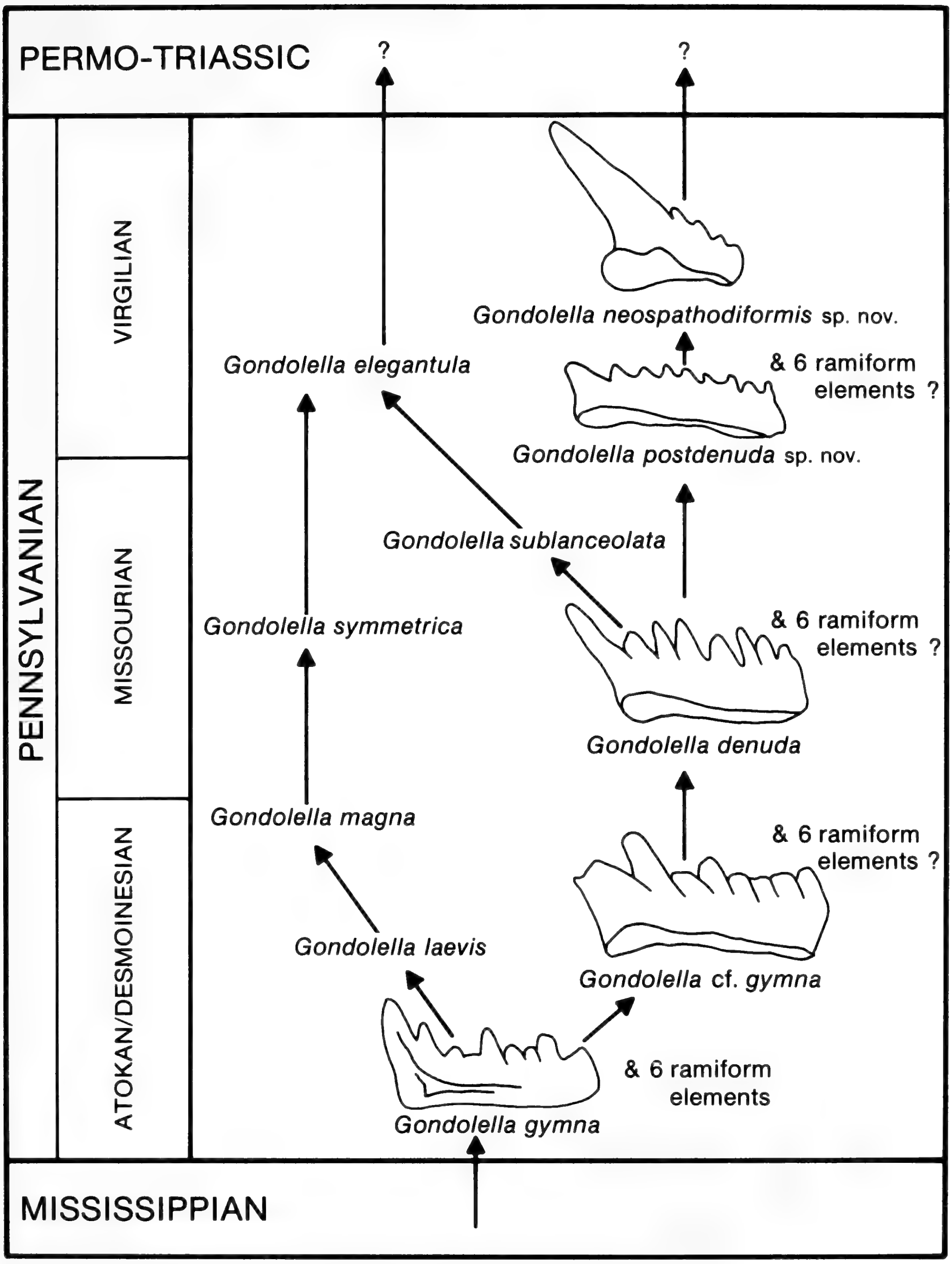


Fig. 4 Evolution of naked species of *Gondolella* by iterative mosaic evolution.

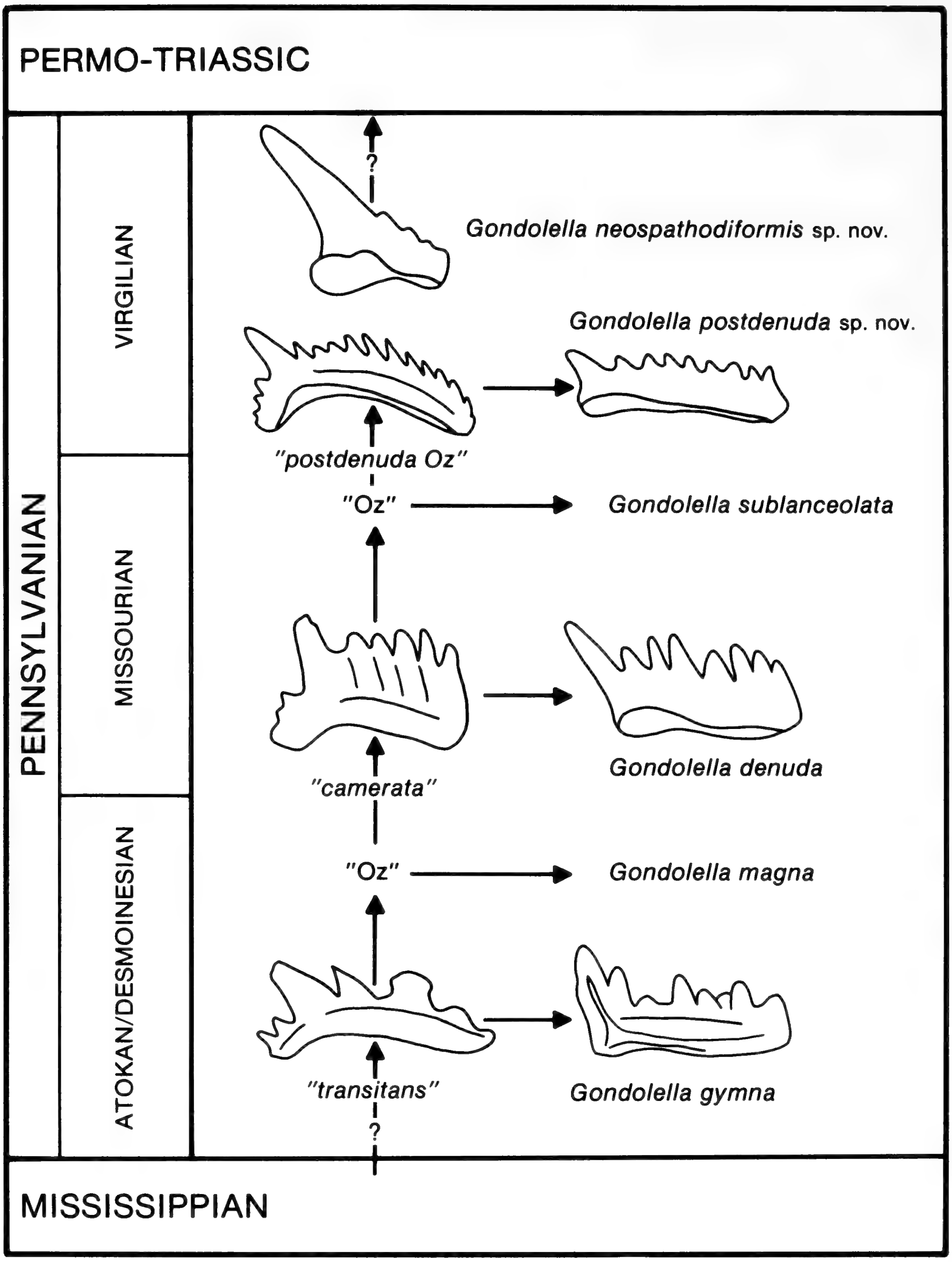


Fig. 5 Evolution of naked and broad-platformed species of *Gondolella* from a stock of Oz-like elements.

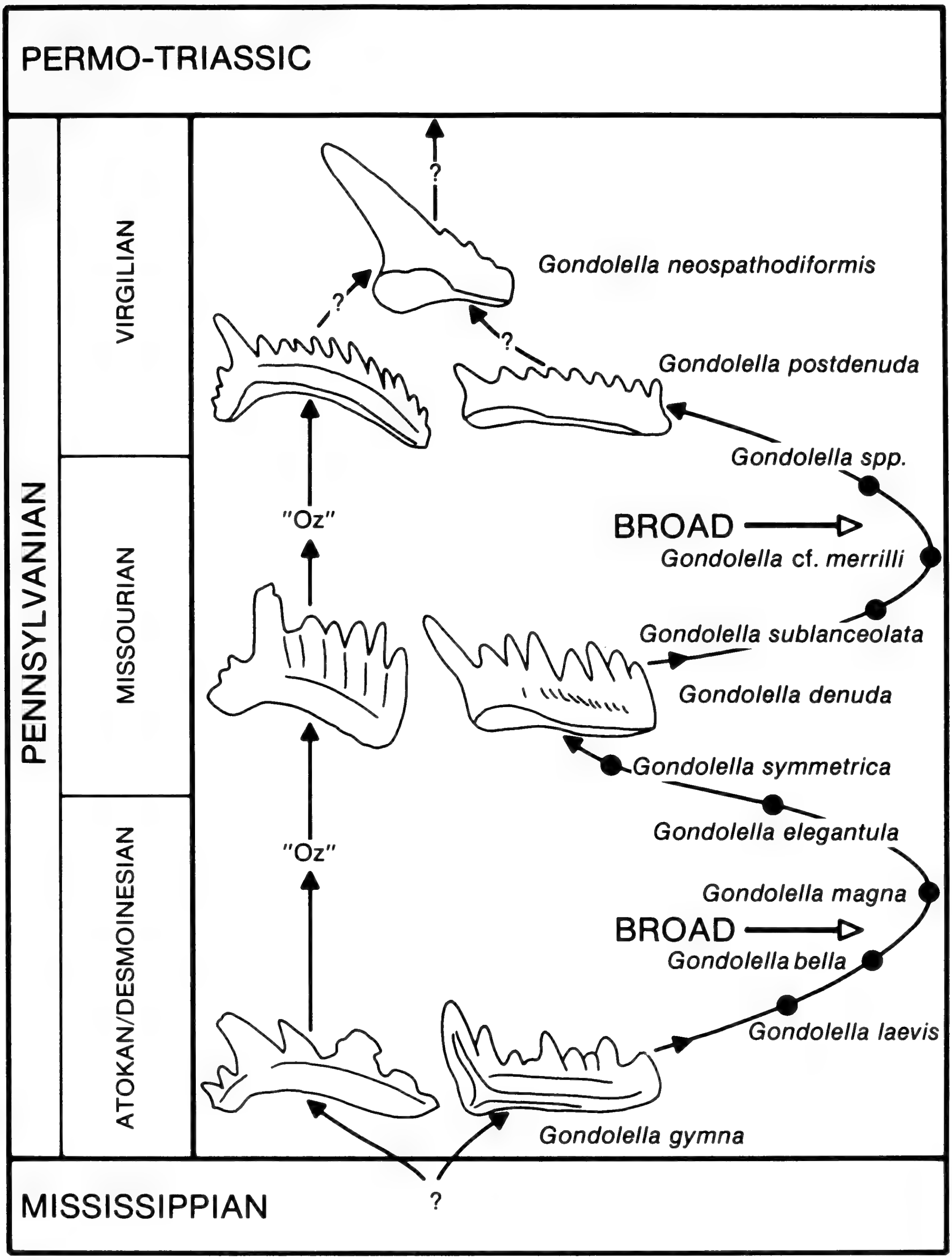


Fig. 6 Evolution of naked species of *Gondolella*. The platform elements are dimorphic and range from being naked to broad-platformed, while the Oz elements remain more or less constant in morphology through time.

Pennsylvanian. One morphotype of this pair (Fig. 6) bore a platform surrogate (the element that we refer to as an Oz element) and as many as five ramiform element types. The other morphotype (Fig. 6) contained the intergrading elements we refer to as the naked and broad-platformed Sp elements, again with as many as five ramiform element types.

This phylogenetic possibility is based not only on the two observations and concepts already outlined but is also dependent on a number of other considerations.

(a) Natural conodont assemblages present on black shale bedding planes from the Stark Shale of Nebraska show the presence of paired Oz elements but lack associated paired platform elements.
(b) Some samples, such as one from the Scammon Formation of western Missouri containing abundant well-preserved Sp elements of *G. laevis*, lack the typical Oz elements that we would have expected in the apparatus of this species. This is despite the fact that Oz elements of another genus, those of species of *Idiognathodus*, are rather abundant in this sample.
(c) The presence of elements having great morphologic similarity in stratigraphic units such as Hushpuckney and Cramer Members of western Missouri and northern Illinois, respectively. More specifically, this refers to naked gondolelliform elements (*G. denuda*) and Oz elements called *Prioniodina* ? *camerata* by Ellison. This point was already raised in the second phylogenetic alternative.
(d) The apparatus of *G. sublanceolata* as reconstructed by von Bitter (1976) contains an element, the Hi element, that functionally could probably have played the part that the Oz element played in the apparatuses of species of *Streptognathodus*, *Idiognathodus*, and *Cavusgnathus* (von Bitter, 1972). The presence of two elements in the above reconstruction that could have taken on this role is anomalous—apparatuses of species of other genera do not have two morphologically similar Oz-like elements. This, added to the fact that most platform-bearing apparatuses usually have a complement of six rather than seven distinct element types (Klapper and Philip, 1971:431–434) supports the possibility that the "*camerata*" element may in fact have functioned in a platform-surrogate role.
(e) Even though Kozur (1976) makes the claim that Permo-Triassic species of *Neospathodus* have an apparatus closely similar in kinds of elements to those of species of *Gondolella*, a number of the species that have been placed in *Neospathodus* (and which we would consider to be Sp elements) strongly resemble the Oz elements of three of the Pennsylvanian naked gondolellid species. This may be support for the idea that these Pennsylvanian Oz elements were functionally Sp rather that Oz elements. This possibility is, of course, exceedingly difficult to demonstrate owing to the fact that even if such dimorphs existed their remains would normally be mixed together after death. If the existence of such dimorphism could be demonstrated by statistical or other means then this knowledge would have considerable impact on the taxonomy of Pennsylvanian gondolellids. For one thing, a number of broad-platformed and naked species would have to be drawn into synonymy.

A consideration of the phylogeny of naked gondolellids has, we believe, important implications for the phylogenies of conodonts both younger and older than those of Pennyslvanian age. Relationships between *Gondolella* and other genera are not known. By pointing out that this group of gondolellids, as distinct from a group of species that more or less cluster about the type species, has some morphologic characters in common with other genera not only suggests possible phylogenetic relationships, but possible similar environmental adaptations as well. In discussing these faunas, nomenclature can, and does, often have an obscuring effect, and it should be noted that once the names are ignored conodont species having many of the characters of naked gondolellids have been found in rocks of Devonian, Mississippian, Permian, and Triassic age. Thus, some species of *Icriodus*, *Pelekysgnathus*, *Eotaphrus*, and *Neospathodus* share important morphologic characteristics with the naked gondolellids, particularly in the aboral loop and the possible presence in some species of *Gondolella* of multiple basal cavity tips. Indeed, Huddle (1934) placed the species *Icriodus nodosa* in *Gondolella* and Butler (1973) placed *Spathognathodus bultyncki* Groessens, a form probably ancestral to the naked gondolellids, in *Pelekysgnathus*.

Spathognathodus bultyncki Groessens (Fig. 13I–L) from the Tournaisian of Belgium has an Sp element morphologically closely comparable to the platform or Sp elements of Pennyslvanian naked gondolellids. Initially, Groessens (1971) included two morphotypes in *Spathognathodus bultyncki*—a platform-like element and a second element bearing a short posterior bar. It was subsequently found (Groessens, 1974) that these two elements have nearly mutually exclusive ranges in Belgium and that in the Lower Carboniferous of some areas, notably in the Canadian Rocky Mountains, the Oz-like element with the posterior bar occurs to the exclusion of the more platform-like element (S. Baxter, pers.comm., 1978). This resulted in two species, *S. bultyncki* and *S.* cf. *bultyncki*, being recognized in Belgium (Groessens, Conil, and Lees, 1973) whereas in the Canadian Mississippian S. Baxter (pers.comm., 1978) is planning to erect a new genus for the Oz-like forms.

It is not known what, if any, ramiform elements were present in the apparatus of *S. bultyncki*. We initially thought that *S. bultyncki* and *S.* cf. *bultyncki* (*sensu* Groessens) could be part of the same apparatus. On the basis of the disparate ranges in Belgium (Groessen, 1974) and the nonoccurrence of the former in the Canadian Rocky Mountains (S. Baxter, pers.comm., 1978), we now believe that this probably represents the start of an evolutionary alternation in which an evolutionary pliable Oz-like element gave rise to a more Sp-like element. This alternation is nearly identical to that which we suggest might have taken place in Pennsylvanian naked gondolellids (Figs. 5, 6).

Spathognathodus bultyncki has not been reported from North America, but *S.* cf. *bultyncki* (*non sensu* Groessens, 1971) (Fig. 13M–N, P–Q) from the Lower Windsor Group of Nova Scotia is very similar and occurs with an Oz element (Fig. 13O) at the single locality from which it is known. It seems likely that these two elements represent the Sp and Oz elements of a single species. *S. bultyncki* Groessens is the best candidate for a Mississippian ancestor for Pennsylvanian naked gondolellids of which we are aware.

Species placed in the Permo-Triassic genus *Neospathodus* Mosher (1968) share many characteristics with the Pennsylvanian naked gondolellids. Not only do they have the typical blade-like form that is not a true platform, but they also have the characteristic loop-like basal cavity. Indeed, there is some question, as is implied by the specific name, of whether *Gondolella neospathodiformis* sp. nov. could not be conveniently placed in what is at present recognized as a Permo-Triassic genus (Sweet *in* Ziegler, 1973). Some species of *Neospathodus* such as *N. pakistanensis* and *N. timorensis* possess short posterior processes. We cannot help but wonder if such elements are homologous in their respective apparatuses to the Oz elements of the naked gondolellid species *G. gymna*, *G. denuda*, and *G. postdenuda*. Alternatively, it may be that these Oz-like elements are not platform surrogates and have taken on the function and position of the platform element as in the fourth and fifth phylogenetic possibilities already outlined. This may be a similar to identical expression of the morphologic (and possibly functional) plasticity and interchangeability postulated between Sp and Oz elements of the naked gondolellids. All of the preceding taken together with Kozur's (1976) claim that the apparatuses of species of *Neospathodus* and *Gondolella* are practically identical may be support for the idea that Pennsylvanian naked gondolellids and Permian and Triassic neospathodids not only are closely related but are part of the same phylogenetic lineage.

Apparatus Element Composition

von Bitter (1972, 1974, 1976) and Merrill (1975) concluded that species of *Gondolella* bore an apparatus consisting of not only a pair of platform (Sp) elements, but also paired and unpaired ramiform elements. von Bitter (1972) was able to partially reconstruct the apparatus of *Gondolella denuda* (*G. postdenuda* sp. nov. herein) and Merrill (1975) reconstructed most of the apparatus of *Gondolella gymna* Merrill and King. Since that time it has been possible to recognize the ramiform elements of *G. postdenuda* sp. nov. as well as those that probably belonged to *G. denuda* Ellison. The uncertainty about the ramiform elements of *G. denuda* stems from the fact that it occurs in the same samples with other, broad platform-bearing species of *Gondolella* and we cannot be sure which ramiform elements belonged with which Sp elements. Some of the ramiform elements almost certainly belonged to *G. denuda*, especially in samples where Sp elements of that species greatly outnumber the Sp elements of all other gondolellid species.

Gondolella gymna, *G. denuda*, and *G. postdenuda* sp. nov. each have similar apparatuses, and the six kinds of ramiform elements cannot generally be distinguished from one species to the next. An exception to this is provided by the Oz elements of the three species. Each mimics the Sp element of the same species and can be distinguished in much the same way as can the respective Sp elements (see Systematic Palaeontology). In general, however, no matter which of the five phylogenetic paths outlined was followed, evolutionary change appears to have been restricted to the paired platform and ozarkodinid elements. *Gondolella neospathodiformis* sp. nov. is known only from Sp elements. The element composition of the naked species, exclusive of *Gondolella neospathodiformis* sp. nov., is directly homologous to that of species of *Gondolella* with broad platforms, as reconstructed for the representative species, *G. sublanceolata*, by von Bitter (1976). The six distinct kinds of ramiform elements present in *G. sublanceolata* (and probably other broad-platformed species of *Gondolella* as well) cannot at present be distinguished from those in the apparatuses of *G. gymna*, *G. denuda*, and *G. postdenuda* sp. nov. This lack of clearcut differences in ramiform element morphology of naked and broad platform-bearing species of *Gondolella* poses problems in apparatus reconstruction when dealing with samples containing both kinds. Fortunately, there are a number of units and/or localities where their occurrence is mutually exclusive, or nearly so, and it is this fact that allows apparatus reconstruction to proceed. For example, although nearly 4000 platform and ramiform elements of the broad-platformed *G. sublanceolata* were recovered from six Pennsylvanian shale samples in western Iowa (von Bitter, 1976; von Bitter and Heckel, 1978) these same samples were totally devoid of the elements of naked gondolellids. The reverse situation has been found to be nearly always true at three localities of the Queen Hill Shale in Kansas and Nebraska (Fig. 1 and Table 2) and to be true in the Seville Member of northwestern Illinois (Fig. 1 and Table 1). The reasons for this mutual exclusiveness are either environmental and/or evolutionary in nature and were discussed in the section dealing with environmental distribution and faunal associates.

The preceding discussion purposely avoids a consideration of the ratios of one element to another present in each of *Gondolella gymna*, *G. denuda*, and *G. postdenuda* sp. nov. It would be unwise to base any discussions regarding such ratios on the material available to us (Tables 1 and 2) because more substantial numerical data are required for such studies.

Systematic Palaeontology

Order Conodontophorida Eichenberg, 1930
Superfamily Gondolellacea Lindström, 1970
Family Gondolellidae Lindström, 1970

Genus *Gondolella* Stauffer and Plummer, 1932

Gondolella Stauffer and Plummer, 1932:41
Illinella Rhodes, 1952:898.

Type Species

Gondolella elegantula Stauffer and Plummer, 1932, by original designation.

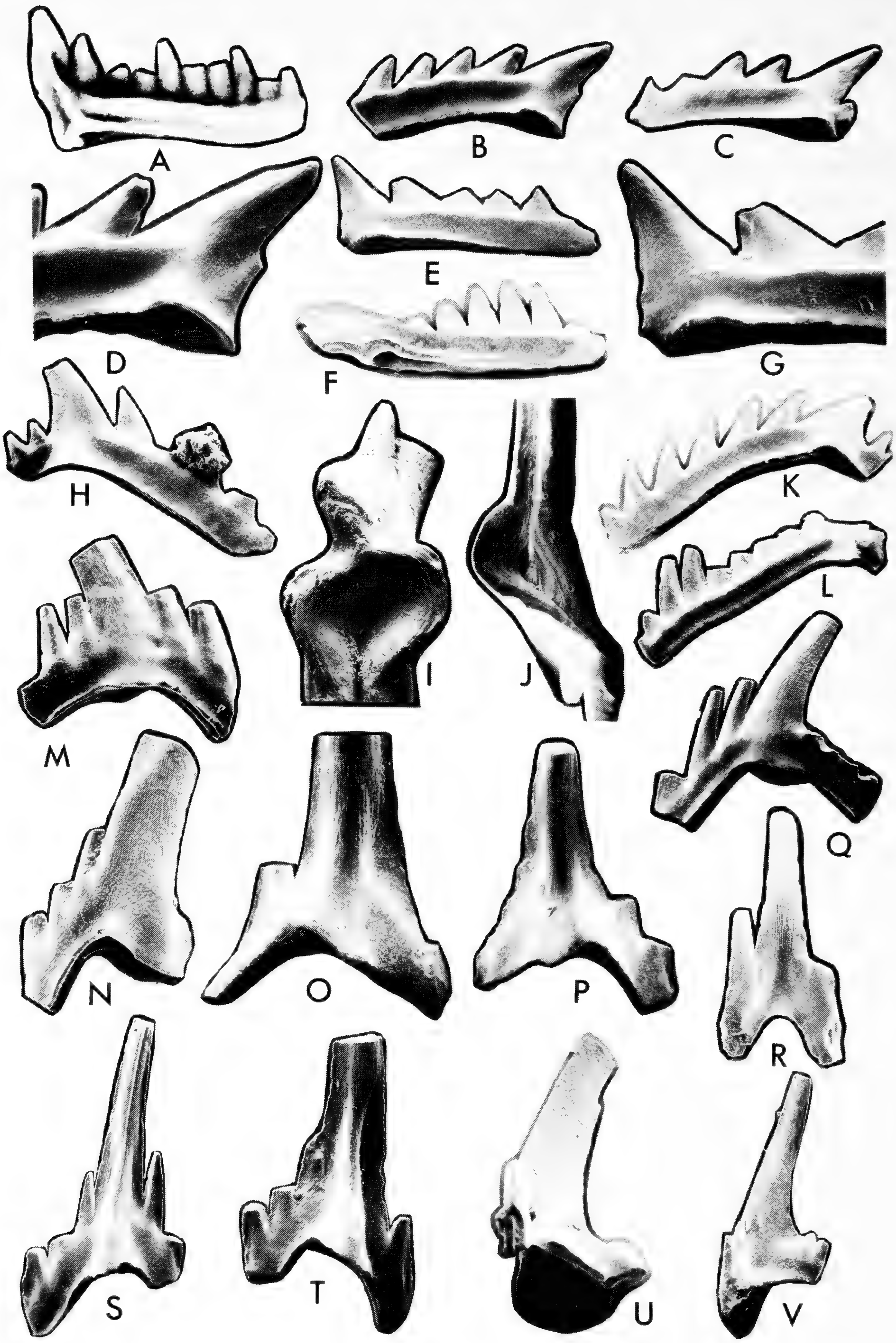
Gondolella gymna Merrill and King, 1971

Diagnosis

A species containing paired Sp, Oz, Lo, Hi, Ne, and Syn elements as well as a probably unpaired bilaterally symmetrical Tr element. Sp element blade-like, narrow, lacking platform, but possessing a conspicuous lateral ridge about two-thirds to three-quarters the height of the blade above the aboral edge and extending the entire length of the anterior blade. A comparison of the Sp element of *G. gymna* with those of *G. denuda* and *G. postdenuda* sp. nov. is provided in Table 3. Sp, Oz, and Hi elements form a symmetry transition as do the Ne and Syn elements.

Sp element (Fig. 7A–G, I)

Gondolella ? sp. A—Koike, 1967:302, pl. 1, figs. 29–32.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Gondolella gymna—Merrill and King, 1971:655, pl. 75, figs. 10–14.
Gondolella gymna—Merrill, 1975:55, fig. 17, only numbers 53 and 55 are Sp elements of *G. gymna*.

Oz element (Figs. 7H, J–L, 10J)

Lonchodina sp. A—Koike, 1967:306, pl. 4, figs. 26–29.
Gondolella gymna—Merrill and King, 1971:655, pl. 75, figs. 7–9.
Lonchodina transitans—Merrill and King, 1971:658, pl. 75, figs. 15–18.

Lo element (Figs. 7N, U, 10K)

Gondolella gymna "Lonchodinid" element—Merrill, 1975:56, fig. 17, no. 51.

Hi element (Fig. 7M, Q)

Gondolella gymna "Lonchodinid-ozarkodinid" element—Merrill, 1975:56, fig. 17, no. 52.

Ne element (Fig. 7O, P)
Syn element (Fig. 7S, T)

Gondolella gymna "Synprioniodinid" element—Merrill, 1975:56, fig. 17, no. 54.

Tr element (Figs. 7R, V, 10L)

Fig. 7 A–V *Gondolella gymna* Merrill and King, Seville Member, Spoon Formation, Kewanee Group, Henry Co., Illinois; locality 14KSSS, sample 14C.

- A Sp element, lateral view of paratype. From Merrill and King (1971: pl. 75, fig. 10), USNM 165023, ×34.
- B Sp element, lateral view, ROM 38061, ×68.
- C Sp element, lateral view, ROM 38062, ×70.
- D Sp element, lateral view, enlargement of posterior end, ROM 38061, ×139.
- E Sp element, lateral view, ROM 38063, ×55.
- F Sp element, aboral-lateral view, ROM 38064, ×42.
- G Sp element, lateral view, enlargement of posterior end, ROM 38063, ×110.
- H Oz element, dextral, outer lateral view, ROM 38065, ×75.
- I Sp element, aboral view, enlargement of posterior end, ROM 38066, ×125.
- J Oz element, dextral, aboral view, enlargement of basal cavity and basal groove, ROM 38067, ×119.
- K Oz element, sinistral, outer lateral view, ROM 38068, ×72.
- L Oz element, sinistral, outer lateral view, ROM 38069, ×37.
- M Hi element, dextral, outer lateral view, ROM 38070, ×87.
- N Lo element, sinistral, outer lateral view, ROM 38071, ×107.
- O Ne element, sinistral, inner lateral view, ROM 38072, ×123.
- P Ne element, dextral, inner lateral view, ROM 38073, ×121.
- Q Hi element, sinistral, outer lateral view, ROM 38074, ×75.
- R Tr element, anterior view, ROM 38075, × 106.
- S Syn element, dextral, inner lateral view, ROM 38076, ×62.
- T Syn element, sinistral, inner lateral view, ROM 38077, ×88.
- U Lo element, aboral, inner lateral view, ROM 38078, ×114.
- V Tr element, lateral view, ROM 38079, ×62.

Table 3 Comparison of the characteristics of the Sp elements of *Gondolella gymna*, *G. denuda*, and *G. postdenuda* sp. nov.

Sp element of *G. gymna* Merrill and King	Sp element of *G. denuda* Ellison	Sp element of *G. postdenuda* sp. nov.
Short denticles	Long denticles	Shortest denticles
Peg-like, only slightly laterally compressed denticles	Elongate, noticeably laterally compressed denticles	Short, laterally compressed denticles
Intermediate number of denticles	Numerous denticles	Fewest denticles
Denticle bases confluent	Denticle bases confluent	Denticle base less confluent
Intermediate length of cusp	Noticeably long cusp	Short, stout cusp
Real posterior process often present	One, rarely two, posterior denticles may be present posterior to cusp	One denticle may be present posterior to cusp
Little arching	Some arching	Some arching
Pronounced lateral ridge	Less pronounced lateral ridge	Less pronounced lateral ridge
Small basal cavity	Large basal cavity	Large basal cavity
Basal cavity not symmetrically rounded and flaring	Basal cavity rounded and flaring	Basal cavity rounded and flaring

DISCUSSION

Sp elements (Fig. 7A–G, I) of this species form a symmetry transition with the Oz element. This element, may, like the Oz element, have several denticles posterior to the cusp (Fig. 7F, I) but is distinguished from the Oz element (Fig. 7H, J–L) by the presence of a closed aboral loop below the cusp (Fig. 7I). The Oz element lacks a closed aboral loop and the basal groove extends into both the anterior and posterior blade (Fig. 7J). The posterior blade of the Oz element and the denticles posterior to the cusp of the Sp element are often missing, the result of structural weakness just posterior to the cusp. The resulting break generally is through the expanded basal cavity below the cusp and often makes it difficult, if not impossible, to state definitely with which of these two elements one is dealing.

The nonplatform elements of *Gondolella gymna* (Fig. 7H, J–V) appear to be completely homologous in kinds of element types present with those of *G. denuda*, *G. postdenuda* sp. nov., and *G. sublanceolata* (von Bitter, 1976), the last a broad-platformed species. Although the ramiform elements of the three gondolellid species bearing naked Sp elements cannot be distinguished from one species to another, an exception to this observation is provided by the Oz element (Fig. 7H, J–L), the characteristics of which are tabulated in Table 4. The Oz element of *G. gymna* is differentiated from that of the younger *G. denuda* by the fact that it possesses fewer, shorter, and more-discrete denticles and by the presence of a strong lateral ridge along the length of the element. The presence of a strong lateral ridge in both the Sp and Oz elements of *G. gymna* (Fig. 7A, B, K, L) is another feature in which these two elements intergrade and mimic one another. With the exception of the Oz element, the ramiform elements of *G. gymna* are apparently indistinguishable from those of *G. denuda* and *G. postdenuda* sp. nov.

Elements of *G. gymna* possess a microsculpture of both parallel and anastomosing ridges (Fig. 10J–L) on their cusps and denticles.

MATERIAL

Figured specimens ROM 38061 to 38079 inclusive; unfigured material ROM 38080 to 38084 inclusive.

DISTRIBUTION

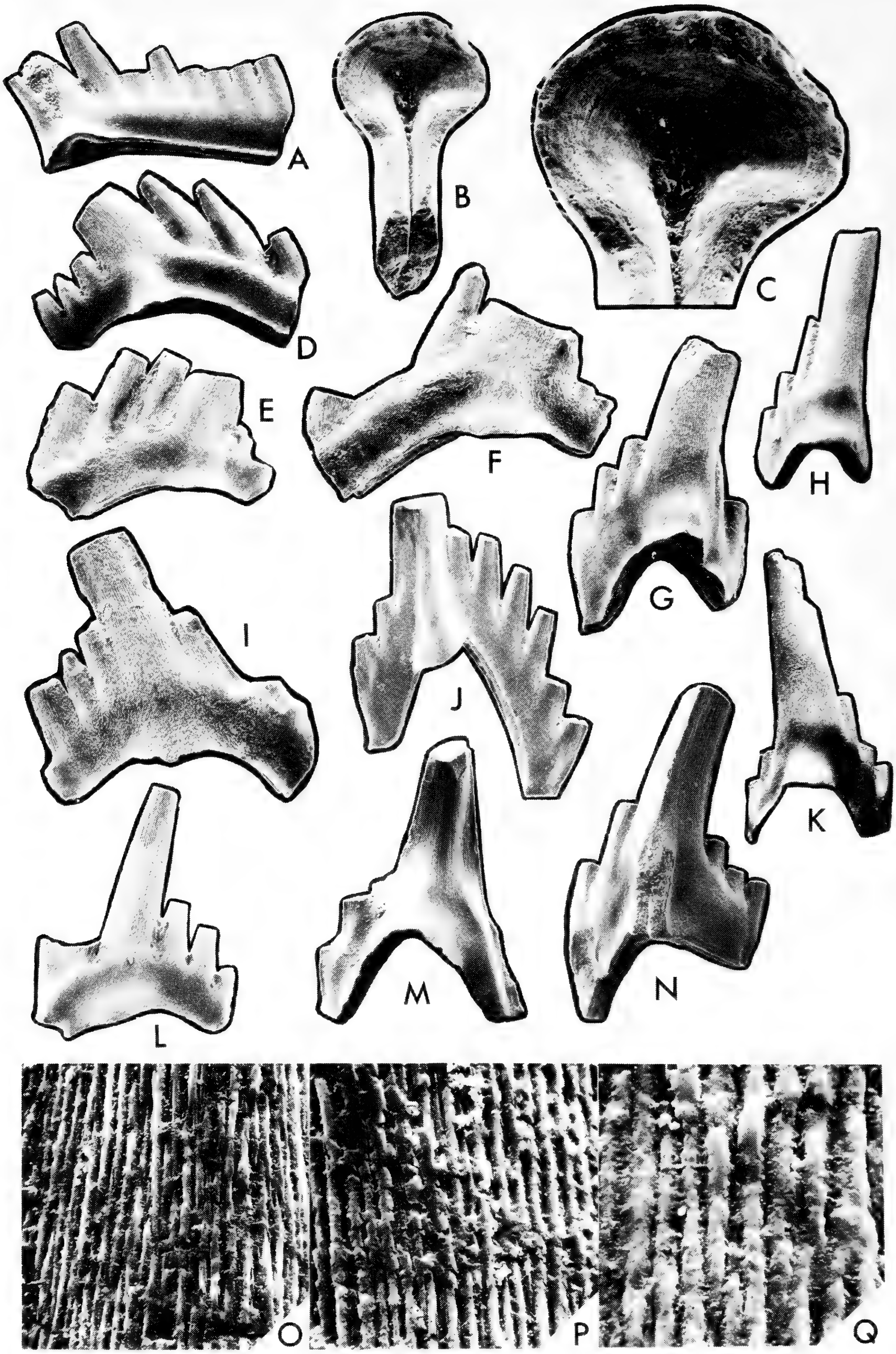
Late Atokan and/or early Desmoinesian of Illinois; late Morrowan to early Atokan, Japan (Fig. 1 and Table 1).

Gondolella cf. *gymna* Merrill and King, 1971

Sp element (Fig. 8A–C, O)

Gondolella gymna—Merrill, 1975:85, fig. 14, no. 22.

?*Gondolella gymna*—Merrill, 1975:85, fig. 16, numbers 38, 39 (probably = Oz elements of *G. bella*).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Possible ramiform elements of *Gondolella* cf. *gymna*.

Oz element (Fig. 8D–F)

?*Gondolella gymna*—Merrill, 1975:85, figs. 14, 23. (Unable to determine from illustration whether complete aboral loop or posterior groove present.)

Lo element (Fig. 8G, H, K, Q)
Hi element (Fig. 8I, L, P)
Ne element (Fig. 8M)
Syn element (Fig. 8J)
Tr element (Fig. 8N)

DISCUSSION

Rare platform specimens (Fig. 8A–C) from the Lonsdale Member in northwestern Illinois and the Holdenville Formation of Jackson Co., Missouri bear a strong

Fig. 8 A–C, O *Gondolella* cf. *gymna* Merrill and King, Sp element, Lonsdale Member, Modesto Formation, McLeansboro Group, Peoria Co., Illinois.
- A Lateral view, locality 2AMGL, sample 2C, ROM 38085, ×59.
- B Aboral view, locality 7AMGL, sample 7D, ROM 38086, ×106.
- C Aboral view, enlargement of aboral view showing basal cavity, locality 7AMGL, sample 7D, ROM 38086, ×209.
- O Detail view of striae on first denticle posterior to the cusp, locality 2AMGL, sample 2C, ROM 38085, ×902.

D–N, P–Q ?Ramiform elements of *Gondolella* cf. *gymna* Merrill and King, Lonsdale Member, Modesto Formation, McLeansboro Group, Peoria Co., Illinois.
- D Oz element, dextral, outer lateral view, locality 2AMGL, sample 2C, ROM 38087, ×55.
- E Oz element, sinistral, outer lateral view, locality 2AMGL, sample 2C, ROM 38088, ×99.
- F Oz element, sinistral, outer lateral view, locality 7AMGL, sample 7D, ROM 38089, ×106.
- G Lo element, sinistral, outer lateral view, locality 7AMGL, sample 7D, ROM 38090, ×114.
- H Lo element, sinistral, outer lateral view, locality 2AMGL, sample 2C, ROM 38091, ×75.
- I Hi element, dextral, outer lateral view, locality 7AMGL, sample 7D, ROM 38092, ×101.
- J Syn element, dextral, inner lateral view, locality 2AMGL, sample 2C, ROM 38093, ×92.
- K Lo element, dextral, outer lateral view, locality 2AMGL, sample 2C, ROM 38094, ×92.
- L Hi element, sinistral, outer lateral view, locality 2AMGL, sample 2C, ROM 38095, ×99.
- M Ne element, sinistral, inner lateral view, locality 2AMGL, sample 2C, ROM 38096, ×119.
- N Tr element, lateral view, locality 2AMGL, sample 2C, ROM 38097, ×132.
- P Hi element, detail view of striae on cusp, locality 7AMGL, sample 7D, ROM 38092, ×902.
- Q Lo element, detail view of striae on cusp, locality 2AMGL, sample 2C, ROM 38091, ×2200.

Table 4 Comparison of the characteristics of the Oz elements of *Gondolella gymna*, *G. denuda*, and *G. postdenuda* sp. nov.

Oz element of *G. gymna* Merrill and King	?Oz element of *G. denuda* Ellison	Oz element of *G. postdenuda* sp. nov.	
Short denticles	Long denticles	Short denticles	Oz elements of species of *Gondolella* that bear broad platforms (*G. bella*, *G. elegantula*, *G. sublanceolata*, etc.) most closely resemble the Oz elements of the naked species that occur nearest them stratigraphically.
Peg-like, only slightly laterally compressed	Laterally compressed	Laterally compressed	
Intermediate number of denticles	Numerous denticles	Fewest denticles	
Denticle bases confluent	Denticle bases confluent	Denticle bases confluent in a web-like manner	
Intermediate length cusp	Long cusp	Intermediate length cusp	
Relatively strong posterior bar	Strong posterior bar	Weak posterior bar	
Arched	Arched	Arched	
Pronounced lateral ridge	Unpronounced lateral ridge	Weak lateral ridge	
Basal cavity subtriangular extending into anterior and posterior bars	Basal cavity subtriangular extending into anterior and posterior bars	Basal cavity subtriangular extending into anterior and posterior bars	

resemblance to the Sp element of *Gondolella gymna* in being laterally compressed with a strong lateral ridge, moderately long denticles and cusp, and in possessing a closed, aboral, loopshaped basal cavity (Fig. 8B, C). These specimens are far removed stratigraphically from typical *G. gymna* (latest *versus* earliest Desmoinesian) and are indeed closer in age to *G. denuda* (early Missourian), which they do not closely resemble. Our tentative assignment results from several factors including stratigraphic separation, lack of specimens of the species from intervening collections of gondolellids, and a paucity of these specimens in our collections. We have been unable to document any specimens of this morphology that Merrill (1975) reported from the Hanover Member. As suggested in the synonymy above it seems likely that the specimens reported on by Merrill (1975) were Oz elements of the broad platform-bearing species, *G. bella*, rather than being narrow Sp elements similar to those that characterize *G. gymna*.

The ramiform elements illustrated under this taxonomic category (Fig. 8D–N) cannot be assigned with certainty to *G.* cf. *gymna* since broad-platformed species of *Gondolella* are abundant in the Lonsdale and Holdenville samples from which the narrow-platformed element has been recovered (Table 1). These ramiform elements could, therefore, also belong to these broad-platformed species (von Bitter, 1976).

Both the platform elements assigned to *G.* cf. *gymna* as well as the ramiform elements that cannot be assigned with certainty to this taxon exhibit a microsculpture of parallel and anastomosing ridges (Fig. 8O–Q).

MATERIAL

Figured specimens ROM 38085 to 38097 inclusive; unfigured material ROM 38098 to 38099, and 38165.

DISTRIBUTION

Late Desmoinesian of Illinois and Missouri.

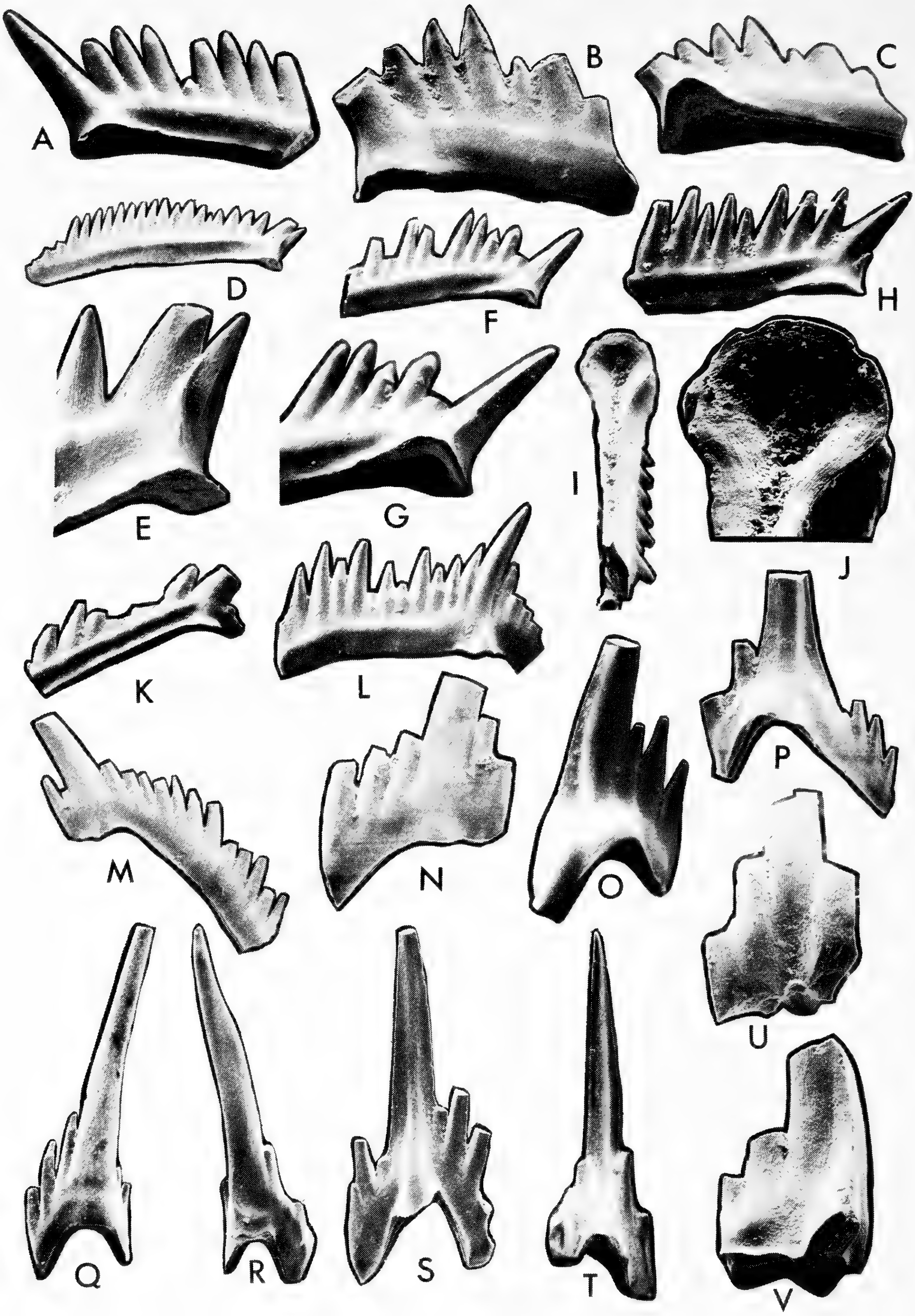
Gondolella denuda **Ellison, 1941**

Diagnosis

A species containing paired Sp, Oz, Lo, Hi, Ne, and Syn elements as well as probably an unpaired bilaterally symmetrical Tr element. Sp element blade-like, narrow, lacking platform. Lateral ridge of both Sp and Oz elements less pronounced than that of the corresponding elements of *G. gymna*. Characterized by possessing numerous long denticles discrete over most of their length in both Sp and Oz elements. Sp, Oz, and Hi elements form symmetry transition, as do Ne and Syn elements.

Sp element (Figs. 9A–J, 10A–D, G)

Gondolella denuda—Ellison, 1941:127, pl. 20, fig. 54; pl. 21, figs. 1, 2, 36.
Gondolella denuda—Branson, 1944:308, 325, pl. 45, figs. 1, 2, 36.
Gondolella denuda—Clark and Mosher, 1966:385, pl. 46, figs. 15–19.
Gondolella denuda—Sweet (*in* Ziegler, 1973):103, pl. 1, fig. 5.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Possible ramiform elements of *Gondolella denuda* Ellison.

Oz element (Fig. 9K–L; 10G)

Prioniodina ? camerata—Ellison, 1941:118, pl. 21, fig. 49.

Syn element (Fig. 9S–T)

Synprioniodina microdenta—Ellison, 1941:119, pl. 20, figs. 43, 44, ?45, ?46.

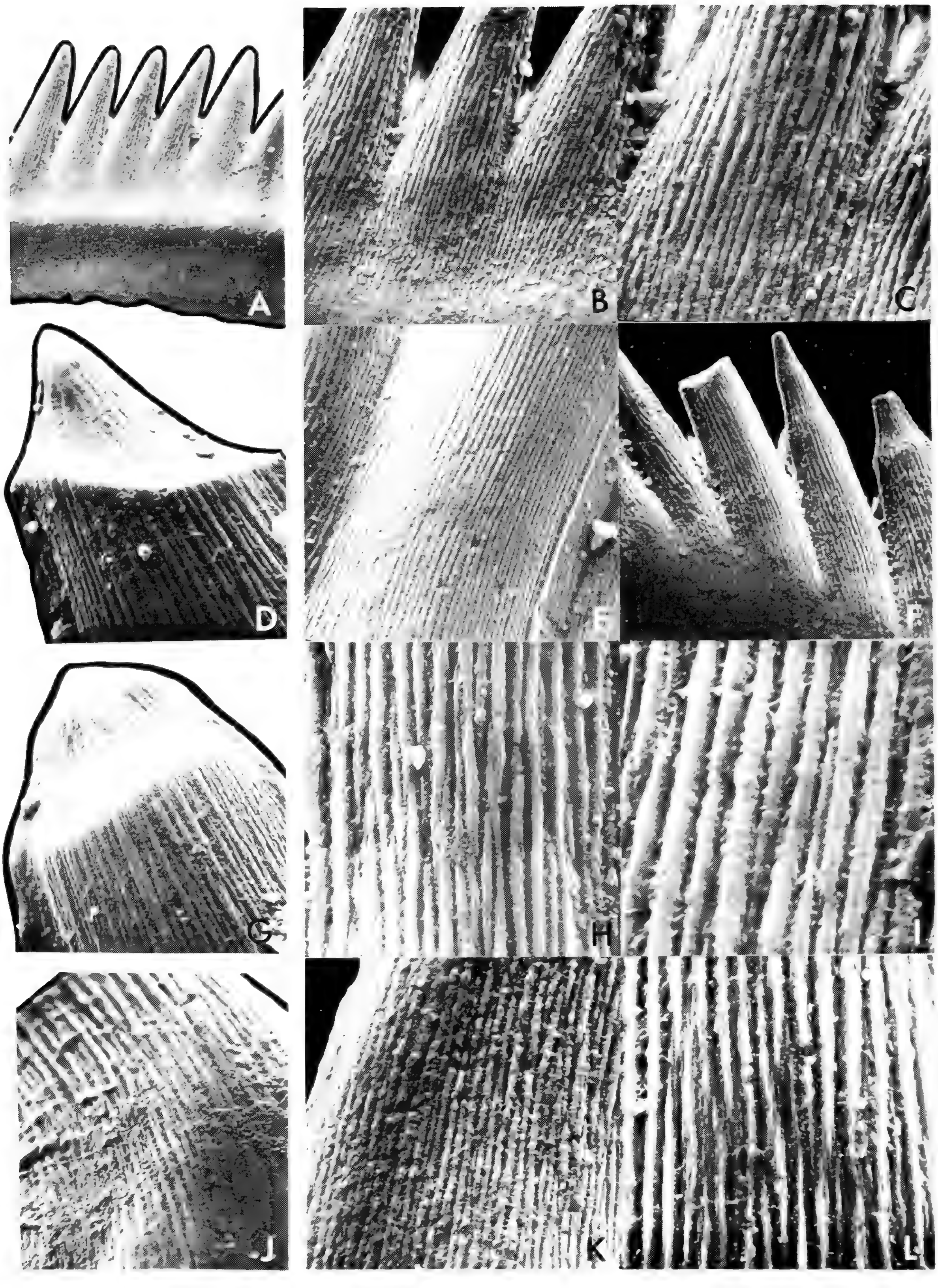
Lo element (Fig. 9Q–R; 10I)
Hi element (Figs. 9M–N, 10F)
Ne element (Figs. 9O–P, 10H)
Tr element (Fig. 9U–V)

Fig. 9 A–J *Gondolella denuda* Ellison.

- A Sp element, lateral view, Cramer Member, Modesto Formation, McLeansboro Group, Bureau Co., Illinois, locality 2AMTC, sample 2B, ROM 38100, ×49.
- B Sp element, lateral view, Lower Brush Creek Member, Conemaugh Group, Muskingum Co., Ohio, locality 39LBCLS, sample 39B, ROM 38101, ×74.
- C Sp element, lateral-aboral view, Lower Brush Creek Member, Conemaugh Group, Muskingum Co., Ohio, locality 39LBCLS, sample 39B, ROM 38101, ×67.
- D Sp element, lateral view, Cramer Member, Modesto Formation, McLeansboro Group, Bureau Co., Illinois, locality 2AMTC, sample 2C, ROM 38102, ×32.
- E Sp element, enlargement of posterior end, Cramer Member, Modesto Formation, McLeansboro Group, Bureau Co., Illinois, locality 2AMTC, sample 2C, ROM 38102, ×125.
- F Sp element, lateral view, Hushpuckney Member, Swope Formation, Kansas City Group, Jackson Co., Missouri, locality 8MKSH, sample 8A, ROM 38103, ×38.
- G Sp element, enlargement of posterior end, Hushpuckney Member, Swope Formation, Kansas City Group, Jackson Co., Missouri, locality 8MKSH, sample 8A, ROM 38103, ×80.
- H Sp element, lateral view, Cramer Member, Modesto Formation, McLeansboro Group, Bureau Co., Illinois, locality 2AMTC, sample 2A, ROM 38104, ×57.
- I Sp element, aboral view, Cramer Member, Modesto Formation, McLeansboro Group, Bureau Co., Illinois, locality 2AMTC, sample 2A, ROM 38105, ×68.
- J Sp element, enlargement of aboral view showing basal cavity, Cramer Member, Modesto Formation, McLeansboro Group, Bureau Co., Illinois, locality 2AMTC, sample 2A, ROM 38105, ×186.

K–V ?Ramiform elements of *Gondolella denuda* Ellison, Cramer Member, Modesto Formation, McLeansboro Group, Bureau Co., Illinois.

- K Oz element, sinistral, outside lateral view, locality 2AMTC, sample 2A, ROM 38106, ×37.
- L Oz element, sinistral, outside lateral view, locality 2AMTC, sample 2C, ROM 38107, ×37.
- M Hi element, dextral, outer lateral view, locality 2AMTC, sample 2C, ROM 38108, ×44.
- N Hi element, sinistral, outer lateral view, locality 2AMTC, sample 2A, ROM 38109, ×88.
- O Ne element, dextral, inner lateral view, locality 2AMTC, sample 2A, ROM 38110, ×75.
- P Ne element, sinistral, inner lateral view, locality 2AMTC, sample 2A, ROM 38111, ×110.
- Q Lo element, sinistral, outer lateral view, locality 2AMTC, sample 2A, ROM 38112, ×63.
- R Lo element, dextral, outside lateral view, locality 2AMTC, sample 2A, ROM 38113, ×55.
- S Syn element, dextral, inner lateral view, locality 2AMTC, sample 2A, ROM 38114, ×69.
- T Syn element, sinistral, inner lateral view, locality 2AMTC, sample 2C, ROM 38115, ×59.
- U Tr element, anterior view, locality 2AMTC, sample 2C, ROM 38116, ×125.
- V Tr element, lateral view, locality 2AMTC, sample 2A, ROM 38117, ×125.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DISCUSSION

The Sp element of *Gondolella denuda* was described in detail by Ellison (1941:107). This description and/or the figures were republished by Branson (1944), Clark and Mosher (1966:385), and Sweet (*in* Ziegler, 1973). It is distinguished from the Sp element of other naked species by the presence of long discrete denticles (Fig. 9A–D, G) as well as other features such as the lack of a pronounced lateral ridge (Table 3). The Oz element of *G. denuda* is similarly distinguished from the Oz element of other naked species of *Gondolella* by the fact that it, like the Sp element of the species, bears rather long discrete denticles (Fig. 9K–L) (a feature that was well shown by Ellison [1941:21, fig. 49]) and also by the lack of a pronounced lateral ridge (Fig. 9K–L). The remaining ramiform elements of this species cannot be distinguished at present from those of broad-platformed species of *Gondolella* (von Bitter, 1976) with which they occur (Table 2).

Ellison (1941) described evolutionary transitions between *G. denuda* and *Prioniodina* ? *camerata* on one hand, and between *G. denuda* and *G. symmetrica* on the other. The first instance is clearly an example of the kind of morphologic plasticity recognized between the Sp and Oz elements of three of the four naked gondolellid species studied. It may represent the morphologic intergradation commonly observed in symmetry transitions found in the elements of conodont species, or as discussed in the phylogenetic section, may represent an instance of functional substitution. The second case, i.e. the transition between the Sp element of *G. denuda* and that of *G. symmetrica*, cannot be documented even after having resampled Ellison's localities.

Fig. 10 A–C *Gondolella denuda* Ellison, Sp element, lateral view, detail of denticles, Cramer Member, Modesto Formation, McLeansboro Group, Henry Co., Illinois, locality 2AMTC, sample 2C.

- A ROM 38102, ×125.
- B ROM 38102, ×317.
- C ROM 38102, ×627.

D, G *Gondolella denuda* Ellison, Sp element, lateral view, detail of denticle showing repair, Hushpuckney Member, Swope Formation, Kansas City Group, Jackson Co., Missouri, locality 8MKSH, sample 8A.

- D ROM 38103, ×770.
- G ROM 38103, ×770.

E, F, H, I ?Ramiform elements of *Gondolella denuda* Ellison, Cramer Member, Modesto Formation, McLeansboro Group, Bureau Co., Illinois, locality 2AMTC.

- E Oz element, lateral detailed view of base of cusp, sample 2C, ROM 38107, ×374.
- F Hi element, lateral detailed view of denticles, sample 2C, ROM 38108, ×220.
- H Ne element, lateral view, detail of cusp, sample 2A, ROM 38110, ×1518.
- I Lo element, outer lateral view, detail of cusp, sample 2A, ROM 38112, ×2200.

J–L *Gondolella gymna* Merrill and King, Seville Limestone, Spoon Formation, Kewanee Group, Henry Co., Illinois, locality 14KSSS, sample 14C.

- J Oz element, lateral view, detail of cusp, ROM 38065, ×726.
- K Lo element, lateral view, detail of cusp, ROM 38071, ×528.
- L Tr element, anterior view, detail of cusp, ROM 38075, ×1056.

MATERIAL

Figured specimens ROM 38100 to 38117 inclusive; unfigured material ROM 38118 to 38124 inclusive and ROM 38167 to 38171 inclusive.

DISTRIBUTION

Lower Missourian of eastern Ohio, northern Illinois, eastern Nebraska, and western Missouri (Fig. 1 and Table 2).

Gondolella postdenuda sp. nov.

Figs. 11, 12

Diagnosis

A species containing paired Sp, Oz, Lo, Hi, Ne, and Syn elements as well as a probably unpaired bilaterally symmetrical Tr element. Sp element blade-like, narrow, lacking platform. Lateral ridge not as pronounced as in *G. gymna*. Main cusp of Sp element shorter than that of *G. denuda* and denticles noticeably shorter and stubbier than in the latter species. Stubby main cusp of Sp element circular to subcircular in cross-section, lacking ridge parallel to its length, as in some specimens of *G. gymna*. Tables 3 and 4 provide a comparison of the characteristics of the Sp and Oz elements of this species with those of *G. gymna* and *G. denuda*.

Sp element (Figs. 11A–H, R, 12A–D)

Gondolella denuda, Sp element—von Bitter, 1972:68, pl. 6, fig. 1a–f.

Oz element (Fig. 11I–J, N, 12E–J)

Gondolella denuda, Oz element—von Bitter, 1972:68, pl. 6, fig. 3a, b.

Lo element (Fig. 11P–Q, S)

Gondolella denuda, Hi? element—von Bitter, 1972:68, pl. 8, fig. 4a, b.

Hi element (Fig. 11K)
Ne element (Fig. 11O)
Syn element (Fig. 11L)
Tr element (Fig. 11M, T)

DESCRIPTION

The Sp element (Fig. 11A–H) of this species is elongate and slightly arched. The element is blade-like and lacks any broadening that could be construed as a platform (Fig. 11H). A lateral ridge extends the full length of the anterior blade halfway between the base of the denticles and the aboral edge. The cusp is posteriorly inclined and is very slightly laterally compressed. Although stouter than the blade denticles, the cusp is generally not much longer than the longest of the series. The blade denticles are also slightly compressed laterally, are short and stubby and reach their maximum length at about the middle of the element. The three or four denticles nearest to the cusp are directed posteriorly whereas the remainder are often nearly vertical. The number of anterior blade denticles varies from seven in small specimens (Fig. 11E) to fourteen in larger specimens (Fig. 11A). There is no posterior blade present although in some Sp elements there is a single small denticle posterior to the cusp (Fig. 11B).

Aborally the Sp element bears a typically gondolellid basal cavity under the cusp (Fig. 11G). The walls of the basal cavity flare outward making this the broadest point of the entire element. The margins of the basal cavity are slightly inverted to form a "lip". Although not generally visible, the basal cavity tip is a rather broad, relatively shallow structure that extends into the cusp. Anteriorly, the basal cavity decreases in width to form a basal groove which extends the full length of the element (Fig. 11G).

The Sp elements are transparent and light brown in colour except in the upper halves of the cusp and some denticles that are white and translucent.

The ramiform elements of *G. postdenuda* sp. nov. (Fig. 11I–Q) appear to be morphologically identical to those of *G. denuda* and *G. gymna* and cannot be distinguished from the nonplatform elements of these two species or of gondolellid species with broad platforms (see von Bitter, 1976). The only exception to this generalization is that the Oz element of *G. postdenuda* sp. nov. can be distinguished from those of *G. gymna* and *G. denuda*. As indicated in Table 4, the Oz element of *G. postdenuda* sp. nov., like the Sp element of that species, has shorter, less fused denticles (Fig. 11I, J) than do both the Sp and Oz elements of *G. denuda*.

The microsculpture of anastomosing and parallel striae is not as well developed in elements of *G. postdenuda* sp. nov. (Fig. 11R–T) as it is in *G. gymna*, *G. denuda*, and *G. neospathodiformis* (Fig. 13A). An unusual feature of the microsculpture of elements of this species is the presence of a hexagonal "honeycomb" structure (Figs. 11R, 12) on elements from Elk Co., Kansas. These hexagonal pits are at present interpreted to be the result of the resorption of calcium phosphate crystallites by the conodont animal.

ETYMOLOGY

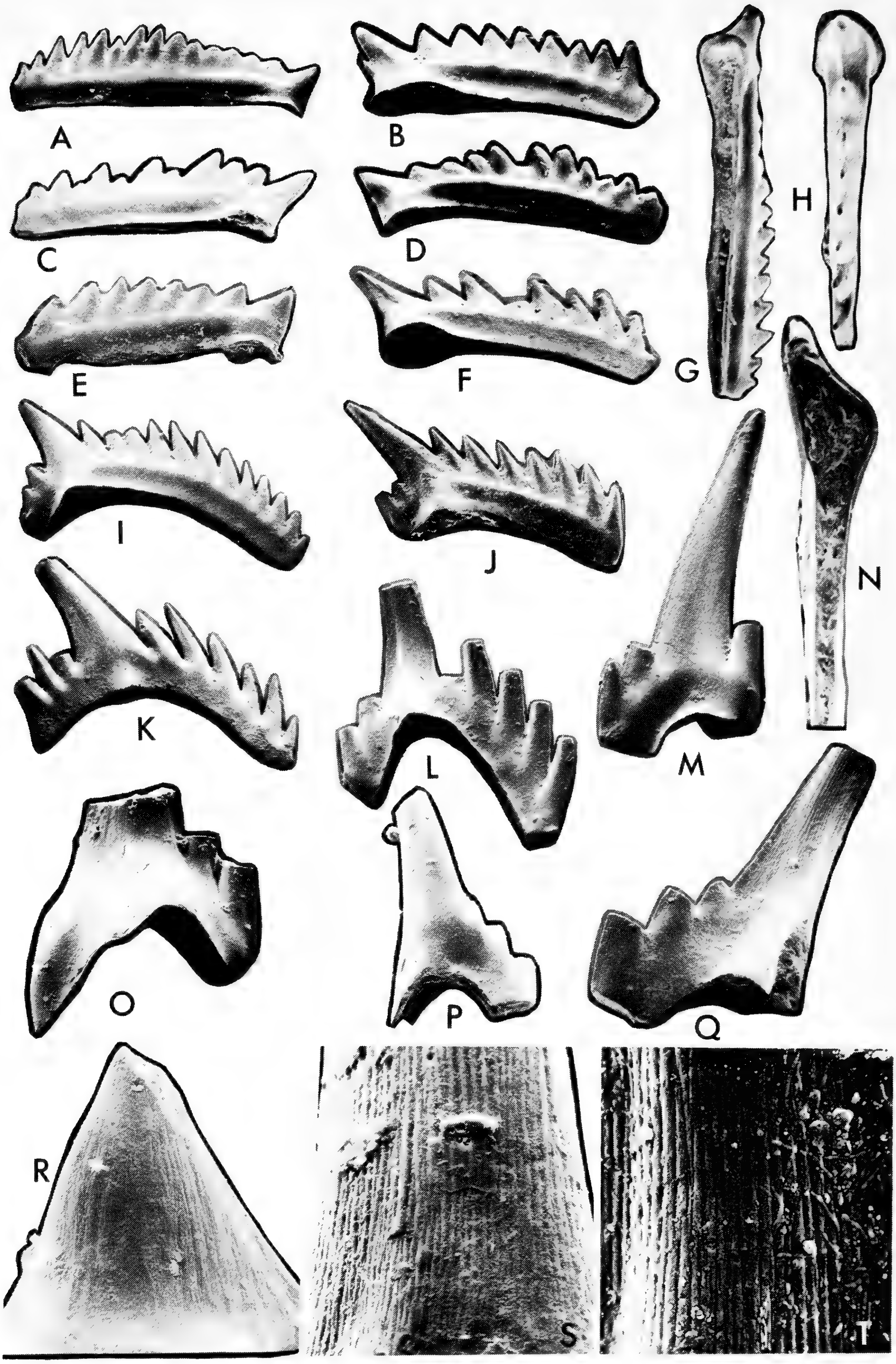
Latin—post, after; alluding to the younger geologic age of the new species; *denuda*—the name of Ellison's species.

MATERIAL

Figured specimens ROM 38125 (holotype), ROM 38126 to 38136 inclusive (paratypes), UKMIP (University of Kansas Museum of Invertebrate Paleontology) 1,900,967 to 1,900,969 inclusive and UKMIP 1,900,997; unfigured paratypes ROM 38137 to 38149 inclusive and ROM 28733, 28717, and 38166.

DISTRIBUTION

Virgilian of Nebraska, Kansas, and Texas.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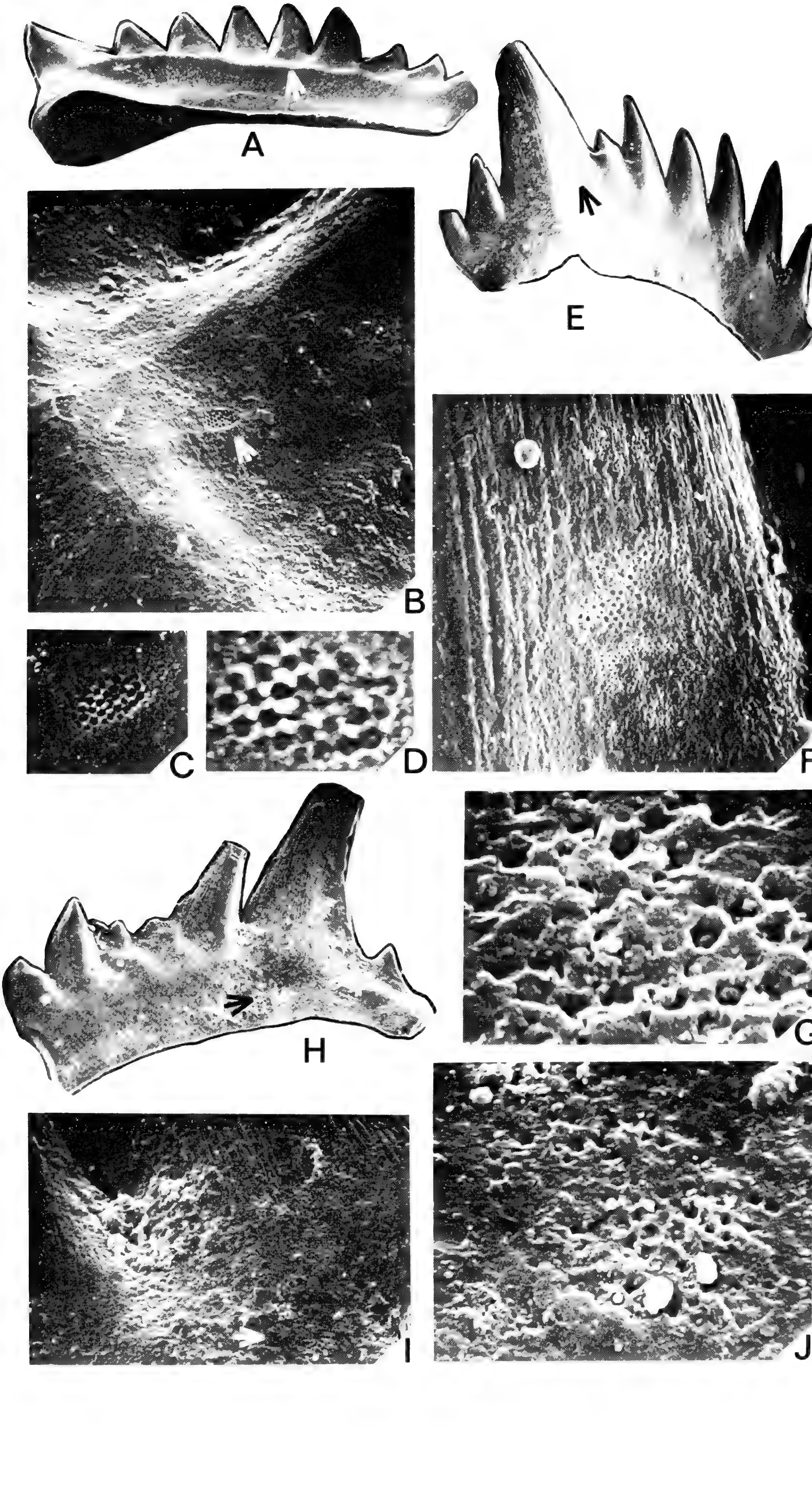
Gondolella neospathodiformis sp. nov.
Fig. 13A–H

Diagnosis

A species based solely on very small, short, Sp elements that apparently lacked associated ramiform elements. Sp element narrow, blade-like, without true platform, lacking lateral ridge; dominated by large, single, laterally compressed cusp under which is a nearly circular basal cavity. Basal cavity forms aboral loop posteriorly and narrows anteriorly into a basal groove of a blade-like, weakly denticulate anterior bar. No posterior blade present.

Fig. 11 A–T *Gondolella postdenuda* sp. nov., Queen Hill Shale, Lecompton Formation, Shawnee Group, Kansas.

- A Sp element, lateral view, paratype, Douglas Co., locality QH-1, sample QH-1-2, UKMIP 1,900,967, ×101.
- B Sp element, lateral view, holotype, Douglas Co., locality QH-1, sample QH-1-2, ROM 38125, ×74.
- C Sp element, lateral view, paratype, Douglas Co., locality QH-1, sample QH-1-2, UKMIP 1,900,968, ×129.
- D Sp element, lateral view, paratype, Douglas Co., locality QH-1, sample QH-1-2, ROM 38126, ×53.
- E Sp element, lateral view, paratype, Douglas Co., locality QH-1, sample QH-1-2, UKMIP 1,900,969, ×121.
- F Sp element, aboral-lateral view, paratype, Elk Co., locality QH-2, sample QH-2-3, ROM 38127, ×87.
- G Sp element, aboral view, paratype, Douglas Co., locality QH-1, sample QH-1-2, UKMIP 1,900,967, ×118.
- H Sp element, oral view, paratype, Douglas Co., locality QH-1, sample QH-1-2, UKMIP 1,900,969, ×175.
- I Oz element, dextral, outer lateral view, paratype, Elk Co., locality QH-2, sample QH-2-3, ROM 38128, ×67.
- J Oz element, dextral, outer lateral view, paratype, Douglas Co., locality QH-1, sample QH-1-2, UKMIP 1,900,997, ×179.
- K Hi element, dextral, outer lateral view, paratype, Elk Co., locality QH-2, sample QH-2-3, ROM 38129, ×92.
- L Syn element, dextral, inner lateral view, paratype, Elk Co., locality QH-2, sample QH-2-3, ROM 38130, ×92.
- M Tr element, lateral view, paratype, Elk Co., locality QH-2, sample QH-2-3, ROM 38131, ×109.
- N Oz element, dextral, aboral view, paratype, Douglas Co., locality QH-1, sample QH-1-2, UKMIP 1,900,997, ×264.
- O Ne element, dextral, inner lateral view, paratype, Elk Co., locality QH-2, sample QH-2-3, ROM 38132, ×154.
- P Lo element, dextral, outer lateral view, paratype, Elk Co., locality QH-2, sample QH-2-3, ROM 38133, ×121.
- Q Lo element, dextral, inner lateral view, paratype, Elk Co., locality QH-2, sample QH-2-3, ROM 38133, ×165.
- R Sp element, detail of cusp showing relative smoothness and location of "honeycomb" structure; paratype, Douglas Co., locality QH-1, sample QH-1-2, ROM 38126, ×440.
- S Lo element, dextral, outer lateral view, detail of cusp, paratype, Elk Co., locality QH-2, sample QH-2-3, ROM 38133, ×603.
- T Tr element, lateral view, detail of cusp, paratype, Elk Co., locality QH-2, sample QH-2-3, ROM 38131, ×880.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DESCRIPTION

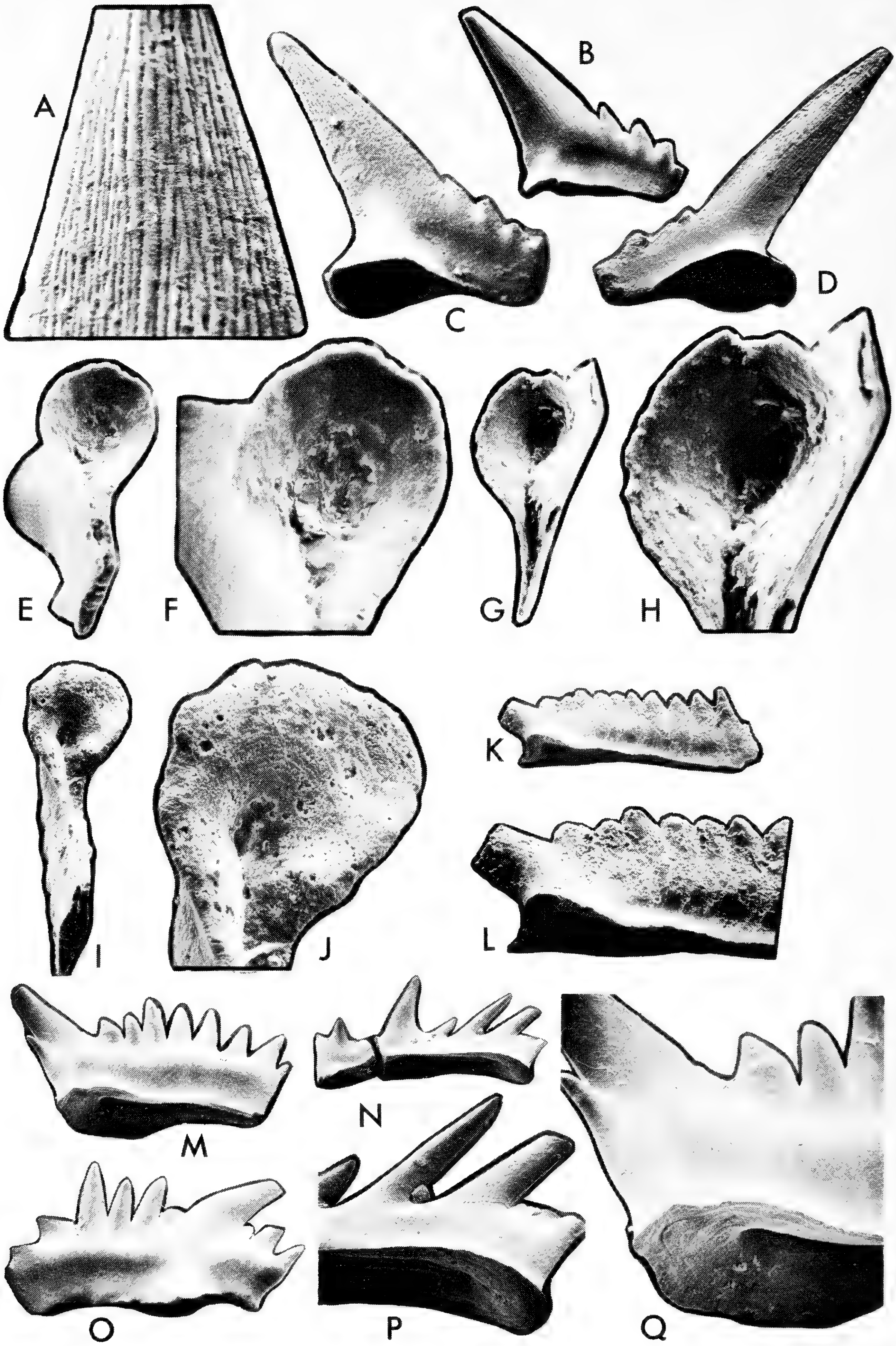
An unusually small species which has a large, laterally compressed, and thus sharp-edged, cusp (Fig. 13B–D). Posteriorly directed cusp is milky white and translucent over most of its length becoming light brown and transparent at a point just above the junction between the cusp and the highest denticle. The lower demarcation of the white matter is relatively sharp and is nearly perpendicular to the length of the cusp. Below this point the element is transparent and light brown in colour. This distribution of colour and diaphaneity is characteristic of the elements of species of *Gondolella* (von Bitter, 1972:68; 1976:5, 6). Anterior to the cusp there is a short blade bearing up to five small transparent denticles (Fig. 13B–D). There is no posterior blade present.

The overall element is, like the cusp, laterally compressed and there is no evidence of the lateral ridge below the denticles that is present on the Sp elements of the three other gondolellid species described. Not only are the Sp elements of this species small but they are also unusually abbreviated, consisting of little else but a large laterally compressed cusp, a short denticulated anterior blade, and a circular basal cavity. The last-mentioned is characteristic for the Sp elements of gondolellid species. The circular basal cavity opens anteriorly into a narrow aboral groove (Fig. 13E–H). A basal cavity tip extends at right angles to the aboral margin from the top of the basal cavity a short distance into the cusp. The microsculpture of this species (Fig. 13A) is similar to that of the other naked gondolellids (this study) and to that of broad-platformed gondolellids (von Bitter, 1976).

DISCUSSION

The above description cannot be applied to any other known Sp (or other) conodont element. The material on which the description of this species is based is exquisitely preserved and is morphologically distinct. The 20 specimens of this species are not fragmentary and to the best of our knowledge there were no other element types present in the apparatus of this species. This is a conclusion that we have reached in spite of the fact that *G. gymna*, *G. denuda*, *G.* cf. *denuda*, and *G. postdenuda* sp. nov. are now known to have had a variety of elements in their apparatuses.

Fig. 12 A–J *Gondolella postdenuda* sp. nov., paratypes, Queen Hill Shale, Lecompton Formation, Shawnee Group, Elk Co., Kansas, locality QH-2, sample QH-2-3.
- A Sp element, lateral-aboral view, ROM 38134, ×144.
- B Sp element, detail of base of fourth denticle posterior to the cusp showing location of "honeycomb" structure, ROM 38134, ×2810.
- C Sp element, enlargement of "honeycomb" structure, ROM 38134, ×3701.
- D Sp element, enlargement of "honeycomb" structure, ROM 38134, ×9880.
- E Oz element, dextral, outside lateral view, ROM 38135, ×208.
- F Oz element, dextral, outside lateral view, "honeycomb" structure on cusp, ROM 38135, ×1477.
- G Oz element, dextral, outside lateral view, enlargement of "honeycomb" structure, ROM 38135, ×7588.
- H Oz element, dextral, inside lateral view, ROM 38136, ×399.
- I Oz element, dextral, inside lateral view, "honeycomb" structure at base of cusp, ROM 38136, ×689.
- J Oz element, dextral, inside lateral view, enlargement of "honeycomb" structure, ROM 38136, ×3547.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ETYMOLOGY

With reference to the morphology of this species which is suggestive of species of *Neospathodus* Mosher.

MATERIAL

Figured specimens ROM 38150 (holotype), ROM 38151 to 38154 inclusive (paratypes); unfigured paratypes ROM 38155, 38156, 38163, and 38164.

DISTRIBUTION

Lower Virgilian, Oklahoma. (See Table 2.)

Fig. 13 A–H *Gondolella neospathodiformis* sp. nov., Heebner Shale, Oread Formation, Shawnee Group, Osage Co., Oklahoma, locality He-7.

- A Sp element, enlarged lateral view of cusp showing striae, holotype, sample He-7-1, ROM 38150, ×792.
- B Sp element, lateral view, holotype, sample He-7-1, ROM 38150, ×154.
- C Sp element, aboral-lateral view, paratype, sample He-7-1, ROM 38151, ×204.
- D Sp element, aboral-lateral view, paratype, sample He-7-1, ROM 38152, ×207.
- E Sp element, aboral view, paratype, sample He-7-Rec., ROM 38153, ×264.
- F Sp element, enlarged aboral view of basal cavity, paratype, sample He-7 Rec., ROM 38153, ×506.
- G Sp element, aboral view, paratype, sample He-7-1, ROM 38154, ×273.
- H Sp element, enlarged aboral view of basal cavity, sample He-7-1, ROM 38154, ×539.

I–L *Spathognathodus bultyncki* Groessens, Tournaisian, Salet, Belgium, sample B(6) 92–95, ROM Acc. No. 74PB24.

- I Sp element, aboral view, ROM 38157, ×92.
- J Sp element, enlarged aboral view of basal cavity, ROM 38157, ×231.
- K Sp element, lateral view, ROM 38158, ×46.
- L Sp element, enlarged lateral view of posterior end, ROM 38158, ×92.

M, N, P, Q *Spathognathodus* cf. *bultyncki* Groessens, Viséan, Windsor Group, Wentworth Formation of Moore and Ryan (1976), Phillips Limestone (Moore, *in* Geldsetzer et al. 1980), Miller's Creek Quarry, Hants Co., Nova Scotia, sample Phil-1-2, ROM Acc. No. 75PB29.

- M Sp element, lateral-aboral view, ROM 38160, ×79.
- N Sp element, lateral-aboral view, ROM 38161, ×44.
- P Sp element, enlarged lateral-aboral view of posterior end, ROM 38161, ×114.
- Q Sp element, enlarged lateral-aboral view of posterior end, ROM 38160, ×183.
- O Oz element, (?) of *Spathognathodus* cf. *bultyncki* Groessens, Viséan, Windsor Group, Wentworth Formation of Moore and Ryan (1976), Phillips Limestone (Moore, *in* Geldsetzer et al., 1980), Miller's Creek Quarry, Hants Co., Nova Scotia, sample Phil-1-1, ROM Acc. No. 75PB28, ROM 38162, ×87.

Acknowledgements

We are indebted to the following members of the Department of Invertebrate Palaeontology, Royal Ontario Museum, for their help and co-operation: Mrs. Hilary Geberl and Ms Maureen Wende who assisted in the preparation of the figures; Miss Joan Burke who typed the numerous drafts and did much of the preliminary editing; and Mrs. LaVerne Russell who, some years ago, did much of the preparation and mounting of specimens and who was the first to locate and recognize the new species *G. neospathodiformis*.

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Literature Cited

BRANSON, E.B.
1944 The geology of Missouri. University of Missouri Studies 19:1–535.

BUTLER, M.
1973 Lower Carboniferous conodont faunas from the eastern Mendips, England. Palaeontology 16:477–517.

CLARK, D.L.
1972 Early Permian crisis and its bearing on Permo-Triassic conodont taxonomy. Geologica et Palaeontologica 1:147–158.

CLARK, D.L. and L.C. MOSHER
1966 Stratigraphic, geographic, and evolutionary development of the conodont genus *Gondolella*. Journal of Paleontology 40:376–394.

COOLEY, D.R.
1952 Facies change in the Oread Limestone in southern Kansas and northern Oklahoma. M.Sc. Thesis, University of Kansas. 61 pp.

ELLISON, S.P., Jr.
1941 Revision of the Pennsylvanian conodonts. Journal of Paleontology 15:107–143.

EVANS, J.K.
1966 Depositional environment of a Pennsylvanian black shale (Heebner) in Kansas and adjacent states. Ph.D. Thesis, Rice University. 166 pp.

GELDSETZER, H.H.J., P. GILES, R. MOORE, and W. PALMER
1980 Stratigraphy, sedimentology, and mineralization of the Carboniferous Windsor Group, Nova Scotia. Joint Annual Meeting, Geological Association of Canada/Mineralogical Association of Canada, Halifax, 1980, Field Trip 22 Guidebook. 42 pp.

GROESSENS, E.
1971 Les conodontes du Tournaisien supérieur de la Belgique; note préliminaire. Service Géologique de Belgique, Professional Paper 4:1–29.
1974 Preliminary range chart of conodont biozonation in the Belgian Dinantian. International Symposium on Belgian Micropaleontological Limits, Namur, Publication 17:1–193.

GROESSENS, E., R. CONIL, and A. LEES
1973 Problèmes relatifs à la limite du Tournaisien et du Viséen en Belgique. Société Belge de Géologie, Bulletin 82:17–50.

GUNNELL, F.H.
1933 Conodonts and fish remains from the Cherokee, Kansas City, and Wabaunsee groups of Missouri and Kansas. Journal of Paleontology 7:261–297.

HUDDLE, J.W.
1934 Conodonts from the New Albany Shale of Indiana. Bulletins of American Paleontology 21(72):1–137.

JEPPSSON, L.
1972 Some Silurian conodont apparatuses and possible conodont dimorphism. Geologica et Palaeontologica 6:51–69.

KLAPPER, G. and G.M. PHILIP
1971 Devonian conodont apparatuses and their vicarious skeletal elements. Lethaia 4:429–452.

KOIKE, T.
1967 A Carboniferous succession of conodont faunas from the Atetsu Limestone in southwest Japan (Studies of Asiatic conodonts, Part VI). Tokyo Kyoiku Daigaku Science Reports, Section C, 93:279–318.

KOZUR, H.
1976 Paleoecology of Triassic conodonts and its bearing on multielement taxonomy. Geological Association of Canada, Special Paper 15:312–324.

LEE, W.
1938 Stratigraphy of the Cisco Group of the Brazos Basin. University of Texas, Publication 3801:11–90.

MENDENHALL, M.E.
1951 Conodonts and fish remains of the Douglas and Shawnee Groups of the Virgil Series (Pennsylvanian) of Nebraska. M.Sc. Thesis, University of Nebraska. 78 pp.

MERRILL, G.K.
1975 Pennsylvanian conodont biostratigraphy and paleoecology of northwestern Illinois. Geological Society of America, Microform Publication 3:1–130.

MERRILL, G.K. and C.W. KING
1971 Platform conodonts from the lowest Pennsylvanian rocks of northwestern Illinois. Journal of Paleontology 45:645–664.

MERRILL, G.K. and S.M. MERRILL
1974 Pennsylvanian nonplatform conodonts, IIa: The dimorphic apparatus of *Idioprioniodus*. Geologica et Palaeontologica 8:119-130.

MERRILL, G.K. and P.H. von BITTER
1976 Revision of conodont biofacies nomenclature and interpretations of environmental controls in Pennsylvanian rocks of eastern and central North America. Royal Ontario Museum, Life Sciences Contributions 108:1–46.

MOORE, R.G. and R.J. RYAN
1976 Guide to the invertebrate fauna of the Windsor Group in Atlantic Canada. Nova Scotia Dept. of Mines, Paper 76–5:1–57.

MOSHER, L.C.
1968 Triassic conodonts from western North America and Europe and their correlation. Journal of Paleontology 42:895–946.

PERLMUTTER, B.
1975 Conodonts from the uppermost Wabaunsee Group (Pennsylvanian) and the Admire and Council Grove Groups (Permian) in Kansas. Geologica et Palaeontologica 9:95–109.

STAUFFER, C.F. and H.J. PLUMMER
1932 Texas Pennsylvanian conodonts and their stratigraphic relations. University of Texas, Bulletin 3201:13–50.

TOOMEY, D.F.
1969 The biota of the Pennsylvanian (Virgilian) Leavenworth Limestone, midcontinent region; part I, stratigraphy, paleogeography, and sediment facies relationships. Journal of Paleontology 43:1001–1018.

von BITTER, P.H.

1972 Environmental control of conodont distribution in the Shawnee Group (Upper Pennsylvanian) of eastern Kansas. University of Kansas Paleontological Contributions 59:1–105.

1974 Element composition and micromorphology of species of *Gondolella* from the Middle and Upper Pennsylvanian of the central U.S.A. Geological Society of America, Abstracts with Programs 6:551. [Abstract].

1976 The apparatus of *Gondolella sublanceolata* Gunnell (Conodontophorida, Upper Pennsylvanian) and its relationship to *Illinella typica* Rhodes. Royal Ontario Museum, Life Sciences Contributions 109:1–44.

von BITTER, P.H. and P.H. HECKEL

1978 Differentiation of black "core" shales in Missourian and Virgilian cyclothems (Pennsylvanian) in Iowa and Kansas, using conodonts. Geological Society of America, Abstracts with Programs 10:510. [Abstract].

von BITTER, P.H. and G.K. MERRILL

1977 Neogondolelliform conodonts of Early and Middle Pennsylvanian age. Royal Ontario Museum, Life Science Occasional Paper 29:1–12.

ZIEGLER, W., ed.

1973 Catalogue of conodonts, volume 1. Stuttgart, E. Schweizerbart. 504 pp.

Appendix

Locality Index of North American Localities (a.b. = above base; all stratigraphic measurements in cm)

Member/ Formation	Sample	Locality Code	Stratigraphic Position	Geographic coordinates
Lonsdale	2C	2AMGL	137–158 a.b.	SW NW sect. 28 T8N R5E Trivoli Twp., Peoria Co., Illinois. Locality: Lonsdale 2 of Merrill (1975).
Lonsdale	6B	6 AMGL	0–61 a.b.	SW NE sect. 28 T8N R6E Logan Twp., Peoria Co., Illinois; in field next to road. Locality: Lonsdale 6 of Merrill (1975).
Lonsdale	7B	7AMGL	69–99 a.b.	W½ NW sect. 34 and E½ SE sect. 33 T8N R6E Peoria Co., Illinois. Along west branch of Copperas Creek. Locality: Lonsdale 7 of Merrill (1975).
Lonsdale	7D	7AMGL	0–61 a.b.	
Lonsdale	7E	7AMGL	Float prob. =7D	
Lonsdale	8C	8AMGL	91–112 a.b.	NW SE sect. 7 T8N R7E Limestone Twp., Peoria Co., Illinois, Locality: Lonsdale 8 of Merrill (1975).
Lonsdale	8D	8AMGL	30–91 a.b.	
Lonsdale	8E	8AMGL	0–30 a.b.	
Lonsdale	11	11AMGL	0–61 a.b.	NW SE sect. 4 T1ON R6E Peoria Co., Illinois. Along ravine. Locality: Lonsdale 11 of Merrill (1975).
Lonsdale	12B	12AMGL	0–61 a.b.	SE SW sect. 4 T11N R7E Akron Twp., Peoria Co., Illinois. In quarry of Princeville Stone Co. Locality: Lonsdale 12 of Merrill (1975).
Lonsdale	13C	13AMGL	0–15 a.b.	NW NW sect. 9 T11N R9E, Chillicothe Twp., Peoria Co., Illinois. Along Coon Creek and tributary above Boy Scout Camp. Locality: Lonsdale 13 of Merrill (1975).
Lonsdale	14B	14AMGL	0–61 a.b.	NE SW sect. 15 T8N R5E, Trivoli Twp., Peoria Co., Illinois. Along creek. Locality: Lonsdale 14 of Merrill (1975).

Holdenville	1	DAHX	0–30 a.b.	NW sect. 28 T48N R29W Jackson Co., Missouri. Locality: 1371 of Ellison (1941).
"Seville"	11D	11KSSSD	76–152 a.b.	NW NE sect. 36 T17N R4W, Buffalo Twp., Rock Island Co., Illinois.
"Seville"	11E	11KSSSE	0–76 a.b.	
Seville	4B	4KSSS	0–46 a.b.	NW SE NW sect. 15 T11N R2W, Monmouth Twp., Warren Co., Illinois. Along S bank of Cedar Creek. Locality: Seville 4 of Merrill and King (1971).
Seville	8A	8KSSS	30–91 a.b.	NW NE SW sect. 24 T15N R4W, Duncan Twp., Mercer Co., Illinois. In cut bank on W side of road. Locality: Seville 8 of Merrill and King (1971).
Seville	8B	8KSSS	0–30 a.b.	
Seville	10-I-h	10KSSS	0–30 a.b.	NE NE sect. 26 T9N R1W, Warren Co., Illinois. Locality: Seville 10 of Merrill and King (1971).
Seville	10-II-d	10KSSS	0–30 a.b.	
Seville	14A	14KSSS	?assumed 61–91 a.b.	SE SE SW sect. 21 T7N R2E Henry Co., Illinois. Locality: Seville 14 of Merrill and King (1971)
Seville	14B	14KSSS	?assumed 30–61 a. b.	
Seville	14C	14KSSS	?assumed 0–30 a.b.	
Seville	16A	16KSSS	15–106 a.b.	SE sect. 22 T6N R1E, Fulton Co., Illinois. Locality: Seville 16 of Merrill and King (1971).
Seville	16D	16KSSS	0–15 a.b.	
Seville	20	20KSSS	Nodules from mine dump	E NW NE sect. 33 T14N R1E, Oxford Twp., Henry Co., Illinois. Mine dump of abandoned Shuter Coal Co. Shaft Mine, W side of U.S. 150, 1.25 mi S of Alpha.
Lower Brush Creek	39B	39LBCLS	0–30 a.b.	E Cen. and SW NW sect. 32, Harrison Tp., Muskingum Co., Ohio. Along road above Cedar Run.
Cramer	2A	2AMTC	61–122 a.b.	NW NW sect. 2 T15N R11E, Bureau Co., Illinois.
Cramer	2B	2AMTC	0–61 a.b.	
Cramer	2C	2AMTC	0–61 a.b.	
Hushpuckney	4	4MKSH	45–60 a.b.	NW NE NE sect. 24 T49N R33W, Jackson Co., Missouri, Locality 2 of Gunnell (1933).

Continued on page 48.

Locality Index continued

Member/ Formation	Sample	Locality Code	Stratigraphic Position	Geographic coordinates
Hushpuckney	5	5MKSH	0–60 a.b.	SE sect. 22 T5ON R32W, Blue Twp., Jackson Co., Missouri. Along road leading to Missouri Portland Cement Co. plant near Sugar Creek.
Hushpuckney	8	8MKSH	30–45 a.b.	Sect. 35 T49 R32W, Jackson Co., Missouri. Locality: 0017E of Ellison (1941).
Stark	1	1MKDS	0–30 a.b.	SE SE NE sect. 28 T49N R33W, Jackson Co., Missouri. Localities: 0141 and 0142 of Ellison (1941).
Stark	6B	6MKDS	20–65 a.b.	SE NE SW sect. 32 T14N R13E, Sarpy Co., Nebraska. City Wide Quarry #6.
	6C	6MKDS	0–20 a.b.	
Heebner	He-2-1	He-2	0–12.7 a.b.	NW SW SE sect. 33 T33S R11E, Chautauqua Co., Kansas. On NE side of Hwy. 99, approx. 1 mi W of Sedan, Kansas. Locality 0097 of Ellison (1941) and Locality 22 of Evans (1966).
Heebner	He-2-2A	He-2	12.7–45.7 a.b.	
Heebner	He-5-1	He-5	0–2.5 a.b.	SE SW sect. 29 T26S R13E, Greenwood Co., Kansas. Along county road.
Heebner	He-7-1	He-7	$\cong$153–$\cong$183 a.b.	SE NE sect. 14 T29N R9E, Osage Co., Oklahoma. Locality 7 of Cooley (1952).
Heebner	He-7 Recolln.	He-7	$\cong$153–$\cong$183 a.b.	
Heebner	He-8-1	He-8	0–60.9 a.b.	SE SE SW sect. 24 T29S R12E, Elk Co., Kansas. 2 mi north of Busby.
Heebner	He-10-1	He-10	0–60.9 a.b.	C sect. 33 T8S R22E, Leavenworth Co., Kansas. At sharp bend in Hwy. 92 just W of Leavenworth town limits.
Heebner	He-14-1	He-14	0–62.2 a.b.	NW sect. 15 T12N R10E, Cass Co., Nebraska. Johannsen Quarry, W of South Bend. Locality 4 of Evans (1966).
Plattsmouth	P-6-1	P-6	0–151.5 above apparent base	SE NE sect. 14 T29N R9E, Osage Co., Oklahoma. Locality 7 of Cooley (1952).

Queen Hill	QH-1-1	QH-1	0–48.3 a.b.	NW NW sect. 24 T12S R18E, Douglas Co., Kansas; 6 mi W of West Lawrence Interchange on Kansas Turnpike. Sampled on N side of Turnpike. Locality 2 of von Bitter (1972).
Queen Hill	QH-1-2	QH-1	48.3–101.6 a.b.	
Queen Hill	QH-2-3	QH-2	24.1–64.8 a.b.	NE NE sect. 7 T29S R12E, Elk Co., Kansas. E side of county road.
Queen Hill	QH-4-2	QH-4	45.7–76.2 a.b.	E½ SW SW sect. 33 T12N R14E, Cass Co., Nebraska. Ace Hill Quarry.
	QH-4-3	QH-4	76.2–83.8	
Queen Hill	2	2VSLQ	unavailable	E½ SW sect. 13 T12N R14E, Cass Co., Nebraska.
Beil	B-1-1	B-1	0–68.6 a.b.	NW NW sect. 24 T12S R18E, Douglas Co., Kansas, 6 mi W of West Lawrence Interchange on Kansas Turnpike, sampled on N side of Turnpike. Locality 2 of von Bitter (1972).
Brown marine shale over Salem School Mbr.	Sal-Sp-3	Sal-Sp	$\cong$427–$\cong$519 a.b.	0.5 mi SE of Salem School, Herron Bend, N side Brazzos River, Young Co., Texas. Ref.: Lee (1938:16). Toomey (1969:1008).
Salem School	Sal-1-2	Sal-1	15.2–40.6 a.b.	

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