# PRAGIAN CONODONT ZONAL CLASSIFICATION IN NEVADA, WESTERN NORTH AMERICA

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## ABSTRACT

A tripartite global zonal scale for the Pragian Stage (Devonian) was recommended by the Subcomission on Devonian Stratigraphy in 1989. Since that time, additions to the data on the two primary lineages used for the subdivision of the Pragian, *Eognathodus* and early *Polygnathus,* have shown: 1) that the Lochkovian-Pragian boundary criterion is useable as defined and is applicable on a global scale, but that the boundary-stratotype section in the Barrandian region of the Czech Republic has serious limitations as a reference section; 2) the criteria for the internal subdivision of the Pragian are not globally applicable; and 3) that the taxon that we have used in Nevada to mark the base of the Emsian is *Polygnathus lenzi,* whose range may be different from that of Australian *P. dehiscens,* the supposed criterion for the base of the Emsian.

The problem of interregional correlation within the Pragian and with the base of the Emsian can be solved only by increasing our understanding of the evolutionary pathways within all lineages and to develop better standards of comparison with the aim of finding a few intra-Pragian interregional correspondences. This paper reviews the Pragian of Nevada and compares it with Alaska, Canada, eastern Australia, and central Europe and suggests a regional scale for use in the western North American Cordillera.

Evolutionary stages within the Eognathodontidae plus the help of *Pedavis* and *Icriodus* make the best scale for Nevada. However, the subdivisions proposed here (*irregularis-profunda* Zone; *profunda–brevicauda* Zone*; brevicauda-mariannae* Zone; *mariannae-lenzi* Zone) are not the same as those of the SDS and cannot be applied on a global scale. The first two are based on evolutionary appearances; the last two on the lowest occurrences of distinctive and widespread taxa in North America.

One new genus, *Masaraella* (type species, *Ozarkodina pandora* Murphy, Matti & Walliser, 1981) and four new species, *Masaraella epsilon*, *Masaraella riosi*, *Gondwania profunda,* and *Pedavis longicauda,* are described.

**Key words: Systematics, zonation, correlation, conodonts, Lower Devonian, Nevada.**

## RESUMEN

La Subcomisión Internacional de Estratigrafía del Devónico recomendó, en 1989, para el Piso Praguiense (Devónico) una escala zonal global que constara de tres partes. Desde entonces, las nuevas informaciones sobre los dos linajes principales de conodontos que se han utilizado para la subdivisión del Praguiense *Eognathodus* y *Polygnathus* primitivos han mostrado lo siguiente: 1) el criterio para el límite Lochkoviense-Praguiense se puede utilizar tal como fue definido y se puede aplicar globalmente, pero la sección del estratotipo en la región de Barrandia (República Checa) tiene limitaciones importantes como sección de referencia. 2) los criterios para la subdivisión interna del Praguiense no se pueden aplicar de manera global. 3) el taxón que se ha venido utilizando en Nevada para indicar la base el Emsiense es *Polygnathus lenzi*, cuyo rango pudiera ser diferente al de *P. dehiscens*, el supuesto índice para la base del Emsiense.

El problema de la correlación suprarregional dentro del Praguiense y con la base del Emsiense sólo se puede resolver mediante la comprensión de los caminos evolutivos dentro de todos los linajes de conodontos y con el desarrollo de mejores estándares de comparación que permitan encontrar algunas correspondencias dentro del Praguienses a nivel suprarregional. Este trabajo revisa el Praguiense de Nevada comparándolo con el de Alaska, Canadá, Australia Oriental y Europa Central, y sugiere una escala regional para el oeste de la *North American Cordillera.*

La mejor escala zonal para Nevada se basa en los estadios evolutivos dentro de los Eognathodontidae, además de datos de los géneros *Pedavis* e *Icriodus*. Sin embargo, la subdivisión propuesta aquí (Zona *irregularis-*

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*profunda*; Zona *profunda-brevicauda*; Zona *brevicauda-mariannae*; Zona *mariannae-lenzi*) no es la misma que la propuesta por la Subcomisión Internacional de Estratigrafía del Devónico y no se puede aplicar a escala global. Las dos primeras zonas se basan en entradas evolutivas, las dos últimas en registros más bajos de taxones característicos de amplia distribución en Norteamérica.

Se describe un nuevo género *Masaraella* (especie típica, *Ozarkodina pandora* Murphy, Matti & Walliser, 1981) y cuatro especies nuevas *Masaraella epsilon*, *Masaraella riosi, Gondwania profunda*, y *Pedavis longicauda*.

**Palabras clave: Sistemática, zonación, correlación, conodontos, Devónico Inferior, Nevada.**

## INTRODUCTION

The presence of conodonts in the Devonian rocks of Nevada was shown by Clark & Ethington (1966), who sampled the then known sections in central Nevada and reported the presence of *Spathognathodus bipennatus nevadensis* Clark & Ethington, 1966 (= *Gondwania nevadensis*) in the type section of the Rabbit Hill Limestone in Copenhagen Canyon, Monitor Range. In this taxon, they included the holotype of *G. nevadensis* and other eognathodontids with a partially sulcate crest on the blade.

Klapper initiated the first systematic sampling program in the Lower Devonian of Nevada in 1966 and partly published the results in 1969 (Klapper, 1969). He put *G. nevadensis* in synonymy with "*Spathognathodus sulcatus* (Philip, 1965)" and recognized that the sulcate spathognathodontids of Nevada and Royal Creek in the Canadian Arctic, which he also identified as "*S. sulcatus*", could be separated into early forms, in which large basal cavities were dominant, and late forms, in which restricted basal cavities were dominant (Klapper, 1969). As a result of his work at Lone Mountain and McColley Canyon, Nevada and additional evidence of the sequential stratigraphic positions of the two forms that was found in the Monitor Range (Matti, 1971; Matti *et al*., 1975; Wise, 1977), Klapper adapted the zonal conodont-based subdivision of Fåhraeus (1971) to the Nevada Lower Devonian (Klapper, 1977b: 35). The forms identified by a large basal cavity that extends to the posterior end of the Pa element, were hypothesized to be characteristic of the early Pragian. The forms with a basal cavity restricted to the quartile behind the midpoint of the element, were hypothesized to be characteristic of the late Pragian.

Based on work in the Salmontrout Formation in Alaska, Lane & Ormiston (1979: 52) adopted Klapper's interpretation of *Eognathodus sulcatus* and named Klapper's late forms *E. sulcatus* subspecies *kindlei,* and a form they regarded as an evolutionary stage intermediate between *E. sulcatus sulcatus* and *E. sulcatus kindlei* as *E. sulcatus juliae*. The name *sulcatus* was used for the earlier Zone and characterized by the presence of *"E. sulcatus sulcatus"* and *E. sulcatus juliae* (Lane & Ormiston, 1979: 45). The subspecies *kindlei* characterized the later Zone. They also modified the zonation proposed by Klapper by adding a *pireneae* Zone above the *kindlei* Zone to accommodate the presence of *Polygnathus pireneae* Boersma, 1973 that they found in the stratigraphic interval mostly above *E. kindlei,* but with a short overlap in their occurrences, and below the lowest occurrence of *Polygnathus "dehiscens"* (= *Polygnathus lenzi* Klapper, 1969). In addition, Lane & Ormiston (1979: 45) pointed out that the modified *sulcatus* Zone has an earlier part, characterized by the morphotypes from Tyers Quarry, Victoria (Philip, 1965), the type locality of *sulcatus,* and also by the specimens from Royal Creek, Canada (Klapper, 1969), and from Alaska (Savage, 1977). The late part of the early Pragian was characterized by their new subspecies, *E. sulcatus juliae*. Their citations for the early part include morphotypes that are assigned here to *Eognathodus irregularis* (Druce, 1971; Pickett, 1980: fig.7 D-F), *G. nevadensis* (Clark & Ethington, 1966: pl. 84 figs. 10, 11), and to *E. sulcatus* s. s. (Philip, 1965: pl. 10 figs. 20, 25). However, it should be emphasized that the Salmontrout section demonstrates only the sequential stratigraphic appearances of *juliae, kindlei,* and *pireneae* in Alaska. Their inference that *E. sulcatus juliae* represents an intermediate stage in the evolution of *Eognathodus* between the morphs from the Tyers Quarry section in Victoria, Australia and the Arctic *E. sulcatus kindlei* is based on their morphologic interpretations and correlation, not superposition. If *juliae* can be shown to be an ontogenetic variant of *kindlei* (as it is here interpreted), the stratigraphic sequence in Alaska would be *kindlei* alone, an overlap of *kindlei* and *pireneae*, then *pireneae* alone.

The word morphotype was used in the above paragraph in the sense of Murphy *et al*. (1981). In subsequent paragraphs, I refer without reference to their classification that used Greek letters to designate coeval Pa element variants (or morphotypes) in the clade and also noted that such variants may have overlapping but different ranges. Although the interpretation of the evolutionary pathways presented by Murphy *et al*. (1981) has changed as a result of new data (Mawson & Talent, 1994; this paper), their terminology is still useful in expressing stratigraphic ranges and it retains nomenclatorial flexibility. It complements Linnaean nomenclature, which expresses relationship. Until now, eognathodontid classification depends on Pa elements. The new nomenclature of Bardashev *et al*. (2002), is selectively employed and commented on below. Type locality of *Spathognathodus bipennatus nevadensis* Clark & Ethington, 1996 (= *Gondwania nevadensis*), no. 26 = COP II 60 feet in Fig. 2.

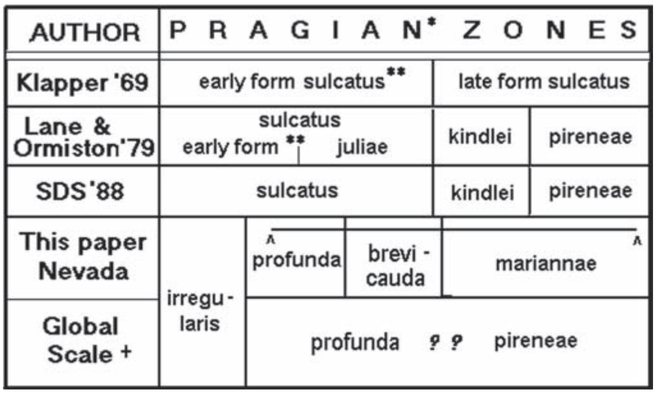
## WORK OF THE SUBCOMMISSION ON DEVONIAN STRATIGRAPHY (SDS)

On the basis of Weddige's (1987) work in the Barrandian, the stratotype for the Lochkovian-Pragian boundary was chosen by the SDS (Subcommission on Devonian Stratigraphy) in 1988 in the quarry by Homolka Hill at Velká Chuchle, southwestern Prague, Czech Republic. The boundary criterion was the appearance of "*Eognathodus sulcatus*" (i. e. the earliest form of *Eognathodus* = *Eognathodus irregularis*) in the lineage postulated by Murphy *et al*. (1981) to connect the morphs in the species *"Ozarkodina" pandora* with those in "*Eognathodus*" ["*Ozarkodina*", as used here, encompasses *Masaraella* n. gen. described herein. The proper identification of the earliest form of Eognathodontidae is *Eognathodus irregularis* Druce, 1971 (= *Eognathodus* sp. Philip, 1965; = *E. sulcatus* η Murphy *et al*., 1981; = *E. eosulcatus* Murphy, 1989)]. *E. irregularis* has a wide geographic distribution including Australia (Druce, 1971; Pickett, 1980), Austria (Schönlaub, 1980), Canada (Klapper, 1969), Germany, and Nevada (Murphy *et al*., 1981) as well as the Barrandian of the Czech Republic. In Nevada, it is in succession above its ancestor, *Masaraella pandora* in three sections in the Toquima Range and makes an excellent indicator of the base of the Pragian. In fact, the Ikes Canyon IV section in Nevada (Murphy, 1989: fig. 5) would have made a far better reference section than the boundary-stratotype in the Barrandian, but had not yet been studied when the latter was selected.

The tripartite subdivision, *sulcatus, kindlei,* and *pireneae,* was adopted by the IUGS as the global standard zonation for the Pragian (Chlupáč & Oliver, 1989). The comparison of these classifications and their supposed correspondences is shown in figure 1 and compared with the classification used herein for Nevada**.**

Since the IUGS action, Carls & Valenzuela-Ríos (1997) and Valenzuela-Ríos (1997) have pointed out some of the deficiencies of the upper Pragian zonation and the choice of the Pragian-Emsian boundary.

A more recent attempt to subdivide the Pragian has been made by Bardashev *et al*. (2002), who based their phylogenies and, thus, their zonation on a supposed chronological arrangement of taxa represented by specimens figured in the literature. In it they paid little attention to known stratigraphic position and arranged the chronological position to suit their phylogenetic interpretation. Their taxonomic constructions are based on the concept that "size and location of the basal cavity are the most important features defining the generic and suprageneric assignments of pectiniform elements" (p. 381). The idea that it can be decided *a priori* what constitutes a generic (or higher taxon) characteristic has led them to construct what they call phylomorphogenetic developments for several groups of conodonts. These constructs ignore both stratigraphic data and apparatus reconstructions even in well-documented genera, such as, *Amydrotaxis* and *Polygnathus*.



| AUTHOR | PRAGIAN* ZONES | | | |
|---|---|---|---|---|
| Klapper '69 | early form sulcatus** | | late form sulcatus | |
| Lane & Ormiston'79 | sulcatus<br>early form ** juliae | | kindlei | pireneae |
| SDS '88 | sulcatus | | kindlei | pireneae |
| This paper Nevada | irregularis | ^ profunda | brevi - cauda | mariannae ^ |
| Global Scale + | irregularis | profunda ? ? pireneae | | |

**Figure 1**. Comparison of zonal classifications with the classifications suggested in this paper for Nevada and for the Global scale. Spacing of categories is arbitrary. * The Pragian Stage was accepted by the SDS in 1988 and ratified by the IUGS in 1989 (Chlupáč & Oliver, 1989). **The early form of Klapper (1969) includes all morphs with the basal cavity reaching the posterior tip of the Pa element and with a sulcate blade; the early form of Lane & Ormiston (1979) equals *E. irregularis* Druce, 1971, *G. nevadensis* (Clark & Ethington, 1966), and *E. sulcatus* s. s. + Indicates distribution in more than one continent. ^—^ Range of *kindlei* in Nevada according to the original diagnosis.

I regard all characters as useful for taxonomic purposes, but those that are consistently present or similar within the same stratigraphical populations or through a specific stratigraphic interval are especially important in taxonomy. However, no particular characteristic has intrinsic value at the generic or familial level etc, nor does it necessarily have the same significance at the same rank throughout the group or during the same time interval.

In the eognathodontids, the character of the basal cavity and the stage of development of the sulcus on the crest of the blade have been the principal features used for classification. However, the use of one feature to the exclusion and in contradiction of others is to suggest that natural selection had a goal. I hope to demonstrate below that the shape and position of the basal cavity is misleading in some cases and useful in others.

## PRESENT WORK

Recent efforts by A. E. H. Pedder and myself (Pedder & Murphy, 1997, 2003, 2004) to integrate the rugose coral biostratigraphy of Nevada with the global conodont zonation for the Pragian-early Emsian have been inhibited because the taxonomy of *Eognathodus* is still poorly understood in spite of the considerable attention it has received (Philip, 1965; Clark & Ethington, 1966; Klapper, 1969, 1977b; Druce, 1971; Fåhraeus, 1971; McGregor & Uyeno, 1972; Cooper, 1973; Telford, 1975; Al Rawi, 1977; Savage 1977; Savage *et al*., 1977, 1985; Lane & Ormiston, 1979; Klapper & Johnson, 1980; Pickett, 1980; Murphy *et al*., 1981; Savage & Gehrels, 1984, 1995; Schönlaub, 1985; Weddige, 1987; Murphy, 1989; Wilson, 1989; Bischoff & Argent, 1990; Mawson & Talent, 1994; Mawson, 1997). Early polygnathids are in the same state (Klapper & Johnson, 1975; Yolkin *et al*., 1989, 1994; Mawson *et al*., 1992; Mawson, 1997). The lack of a stable taxonomy for these two groups renders the zonation adopted for the interval by the IUGS inapplicable to Nevada.

This paper summarizes the morphology and stratigraphy of the eognathodontids and *Pedavis* in particular in the Pragian of Nevada and compares it with the successions in Canada, Alaska, and Australia. I have taken into account all published information that has a stratigraphic context and have drawn also on unpublished information from my own as well as the collections from (1) the Tyers and Boola Quarries housed at Macquarie University, which were kindly put at my disposal for study by Professors R. Mawson and J. A. Talent during the AUSCOS I Conference in 1995; (2) unpublished material from the AMOCO collections of the Salmontrout River section of Alaska (Lane & Ormiston, 1979) deposited at The University of Iowa and loaned to me through the courtesy of J. Golden, curator of collections.

## TAXONOMIC AND BIOSTRATIGRAPHIC BASIS FOR THE ZONAL SUBDIVISION OF THE PRAGIAN

The serious contenders for use in the establishment of a zonal scheme for the subdivision of the Pragian in Nevada are the events within the Eognathodontidae and the genera *Latericriodus, Pandorinellina, Pedavis, Polygnathus,* and *Criteriognathus* or some combination of events using these taxa. Unfortunately, dacryoconarid tentaculites, graptolites, fish, and brachiopods with some exceptions are either not common in the Pragian or they do not have globally distributed lineages that may be used in correlation.

Brachiopods of Nevada were studied intensively for over thirty years by the late J. G. Johnson who developed criteria for recognizing the brachiopod zones set up earlier by Merriam (1940) and a parallel set of stacked and numbered faunal intervals based on brachiopods. It can now be shown that Faunal Intervals 5-7 are in part biofacies: the oldest interval, Number 5, (primarily the *Rensselaerina* fauna) occurs in the upper half of the Pragian in the COP II section (Fig. 2) and the interval 6 or *Oriskania* fauna occurs in the uppermost beds of the COP II section near the end of the Pragian. Faunal interval 5 overlaps the lower range of *Pseudogondwania kindlei μ* and is above the range of *Pedavis brevicauda*. At Willow Creek XI, sample 6 with the lowest occurrence of *P. kindlei μ*, J. G. Johnson (letter, 1990) reports the *Trematospira* Subzone (F.I. 6) followed by the *Costispirifer* Subzone (F. I. 7) at WC XI, sample 10, and the *Acrospirifer kobehana* Zone

**Figure 2**. Relationship and ranges of Eognathodontid and other critical species found in the Copenhagen Canyon II (COP II) section at Rabbit Hill, Copenhagen Canyon, Monitor Range, Nevada with the ranges of important sections exposed in other areas, ranges of important *Pedavis* species, and relative positions of faunas based on taxa other than conodonts.

Along the left side of the diagram are abbreviations for the stage and zonal names as follows: L, Lochkovian Stage; I-P, *irregularis-profunda* Zone; P-B, *profunda-brevicauda* Zone; B-M, brevicauda-mariannae *Zone;* M-L, *mariannae-lenzi* Zone; E, Emsian Stage.

Columns on the left represent the approximate span of the following sections with respect to the COP II section: I - Royal Creek, Yukon Territory, Canada; II – IK IV, Toquima Range, Nevada; III - Boola Quarry, Victoria, Australia; IV – Salmontrout River, eastern Alaska; V – Mill Canyon , Toquima Range, Nevada; VI – Willow Creek XI, northern Roberts Mountains, Nevada. Footages for COP II section, Copenhagen Canyon, Monitor Range, Nevada to scale are to the right of the columns. All other stratigraphic positions are correlated to the Copenhagen Canyon section. IK IV 7A and IK IV 1A represent the base and top of the local range of *Pedavis longicauda* n. sp. in the McMonnigal Limestone at Ikes Canyon (Murphy, 1993: fig. 2), Toquima Range, Nevada.

The lower horizontal shaded area represents the range of *Pedavis longicauda* n. sp. in the IK IV section projected into the COP II section. The upper two horizontal shaded areas represent the ranges of *Pedavis brevicauda* and *P. mariannae* at COP II, the type section of the Rabbit Hill Limestone, Copenhagen Canyon, Monitor Range, Nevada. The genera of *Eognathodontidae* are represented by areas with contrasting density of stippling. A space is left in the diagram between the top of the Pragian and the base of the Emsian to indicate that the regional base of the Emsian in Nevada is chosen on the basis of *Polygnathus lenzi* whose stratigraphic position may not coincide with the base of the Emsian in other regions. Brachiopod faunal intervals 5 and 6 of Johnson (1977) were established on the basis of their occurrences in the COP II section and are shown in two columns at the right side of the diagram. The range of *Monograptus thomasi* is plotted as it occurs in the COP II section. The Lochkovian-Pragian boundary is based on the appearance of *Eognathodus irregularis* in bed 20A in the upper part of the Mill Canyon section, Toquima Range, which mainly is older than COP II.

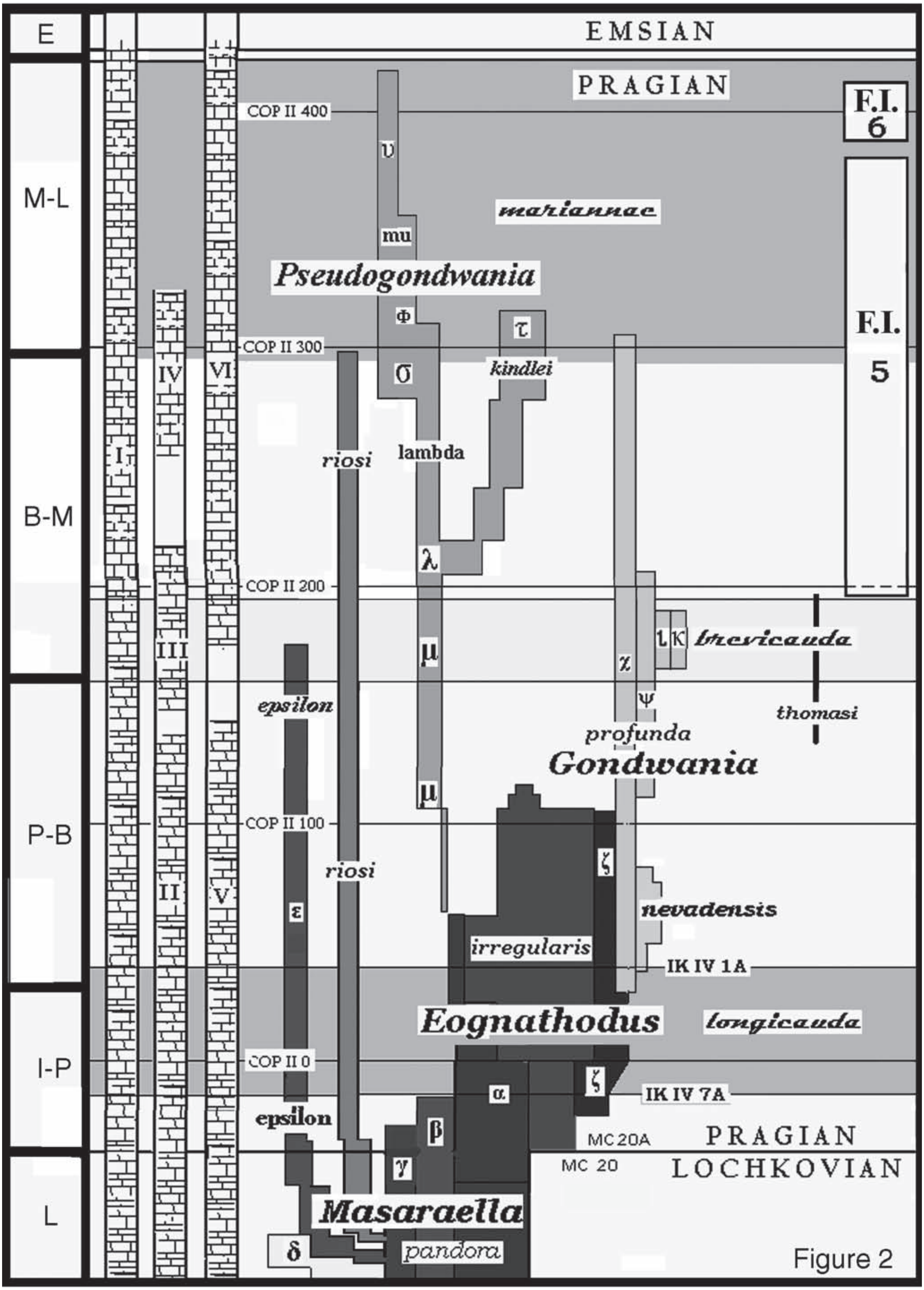

E
EMSIAN
PRAGIAN
F.I. 6
COP II 400
υ
M-L
mariannae
mu
Pseudogondwania
Φ
τ
F.I. 5
COP II 300
IV
VI
σ
kindlei
I
riosi
lambda
B-M
λ
COP II 200
III
ι κ brevicauda
μ
χ
epsilon
ψ
thomasi
profunda
Gondwania
μ
COP II 100
P-B
riosi
II
V
ε
ζ
nevadensis
irregularis
IK IV 1A
Eognathodus
longicauda
COP II 0
I-P
α
ζ
IK IV 7A
epsilon
β
MC 20A
PRAGIAN
γ
MC 20
LOCHKOVIAN
L
Masaraella
δ
pandora

Figure 2

(F. I. 8-9) at WC XI, sample 16 (178 feet), above the last occurrence of *P. kindlei μ* (134 feet), but significantly below the entry of *Polygnathus lenzi* (used as the base of the Emsian in the North American Cordillera) at WC XI 21 (239.5 feet). Based on what we know of the ranges of the conodont taxa, the *Renssellaerina* fauna (F. I. 5) must be at least partly equivalent to the *Trematospira* fauna (F. I. 6); the *Oriskania* (F. I. 6) fauna must be equivalent to the upper part of the *Costispirifer* fauna (F. I. 7). This example illustrates why it is so difficult to establish an effective zonation based on brachiopods in the Lower Devonian.

Pragian ostracodes are relatively rare in Nevada (Berdan, 1986) and their study mostly available in unpublished theses (Christiansen, 1980; LeFebvre, 1988; Luptowitz, 1990). Therefore, I restrict my discussion to conodont genera.

The use of an icriodontid-based zonation integrates other local biostratigraphies based on brachiopods, corals, other conodonts, ostracodes, and fish, but involves the use of endemic faunal elements and, therefore, either the eognathodontids or *Pedavis* must be employed to correlate with other regions. *Pedavis* is not abundant and study of its apparatus composition and evolution is still in its infancy, but the taxa present are distinctive and easily identified and, therefore, play an important supporting role, but not a definitive one. Early *Polygnathus* taxonomy, as mentioned above, is still in dispute and, although the group is important, it is not well represented in the faunas and would cover only half of the stage. *Pandorinellina* and *Criteriognathus* citations are usually referred to the wastebasket terms, *P. optima,* or *C. miae* or *C. steinhornensis* and, although the citations are numerous, the Pragian forms of these taxa are almost unstudied. The sequences within eognathodontids are best known, but are fragmentary and their interrelations are not well understood. Nevertheless, they have been and probably will continue to be the most useful for interregional correlation.

## EVOLUTION OF EOGNATHODONTIDAE

Hypotheses concerning the evolution of eognathodontids have become more complex with the increase in the information available and so this review suggests a branching pattern rather than our earlier single-lineage hypothesis (Murphy *et al.*, 1981). A summary diagram is shown in figure 2.

Early studies adopted a relatively broad view of species composition as reviewed above. The rather different morphologies shown by Philip (1965) for the holotype and paratype of *E. sulcatus* were accepted as growth stages or variants of the same taxon, although it was evident from Philip's (1965: 95) description that the specimens were different morphologically, came from a composite sample, and may represent different stratigraphic levels and different taxa (Murphy *et al.*, 1981: 752). In recognition of this, Mawson & Talent (1994) restudied the type locality at Tyers Quarry in Victoria, and presented a detailed report of the *Eognathodus* stratigraphy of the limited sequence at Tyers and also at the thicker section of the nearby Boola Quarry. Their work is essential to the understanding of eognathodontid taxonomy, but unfortunately these sections in Victoria span only a short part of the Pragian so the remaining history has to be uncovered in other areas.

The early history of the eognathodontids was inferred on the basis of sections in the Frankenwald, Germany and in the Monitor and Toquima Ranges, central Nevada where the members of the lineage *"Ozarkodina" pandora*-*"Eognathodus sulcatus"* occur in sequence (*Ozarkodina* is enclosed in quotation marks here because *pandora* is not a true *Ozarkodina* as restricted by Murphy *et al.* (2004) and is described below as *Masaraella* n. gen. *E. sulcatus* is used in the broad sense of early authors). Murphy *et al.* (1981) interpreted these sequences as being comprised of a series of morphs that are variants within a lineage. As evolution proceeded, some morphs were added and others dropped out. The result was an incremental evolution from *"O". pandora* to *Eognathodus*. The change seen in Nevada was from a relatively normal spathognathodontid Pa element, characterized by the *pandora* α and β morphs in the upper Lochkovian with an increasingly broader range of variability just below the Pragian boundary where the variability includes all of the *pandora* morphs except δ. At the boundary, the variability is augmented with the addition of *Eognathodus irregularis*. I now modify the basic interpretation somewhat because the substantial increase in the data base suggests that taxonomic differences exist between Nevada and Australia. A phylogenetic tree with more than one branch better fits the present data as already suggested by the works of Mawson & Talent (1994) and Bardashev *et al.* (2002).

Several pathways seem possible to explain the Nevada data. I believe it probable that the true explanation will involve some combination of them. With this in mind, the following stages of development of the Pa elements in the clade are envisioned:

1) The transition from a more or less centrally placed basal cavity to a basal cavity that expanded to the posterior end of the element (corresponds with the transition to *Masaraella pandora* (Murphy *et al.*, 1981) in the late Lochkovian).

2) Development of nodes or ridges on the basal platform lobes (different morphs of *Masaraella* in the late Lochkovian; Murphy *et al.*, 1981).

3) Extreme variability with the loss of a prominent cusp and modification of the crest of the blade from aligned, palisade or needle-shaped denticles to fused, suppressed, or disorganized, more or less tuberculate denticulation with concomitant increase in blade size and thickness (transition to Eognathodontidae across the Lochkovian-

Pragian boundary; Murphy, *et al*., 1981; Murphy, 1989; this paper).

4) Development of a sulcus on the crest of the blade either by indentation or ridge and node development (later forms of *E. irregularis*) resulting in three general kinds of sulci: a) a shallow flat sulcus on a thick blade that in Australia commonly also developed disorganized nodes between the rows of marginal nodes as in *E. sulcatus* s. s. (Mawson & Talent, 1994: figs. 8I-8P); b) a deeper sulcus on a thick blade bordered by lateral rows of nodes (*G. profunda* n. sp., Nevada, Alaska, Australia; Figs. 7.11, 7.13-7.16); c) an elongate ridge bordered by a row of nodes at the crest of a thin blade (*E. irregularis,* Nevada, Figs. 7.6-7.8, and 7.10). I suggest that these three morphotypes, of which only the last two continue in Nevada, are the survivors of the multifaceted variation that occurred from the base of the Pragian into the base of the *profunda-brevicauda* Zone and that they form the root stocks of the later Pragian eognathodontids.

The deeply and shallowly sulcate forms are both fully sulcate; i. e. the sulcus extends from a position posterior of the cockscomb to the posterior end of the element (e.g. Klapper, 1969: pl. 3, fig. 5). The ridge-and-node morphs, on the other hand, are only partially sulcate, i.e. sulcate from the posterior of the cockscomb to a position more or less above the peak of the basal cavity (e.g. Murphy *et al*., 1981: pl. 2 figs. 12, 27, 29, 32)

5) The deeply sulcate forms have at least three manifestations in Nevada: *G. profunda* n. sp. χ new morph (Figs. 7.11, 7.13-7.15; in part the λ morph of Murphy *et al*., 1981: pl. 3 figs. 1, 2, 11; in part κ morph of Murphy *et al*., 1981: pl. 3 figs. 9, 10) with a wide sulcus bordered by more or less straight and parallel rows of nodes; ψ new morph with a very deep sulcus bordered by variously curved rows of nodes (Figs. 7.32-7.41); ω new morph with a straight blade with a deep, narrow sulcus bordered by rows of elongate nodes (Figs. 8.6-8.8; in part the ι and κ morphs of Murphy *et al*., 1981: pl. 2 figs. 1-6, pl. 3 figs. 12-14). All deeply sulcate forms disappear by the early part of the late Pragian (base of *mariannae-lenzi* Zone) and leave only the partially sulcate forms in the latest Pragian.

6) The partially sulcate branch begins in the late part of the early Pragian (*profunda-brevicauda* Zone) with narrow, short-bladed morphs with posterior, heart-shaped basal cavities (Figs. 8.9-8.11; IK IV 4C). They tend to lengthen the blade and constrict the basal cavity in the progressively higher parts of the section (Figs. 8.12, 8.13; IK IV 1A; Fig. 7.17, COP II 106' = *Pseudogondwania kindlei* and related forms). I emphasize here that all forms in this category would be identified as the species *kindlei* according to the original diagnosis (Lane & Ormiston, 1979: 54) and, therefore, the taxon as diagnosed by Lane and Ormiston is not suitable as the name bearer of the SDS zone for the middle Pragian.

7) A split in the lineage of partially sulcate forms occurs in the middle Pragian with one branch retaining the more primitive single row of denticles on the crest of the posterior blade (= *μ* morph of Murphy *et al*., 1981). In the other, the posterior blade denticles become disorganized (Figs. 7.18-7.28; = *kindlei* τ morph as redefined here), especially in large specimens, and the sulcus may (Fig. 7.30) or may not (Figs. 7.19-7.27, 7.29) reach the posterior tip of the blade. Both branches retain the elongated anterior process and the slim blade with a shallow sulcus. The tendency to develop a bend in the posterior blade that had been present since the late Lochkovian *M. pandora* morphs dominates the morphs from at least the base of the *mariannae-lenzi* Zone and through the remainder of the Pragian.

The history of *Masaraella* and its transition into the Eognathodontidae as outlined immediately above is derived from the central Nevada sections where the latest Lochkovian (*gilberti-irregularis* Zone) is characterized by an abundance of *M. pandora* and is represented by several morphs, especially the α, β, and ζ morphs (Figs. 6.21-6.31; COP IV section in Murphy & Matti, 1983: Table 1) and icriodontids (Murphy & Cebecioglu, 1984: figs. 2A-2F). Correlation of the COP IV section in the Monitor Range and the MC section in the Toquima Range was made by Murphy & Berry (1983) using Shaw's method of graphic correlation. The base of the Pragian is best developed in the MC and IK IV sections in the Toquima Range where the evolutionary appearance of *E. irregularis* is documented. During the earliest Pragian, represented best by the MC, IK IV, and TO-I sections in the Toquima Range (Murphy, 1989; Valenzuela-Ríos, 1994), the predominant taxa are the α, β, ζ, and ε morphs and *E. irregularis* (*irregularis-profunda* Zone; Figs. 6.2-6.19) and icriodontids (Murphy & Cebecioglu, 1984: figs. 2G-2R). Early *E. irregularis* from these localities generally has a straight blade and very large basal cavity open to the posterior end, a relatively simple denticle pattern with one or a few denticles off the main line of denticles, and a single row of posterior denticles. Even in the earliest occurrences there is considerable variation in denticle pattern (e.g. MC 20A, Figs. 6.14-6.17) and basal cavity shape in both *E. irregularis* and the *M. pandora* morphs (Figs. 6.2-6.8, 6.10-6.19). In the upper part of the *irregularis-profunda* Zone and the *profunda-brevicauda* Zone, *irregularis* exhibits an extremely wide range of variation (Figs. 7.3-7.6; Murphy *et al*., 1981: pl. 2 figs. 17-19, 25; Murphy, 1989: figs. 1.2, 1.4-1.9) that still includes *M. pandora* α at one extreme. It is the common form at that level while the *profunda* χ morph (Fig. 7.11) is relatively rare. The extreme variation in *irregularis* that characterizes the lower levels of the *profunda-brevicauda* Zone is short-lived, but contains the lowest occurring members of the main eognathodontid taxa that characterize the remainder of the Cordilleran Pragian.

The early *profunda* χ morph is straight in upper view and has even rows of denticles bordering a modest to deep sulcus that, except for the cockscomb, occupies the entire upper edge of the blade to the posterior end (= fully sulcate; Figs. 7.11, 7.13-7.16). This differs from all of the other contemporaneous variants, which have a single row of denticles on the posterior crest of the blade. Although members of the Alaskan sequence (= *P. kindlei*) described by Lane & Ormiston (1979: pl. 4 figs. 1-9, 12, 13) have a sulcus that extends onto the posterior blade, they probably do not develop out of early *profunda* χ because the *profunda* χ morphs are proportionally more robust, the blades are consistently straight and lack a posterior bend, the sulcus is deeper, and the anterior process is relatively shorter. In addition, the Alaskan specimens generally develop the posterior sulcus only in large specimens whereas small specimens have a single row of denticles on most or all of the posterior process (Figs. 8.19-8.23; Lane & Ormiston, 1979: pl. 4, fig. 9). This seems an easier pathway than developing the Alaskan forms out of *profunda* χ, even though their ranges overlap from 295-306 feet in the COP II section (Fig. 7.29, Bed 33 and Fig. 7.31, Bed 28, Salmontrout Formation Section 1) and *profunda* χ maintains a more robust Pa element and shorter anterior blade throughout its range (Figs. 8.24, 8.25).

A second variant (Figs. 7.6-7.10) originating early in the *profunda-brevicauda* Zone is the probable ancestor of a narrow and long-bladed group of morphs with restricted basal cavities characterized by "*E. sulcatus* λ and *μ*" (Murphy *et al.*, 1981) and figured here (Figs. 7.17-7.31). Figs. 7.18-7.26, from COP II, and 7.27-7.31 from Alaska (see also Lane & Ormiston, 1979: pl. 4, figs. 1-5), illustrate the close morphologic similarity between specimens from the Salmontrout Formation, type area for *kindlei,* and specimens from the Copenhagen Canyon section in Nevada. The name *Pseudogondwania kindlei* is used for this lineage of morphs and includes "*E. juliae*" of Lane & Ormiston (1979), as well as the *E. sulcatus* λ and *μ* morphs mentioned above.

The present data and the patterns that can be inferred from them suggest that gaps in our knowledge still exist in both Alaska and Nevada, but the presence of some morphologic correspondences and the occurrence of three distinctive *Pedavis* species, *P. longicauda* n. sp., *P. brevicauda,* and *P. mariannae* may afford some control on the relative stratigraphic positions of the other collections. Other possible correlations may be based on the presence of *Monograptus thomasi* in the Copenhagen Canyon (at 128 to 144 feet) and northern Simpson Park Range (SP VIII) sections (Fig. 2) in the upper *profunda-brevicauda* and lower *brevicauda-mariannae* Zones (Berry & Murphy, 1972; Murphy & Berry, 1983) and in Australia. The study of dacryoconarid tentaculites that occur in the Tyers Quarry may be an independent test of the correlation proposed here between the COP II section and Tyers-Boola sections in Victoria.

## ZONATION

The conodont-based, regional zonal classification of the Pragian for Nevada and the western North American Cordillera proposed (Table 1) uses both the evolution within the eognathodontids, as it is seen in Nevada, for the lower part of the stage and the appearances of *Pedavis mariannae* and *Pedavis brevicauda* as indicators of the upper parts of the stage. At present, I see no obvious way consistently to separate the upper part of the stage using eognathodontids because the derivation of *P. kindlei* remains uncertain owing to the paucity of information concerning Cordilleran eognathodontids in the *brevicauda-mariannae* Zone. I have suggested, therefore, that the two *Pedavis* species

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|---|
| **Emsian, approximate base - lowest occurrence of *Polygnathus lenzi* Klapper, 1969 ≠ *P. dehiscens* Philip & Jackson, 1967, ≠ *P. excavata* Carls & Gandl, 1969.**<br>**Zone name = *lenzi-gronbergi* Zone.** |
| **Upper Pragian - appearance of *Pedavis mariannae* Lane & Ormiston, 1979.**<br>**Zone name, *mariannae-lenzi* Zone** |
| **upper Middle Pragian - appearance of *Pedavis brevicauda.***<br>**Zone name = *brevicauda-mariannae* Zone.** |
| **lower Middle Pragian - appearance of *Gondwania profunda.***<br>**Zone name = *profunda-brevicauda* Zone.** |
| **Lower Pragian - appearance of *Eognathodus irregularis* Druce, 1971.**<br>**(= *E.* sp. Philip, 1965; = *E. sulcatus* η morph, Murphy *et al.*, 1981);**<br>**= *E. eosulcatus* Murphy, 1989.**<br>**Zone name = *irregularis-profunda* Zone.** |

**Table 1**. Pragian zonation of Nevada.

be used in Nevada with the understanding that their origin is in doubt, but that they are distinctive taxa of wide distribution, the former between western North America and Australia and the latter within western North America. *Polygnathus pireneae* may be a better guide for the upper Pragian when a better understanding of its ontogeny is known and its variation is established in the Pyrenean type region. So far after several attempts, Valenzuela-Ríos (personal communication) has been unable to recover adequate material from the sites where Boersma (1973) collected the types. The proposed zonation gives a more realistic picture of the biostratigraphy within the Pragian. I offer it with the hope that a new analysis of the Nevada faunas will lead to a better understanding of correlation within the Pragian. The zones are named according to the system suggested in Murphy (1977) and are shown in table 1. The Pa elements assigned to *E. sulcatus* ι and κ by Murphy *et al*. (1981) are restricted herein by the removal of morphs with a very deep sulcus (Murphy *et al*., 1981: pl. 3 figs. 1, 2, 9-11) and their assignment to the *G. profunda* ψ morph, which is described below. The lowest occurrence of *Polygnathus lenzi* Klapper (= *P. "dehiscens"* of Klapper, 1977a, 1977b, and subsequent authors) is used to approximate the base of the Emsian.

## THE PRAGIAN STRATIGRAPHY OF NEVADA

The dated Pragian rocks in Nevada show three lithologic associations (Fig. 3):

1) Pragian rocks in the westernmost outcrops are predominantly dolomitic lime mudstone and wackestone with only rare graded beds. This facies of the Rabbit Hill Formation is known from the Cortez Range (Johnson, 1972), northern Simpson Park Range (Johnson & Murphy, 1969), and Toquima Range (Murphy & Anderson, 1991). I place the formation name in quotation marks in figure 3 to indicate that there are differences in the bedding characteristics of these rocks from those in the type section and that they lack the abundant sponge spicules replaced by iron oxides of the fine-grained rocks in the typical Rabbit Hill Formation. Strong bioturbation and the orangish weathering color of oxidized sedimentary rocks are characteristic. In addition, they may have abundant ostracodes, a few scattered brachiopods, trilobites, and orthocones not present in the typical Rabbit Hill Formation. These rocks are difficult to date but collections from many isolated localities indicate that they are a more basinal facies of the same biostratigraphic interval as the type section of the Rabbit Hill Formation.

2) The Rabbit Hill Formation (Merriam, 1975) is characteristic of the second association, which clearly represents higher energy deposits than the far western facies and has been interpreted as having been deposited on a slope or slope-basin transition (Matti *et al*., 1975). These rocks crop out at several localities in the Monitor Range and include well aerated carbonates with deep-water indicators, such as, graded bedding and intraformational folding, interbedded with *Chondrites* burrows in fine-grained light, orangish weathering lime mudstone. A diverse conodont, brachiopod, and sponge fauna has been recovered from the resedimented beds and a few graptolites from the dominantly fine-grained interbeds.

3) An eastern belt of well-aerated, shallow-water marine limestone and dolomitic limestone crops out in the ranges west of Eureka. These rocks have yielded a fauna of conodonts (especially icriodontids), brachiopods, corals, bryozoans, pelmatozoans, trilobites, ostracodes, nautiloids, bivalves, gastropods, tentaculites, sponges, fish, and burrowing organisms. Calcareous algae also are commonly present. The sedimentary structures in some parts of the interval, such as, oriented shells and shelter porosity, are indicative of deposition above the base of wave action. In some parts of the interval, features are also present that indicate that some of the rocks accumulated below normal storm-wave base. These include thorough bioturbation in some beds and preservation of burrowing patterns in others. These lithologies are normally assigned to the Kobeh Member of the McColley Canyon Formation (Murphy & Gronberg, 1970; Johnson, 1970; Johnson & Murphy, 1984; Luptowitz, 1990). Sections through the Kobeh are known from the Sulphur Springs Range (Carlisle *et al*., 1957), the Roberts Mountains (Luptowitz, 1990), Lone Mountain, Mahogany Hills (Murphy & Gronberg, 1970),

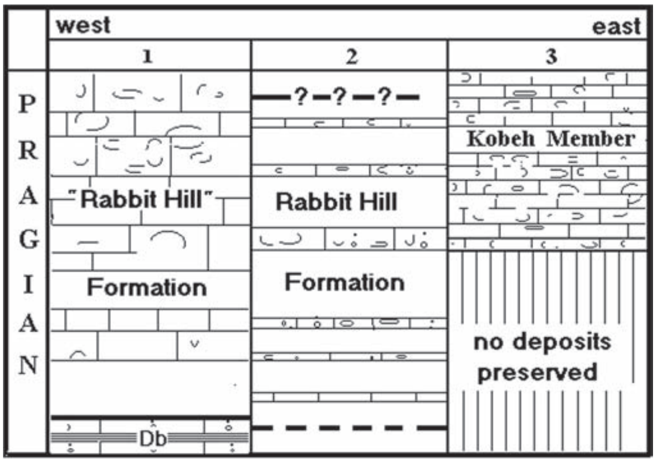


**Figure 3**. Generalized Pragian facies relations in central Nevada. Db – Bastille Limestone. Heavy horizontal lines indicate formation boundaries. Column 1 - the "Rabbit Hill" beds (Mill Canyon, Toquima Range) continue into the Emsian. Column 2 – the type Rabbit Hill Limestone (Rabbit Hill, Monitor Range), the base is not exposed, upper contact is faulted. Column 3 – Kobeh Member (Willow Creek, northern Roberts Mountains) begins in *brevicauda-mariannae* Zone and has *Polygnathus lenzi* in the upper few beds.

the northern Antelope Range (Johnson *et al.,* 1985), and Hot Creek Canyon (McGovney, 1977).

In the Combs Peak area just west of Eureka, Nevada, the Kobeh shows tongues of a still more eastern facies, which has been named the Beacon Peak Dolomite (Nolan *et al.*, 1956). The Beacon Peak occupies the stratigraphic interval of the McColley Canyon Formation to the east of Eureka. Although the Beacon Peak may show relicts of original textures and fossils, identifiable material is rare, thus, its correlation with the McColley Canyon is based on stratigraphic position of the interdigitations that are found in the Eureka District and Sulphur Springs Range.

## CRITICAL SECTIONS

Five sections in central Nevada are critical to our present understanding of the Pragian: Ikes Canyon and Mill Canyon sections in the Toquima Range, Rabbit Hill section in the Monitor Range, Wenban Peak section in the Cortez Range, and Willow Creek section in the Roberts Mountains (Fig. 4). The first two sections show the transition from Lochkovian to Pragian. The second two sections show the internal sequence through most or all of the Pragian and the last shows the middle and upper Pragian and contact with the Emsian. Other Pragian sections have been studied, but eognathodontids are either absent or sporadically distributed in them and, thus, none of the other sections is of help in verifying the evolutionary patterns within the family. These five sections are discussed briefly below and the occurrences of critical taxa are noted.

Several sections have been made through the McMonnigal Limestone at Ikes Canyon (Toquima Range), but only the IK IV and TO I sections (Murphy, 1993) have yielded information concerning the mode and timing of evolution in the eognathodontid clade. *E. irregularis* occurs in both sections, but the circumstances of its entry (staggered entry of taxa rather than entry all in one bed) in the IK IV section suggest that it is a more complete representation of the Lochkovian-Pragian transition than is found in the TO I section (Murphy, 1989). These two sections together and the MC section farther south in the Toquima Range are the best expression of the uppermost Lochkovian and lowest Pragian yet discovered in Nevada.

The Mill Canyon section (Toquima Range) is in the Bastille Limestone (Kay & Crawford, 1964; Murphy & Anderson, 1991: fig. 7) and ranges from upper *eleanorae-trigonicus* Zone to the *profunda-brevicauda* Zone. The Lochkovian-Pragian boundary is between beds 20 (174’) and 20A (175’) based on the occurrence of *Masaraella pandora* ζ*-Eognathodus irregularis* (an intermediate variety) in bed 20 and *E. irregularis* in bed 20 A (Murphy & Matti, 1983: Table 3; Murphy, 1989: fig. 7). A deep- or quiet-water mudstone at least partially Pragian in age lies above, but has not yielded significant fossils except from bed 27 where *G. profunda* was recovered (LeFebvre, 1988; Murphy & Anderson, 1991: figs. 2-5).

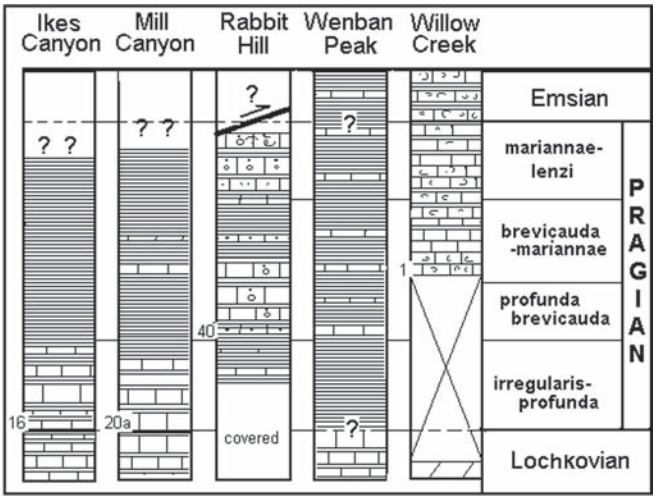


**Figure 4**. Critical sections for the study of Pragian stratigraphy in central Nevada. Numbers to the left of the columns refer to critical samples for that particular section. Ikes Canyon Section – McMonnigal Limestone below, unnamed lime mudstone above; *Eognathodus irregularis* lowest occurrence is in sample 16. Mill Canyon section– Bastille Limestone below, unnamed lime mudstone above; *E. irregularis* lowest occurrence in sample 20A. Rabbit Hill section– Rabbit Hill Limestone – *G. profunda* χ morph lowest occurrence in bed 40. Wenban Peak section – Wenban Limestone. Willow Creek section – Kobeh Member unconformably on Lone Mountain Dolomite; base of Kobeh (1) has association of *G. profunda* χ morph, *Pedavis brevicauda* and *P. kindlei* λ morph.

The lowest fossils recovered from the Rabbit Hill section in the Monitor Range are dated as the lower part of the *profunda-brevicauda* Zone on the basis of *E. irregularis* with morphs *M. pandora* α and ε, and *G. profunda* χ. Icriodontids are common but the other taxa are rare and very large samples are required to obtain a few specimens. Large intervals of burrowed siltstone lie between samples. *Pseudogondwania kindlei μ* (= *E. sulcatus μ*, Murphy *et al.*, 1981) dominates the upper part of the section, but the section is faulted before reaching the Emsian. Thus, the section at Rabbit Hill is missing the lowermost and the uppermost parts of the Pragian and although relatively complete (*sensu* Sadler, 1981) with icriodontids in almost every sample, it has only a few beds with biostratigraphically significant faunas.

The most complete section is in the southern Cortez Mountains at Wenban Peak (Christiansen, 1980) where the section ranges from low in the Silurian through most of the Emsian with only one small fault of known displacement. Above the Lochkovian, the rocks are almost entirely basin lime mudstones that contain a megafauna of small crinoids, a few brachiopods, trilobites, dacryoconarids, and even fewer straight cephalopods scattered in the rock. Small, mostly unornamented ostracodes are exceedingly abundant in many beds and conodonts, especially icriodontids, are preserved in a moderate number of beds throughout the section (Christiansen, 1980). The section is important because of the sequence of the icriodontid taxa that is associated from place to place with eognathodontids, *Pedavis,* or *Polygnathus* and may as a consequence be tied in to the other sections.

The Willow Creek section (WC X, WC XI, LRF) in the northern Roberts Mountains rests unconformably on the Lone Mountain Dolomite. The lower half of the Pragian is missing, but a few feet of *brevicauda-mariannae* Zone and the *mariannae-lenzi* Zone are present. Here the section shows the superposition of the *kindlei μ-lenzi* and *lenzi-gronbergi* Zones, but conodonts are scarce and there is no overlap of the characterizing zonal taxa. These sections have also yielded several important ostracode faunas (Luptowitz, 1990).

## CORRELATION WITH ALASKA

Correlation of the Pragian of Nevada with that of eastern Alaska (Salmontrout River Formation, Lane & Ormiston, 1979) depends largely on the association of *Pedavis mariannae*, *Pseudogondwania kindlei* and *Polygnathus pireneae* in both regions.

*P. mariannae* was described from the Salmontrout and its range is given as sample 35 to 41 (280-458 feet) in section 1 (Lane & Ormiston, 1979: 51, T. 1). The range was documented with figured specimens from samples 35 and 40. The specimen from sample 41 may be disputed on the grounds that it has a different shape and only three processes, but the ornamentation is similar and it probably belongs to the *P. mariannae* apparatus. If we allow the identification of this specimen as *mariannae*, the range of *P. mariannae* begins within the range of *Pseudogondwania kindlei* in the Salmontrout section and terminates in the same bed as *kindlei* terminates. In Nevada, *P. mariannae* τ morph is positively identified from COPII 335 to COP II 378 feet (Figs. 8.1, 8.2), a second morph, *Pedavis mariannae* α morph (Murphy & Matti, 1983: pl. 8 figs. 1, 5, 6, 9, 11), that differs from the holotype of *P. mariannae* in having a shorter spindle, enters the COP II section at 295 feet. Above 378 feet are six specimens that may extend the range of *mariannae* to the top of the COP II section. An immature specimen from COP II 404 feet (Fig. 8.3) may be compared with a specimen from bed 36 of the Salmontrout (Fig. 8.4) and permissibly extends the range of *mariannae* to 404 feet in Nevada. Four fragments that together suggest the τ morph is present occur at COP II 412 feet. A sixth Nevada specimen (Fig. 8.5) in my uppermost sample at COP II and just below the faulted top of the section is similar to the specimen with three processes from Salmontrout bed 41 mentioned above. As with that specimen, it has the same type of surface ornamentation and probably belongs to the *mariannae* apparatus. Thus, I have indicated in figure 2 that the range of *mariannae* extends to the top of the COP II section, but no data support a higher range either in Alaska or Nevada. I infer that *P. mariannae* is limited to the late Pragian although Yolkin *et al*. (1989: fig. 1) have indicated its presence in the lowest Emsian in a range chart (1989: 239, fig. 1) where they show the range of *P. mariannae* extending into the range of "*Polygnathus dehiscens* (early form)" in the Zinzilban gorge section, Zeravshan Range in western Siberia. From plates kindly sent to me by L. Apekina in 1990, a *Pedavis* species very close to *P. mariannae* occurs in the Zinzilban section. Minor details of the platform element, such as, a very short posterior process, more attenuate main process, and different angle of the posterior process with respect to the main process, suggest that this form is a later member of the *P. mariannae* lineage and that the position of the transition between it and *P. mariannae* will be a close approximation of the Pragian-Emsian boundary.

The specific name *kindlei* was originally assigned to material that Lane & Ormiston (1979) described from the Salmontrout Formation in eastern Alaska. It occurs there with *Pedavis mariannae* and *Polygnathus pireneae,* but it is present also much lower in the section than either of the other two taxa have been found (Lane & Ormiston, 1979: Table 1). The original characterization separates *kindlei* from other eognathodontids solely on the basis of the position of the basal cavity (Lane & Ormiston, 1979: 54), but, as indicated above, the denticulation patterns of the upper edge of the blade also seem important in the discrimination of taxa. In this respect, the limits of the variation found in samples from Alaska and Nevada are not exactly the same but they certainly overlap. *P. kindlei* occurs in beds 30-41 of the Salmontrout (Lane & Ormiston, 1979: T. 1a). On figures 7.27-7.31, I have figured five additional specimens of *P. kindlei* from beds 28-36 of the Salmontrout from Lane and Ormiston's collection (Lane & Ormiston, 1979) for comparison with the Nevada specimens from COP II 295 feet that I have identified as *P kindlei* tau morph (Figs. 7.18-7.26).

*Polygnathus pireneae* was described from the central Spanish Pyrenees and is based on small specimens (0.45 mm maximum) that Boersma (1973: 287) distinguished by their narrow, high platform, lack of adcarinal grooves, and ornamentation of the platform consisting of "nodes or short ridges that reach the carina in adult specimens, but which do not cross the platform at the posterior." Unfortunately, Boersma did not figure a specimen that shows what he considered to be adult ornamentation and he gives no indication of the size at which adult ornamentation is present. Lane & Ormiston's (1979: pl. 5 figs. 2, 3) figured specimen from bed 37, the lowest occurrence recorded in the Salmontrout is 3 times the length of Boersma's specimens and differs in having a fused keel that extends to the posterior tip of the platform. However, the other two specimens listed from bed 37 (figured here Figs. 8.14, 8.15) are somewhat smaller and more closely resemble Boersma's specimens. The figured specimens (Lane & Ormiston, 1979: pl. 5 figs. 28-34) from bed 44 do not appear on their range chart, but are also smaller and more like Boersma's specimens than the large specimen from the base of the range. The same is true in Nevada (Murphy & Matti, 1983: pl. 1 figs. 34-38) where the smallest specimen more closely resembles the Spanish forms than the larger ones. Some of the larger Nevadan specimens, however, have a tendency to develop transverse ridges that almost cross the posterior part of the platform. I believe, that these data demonstrate that Boersma's specimens are juveniles and, therefore, that the Alaskan and Nevadan specimens are correctly identified as *Polygnathus pireneae*.

The overlap of *Pedavis mariannae, Pseudogondwania kindlei, and Polygnathus pireneae* in beds 37-41 in the Salmontrout Formation and the co-occurrence of the latter two at 295' in the COP II section at Rabbit Hill, Nevada supports the correlation of the Alaskan and Nevadan sections at these levels. A significant gap in biostratigraphic data exists in the Salmontrout below the occurrences of the *Eognathodus* fauna so that no data on the early history of the genus is available from the Alaskan sections (Lane & Ormiston, 1979: fig. 5). The Emsian boundary is approximated in Alaska and Nevada by the appearance of *Polygnathus lenzi*, which overlaps the range of *P. pireneae* in Alaska, but not in Nevada.

## CORRELATION WITH CANADA

The section along Royal Creek in the Wernecke Mountains of Yukon Territory, Canada was collected by A. Lenz and studied by Klapper (1969, 1977b) who based his early estimates of the biostratigraphy of the Pragian on the Royal Creek data and on his concurrent studies in central Nevada.

Some of the Royal Creek samples were bulk samples taken from stratigraphic intervals rather than individual beds. These bulk samples obviously provide opportunity for mixing faunas and overlap of ranges that are not seen in nature. However, the section is thick and so minimal spurious data have been detected and the general controls on the sequence are adequate to support the conclusions reached by Klapper detailed above concerning the succession within the eognathodontids. However, even in the 1969 paper, Klapper detected problems with the use of the size and position of the basal cavity as an indicator of stratigraphic position: "Although the stratigraphic distribution of the two kinds of basal cavities mentioned in the description of *Spathognathodus sulcatus* **is somewhat inconsistent**, the more extensive, heart-shaped cavity dominates in the lower range (RC 1 405-492 feet) of the species while the more restricted cavity is common in the upper range (RC 1, 647-750 feet)." If the specimens figured by Klapper (1969: figs. 1-4) are compared with specimens from the Monitor Range (IK IV 1A, Figs. 6.48, 6.49), it will be seen that the same morphs of *Eognathodus irregularis* and early "*sulcatus*" are present in both samples. In the middle part of the Royal Creek section (RC1 466-492), the deeply sulcate *profunda* χ morph dominates the assemblage (Klapper, 1969: pl. 3, figs. 5-15 from Royal Creek; Figs. 7.32-7.41 from WCX, base of the section) and is accompanied by *Pedavis brevicauda* just as it is in Nevada and Australia.

The documented range of *P. brevicauda* is short in all three regions of its occurrence and, although Mawson & Talent (1994: 47) have identified specimens in Fåhraeus (1971) and in Uyeno (1991) that they use to extend its range, these identifications can be discounted as discussed in the systematics section of this paper. The higher parts of the Royal Creek section are dominated by eognathodontid morphs with more elongate anterior processes, slender blades and generally more restricted basal cavities.

*Pandorinellina* species are rare or absent in most sections in Nevada except for *Pandorinellina? boucoti,* which occurs in the IK IV section in the Toquima Range as a series of three morphs (α, β, and γ) that appear sequentially (Murphy, 1993). Two of these same morphs (α and β) were found to appear in the same sequence at Royal Creek, in Yukon Territory (Klapper, 1969). *P. boucoti* α morph ranges from the high Lochkovian at least to the *profunda-brevicauda* Zone at Royal Creek, which is somewhat higher than it has been found in Nevada.

Professor Klapper has kindly verified that *Pand. philipi–>Pand. exigua* (Klapper, 1969: pl. 5 figs. 1-7) is present at the top of the WC XI section in the northern Roberts Mountains with *Polygnathus lenzi,* thus, showing the same association as found at the base of the Emsian in Canada. *Pandorinellina philipi* has not been found in Nevada.

Thus, there are three faunal associations at Royal Creek that match those in eastern Alaska and Nevada. The zonation proposed here for Nevada seems applicable also in Canada.

## CORRELATION WITH THE BARRANDIAN AND GERMANY

In the Barrandian, Weddige (1987) has claimed the presence of the *pandora-irregularis* transition in the type area of the Pragian at Velká Chuchle and Cikánka. However, the sequence of forms is not documented by figured specimens from a single section. Correlation between sections is implied. Other sections in the Barrandian have been studied by Slavík (2001) who found no eognathodontids in his sections and who points out (p. 254) some of the inadequacies of the IUGS global subdivision of the Pragian in its type region. Slavík (2001: 266) and Slavik & Hladil (2004: 145) also repeat the claim of Schönlaub in Chlupác *et al.* (1985) that *Caudicriodus steinachensis* η is a good marker close to the base of the Pragian in the Barrandian. This taxon starts well down in the Lochkovian in other regions (Klapper & Johnson, 1980: table 3) and should not be used without verification by other taxa that the occurrences are indeed Pragian. This all suggests to me that the Barrandian is not a good place to put reference sections based on conodonts for the external and internal boundaries of the Pragian.

The condensed section in the Frankenwald, Germany, which exposes only a few thick beds of limestone, but gives the opportunity to see the Lochkovian-Pragian transition and some of the section immediately above and below the boundary, was described by Murphy *et al.* (1981: fig. 9). The lower three beds exposed in the Flemersbach quarry in the Frankenwald produced an upper Lochkovian fauna mainly of *Masaraella pandora* morphs (beds GPIM Gö 1821-1823). According to Murphy *et al.* (1981: fig. 9), the next bed in the sequence contained several specimens of *Eognathodus sulcatus* eta morph (= *Eognathodus irregularis*). The beds above yielded only sparse collections but they included both *pandora* morphs and two *Gondwania* morphs with restricted sulci and large basal cavities like those found in Nevada in the upper *irregularis-profunda* and lower *profunda-brevicauda* Zones. Al Rawi (1977) also has figured a similar specimen from the Frankenwald. O. H. Walliser has permitted study of an unfigured specimen of *G. profunda* χ in his collection (G-P Institut, Göttingen Wa 1868) from the Frankenwald. Thus, although specimens are rare or absent in middle European sections, the sequence of late *pandora* and early *Eognathodus* morphs is similar to those of Nevada, but late Pragian *Eognathodus* have not yet been discovered in western Europe.

## CORRELATION WITH AUSTRALIA

Druce (1971: pl. 4 figs. 4-7) described *Eognathodus irregularis* from the Garra Formation in New South Wales, but its stratigraphic significance at that time was a matter of speculation. The later work of Wilson (1989) on the Garra put the faunas in stratigraphic context and demonstrated that the earliest Pragian is represented in New South Wales. Wilson reports a co-occurrence of *Amydrotaxis praejohnsoni* Murphy & Springer, 1989 (his *johnsoni* beta, Wilson, 1989: pl. 10 figs. 1, 2, and 5, Table 1) and *E. irregularis* from his GCR section. This would indicate an extension of *praejohnsoni* into the Pragian or a very early record of *E. irregularis* in the Lochkovian. Unfortunately he didn't figure any *praejohnsoni* from the part of the section that overlaps the range of *E. irregularis,* and, thus, these identifications need to be verified.

Farther south in Victoria, the Pragian section at Tyers Quarry and at nearby Boola Quarry rests on an unconformity and the early part of the Pragian is missing as inferred from the co-occurrence in the Boola Quarry section of *Gondwania* morphs with *Pedavis brevicauda* only 1 meter above the base of the section (Mawson & Talent, 1994: Table 1). This is probably also true along the southeastern edge of the continent at Waratah Bay as already suggested by Mawson & Talent (1994: 43) in their refutation of the taxonomic assignments of Bischoff & Argent (1990) of fossils from the Waratah Bay sequence. They (Mawson & Talent, 1994: 43, 44) also doubt the documentation of the upper part of the Pragian at Waratah Bay by the presence of *Polygnathus pireneae* and "*Eognathodus sulcatus* $\mu$". I agree with Mawson and Talent and add that denticle configuration of the blade and the shape of the basal platform lobes of the $\mu$ morph differ in essential ways from those figured by Bischoff & Argent (1990: pl. 2 figs. 26-32, pl. 3 figs. 1-3). Thus, there is no evidence based on an occurrence of an eognathodontid that any part of the two sequences in Victoria is late Pragian and the assessment of Mawson *et al.* (1988: fig. 2) that the sections in southeastern Australia do not record upper Pragian strata still seems reasonable. The inferred relationships of eognathodontid species ranges in the sections in central Nevada, Arctic North America, central Europe, and Victoria, Australia are shown in figure 5.

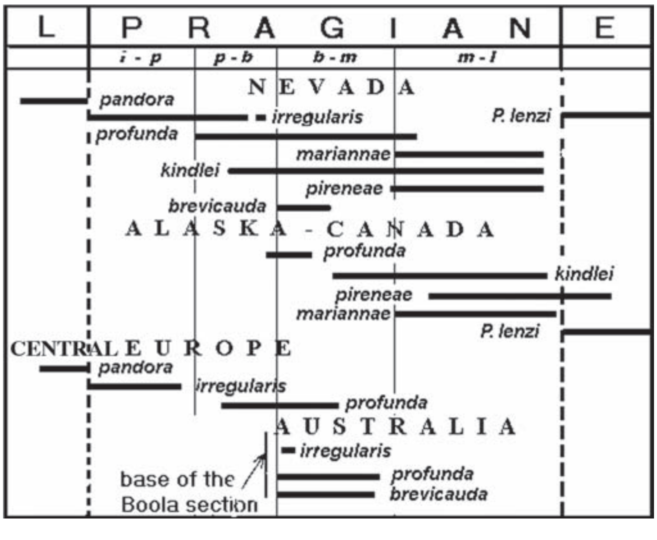


**Figure 5**. Comparative conodont range chart of main areas of study of the Pragian Stage. Identifications are based on my observations of the collections from these areas and do not in all cases reflect those of the original authors. L – Lochkovian; E –Emsian. The Boola section is in Victoria adjacent to the type area of *E. sulcatus* (see Mawson & Talent, 1994).

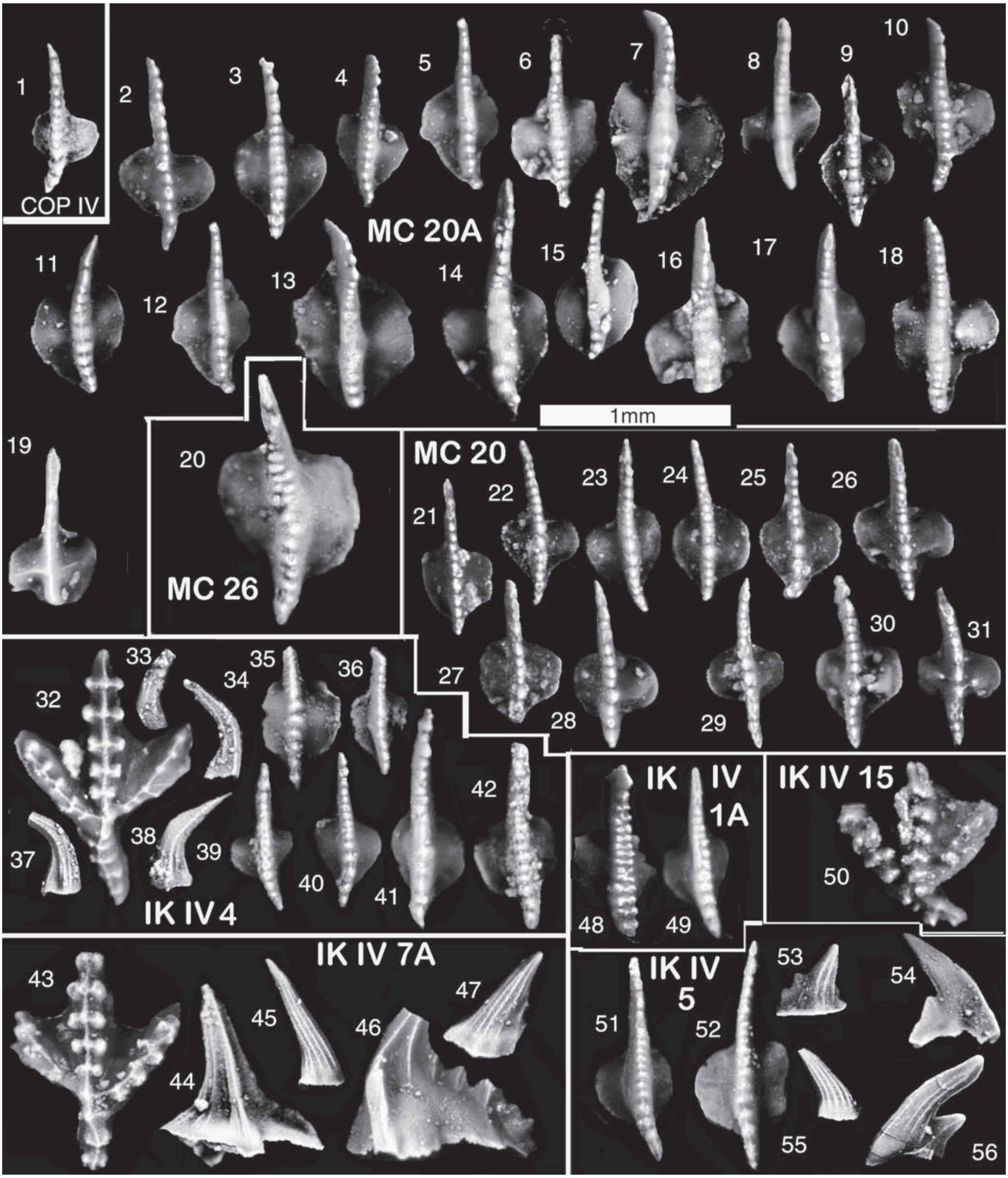
## CONCLUSIONS

This review suggests the following:

1. The boundary-stratotype section and region for the lower Pragian is not satisfactory and should be relocated.

2. The internal subdivision of the Pragian as envisioned by the SDS has serious limitations and is inapplicable as a global standard of comparison (Valenzuela-Ríos, 1997).

3. The four subdivisions suggested for Nevada, although not ideal, are applicable in western North America.



4. A new taxonomic nomenclature is needed for the Eognathodontidae and the one proposed by Bardashev *et al.* (2002) can be adapted to fill part of this need.

5. *Eognathodus sulcatus* is unsatisfactory as a zonal name bearer for the early Pragian because of its late appearance in the stage, its limited geographic distribution, and insufficient data to assess infraspecific variation.

6. *Pseudogondwania kindlei* is unsatisfactory as the name bearer for the second zone of the Pragian because of its long range, however, the τ morph appears to be useful in correlation between the high parts of the Pragian sections in Nevada and Arctic North America.

7. *Polygnathus pireneae* Boersma is unsatisfactory as the name bearer for the highest Pragian zone because its adult morphology is as yet unknown and, thus, its range is unknown (Valenzuela-Ríos, 1997).

8. Johnson's (1974) brachiopod intervals 5 and 6 based on collections from Rabbit Hill at COP II are both in the upper half of the Pragian and not as depicted in his last work (Johnson *et al.*, 1996) and the base of the Rabbit Hill Limestone is significantly below the known occurrence of brachiopod fauna 5.

9. The transgression that begins the global cycle 1a of Johnson *et al.,* (1996) as recorded at Willow Creek in Nevada is slightly younger in Nevada (lower *brevicauda-mariannae* Zone) than the record at Tyers and Boola in Australia (upper *profunda-brevicauda* Zone).

10. Nevada has the most complete sections and most diverse faunas, which should be evaluated as the standard reference section for the Pragian.

## SYSTEMATIC PALEONTOLOGY

### Introduction

Bardashev *et al.* (2002) have proposed a comprehensive classification of the taxa normally assembled in *Eognathodus* and early *Polygnathus* and have given Linnaean names to a large number of specimens figured in the previous literature. Because it is incumbent upon us to respect priority even if we do not agree with the philosophy underlying a classification, these names must be used except in cases where they clearly are not valid. In the paragraphs that follow, I discuss first the reason that the classification of Bardashev *et al.* (2002) fails and then the new nomenclature.

Bardashev *et al.* (2002: 381) concluded that for taxa normally put in *Eognathodus*: 1) only the Pa elements should be used in establishing conodont nomenclature; 2) "The size and location of the basal cavity are the most important features defining the generic and suprageneric assignments of pectiniform elements; 3) the kind of symmetry shown by the basal platform lobes is an important diagnostic feature.

Point 1. The importance of the Pa element in conodont taxonomy is obvious. However, it has been clear for more than thirty years that the Pa element doesn't tell the whole story and that many lineages have very distinctive apparatus elements that can not be mistaken for those in other lineages even if the apparatuses of closely related species in the same lineage are difficult to distinguish (Jeppsson, 1969; Klapper & Philip, 1971, 1972; Sweet, 1988).

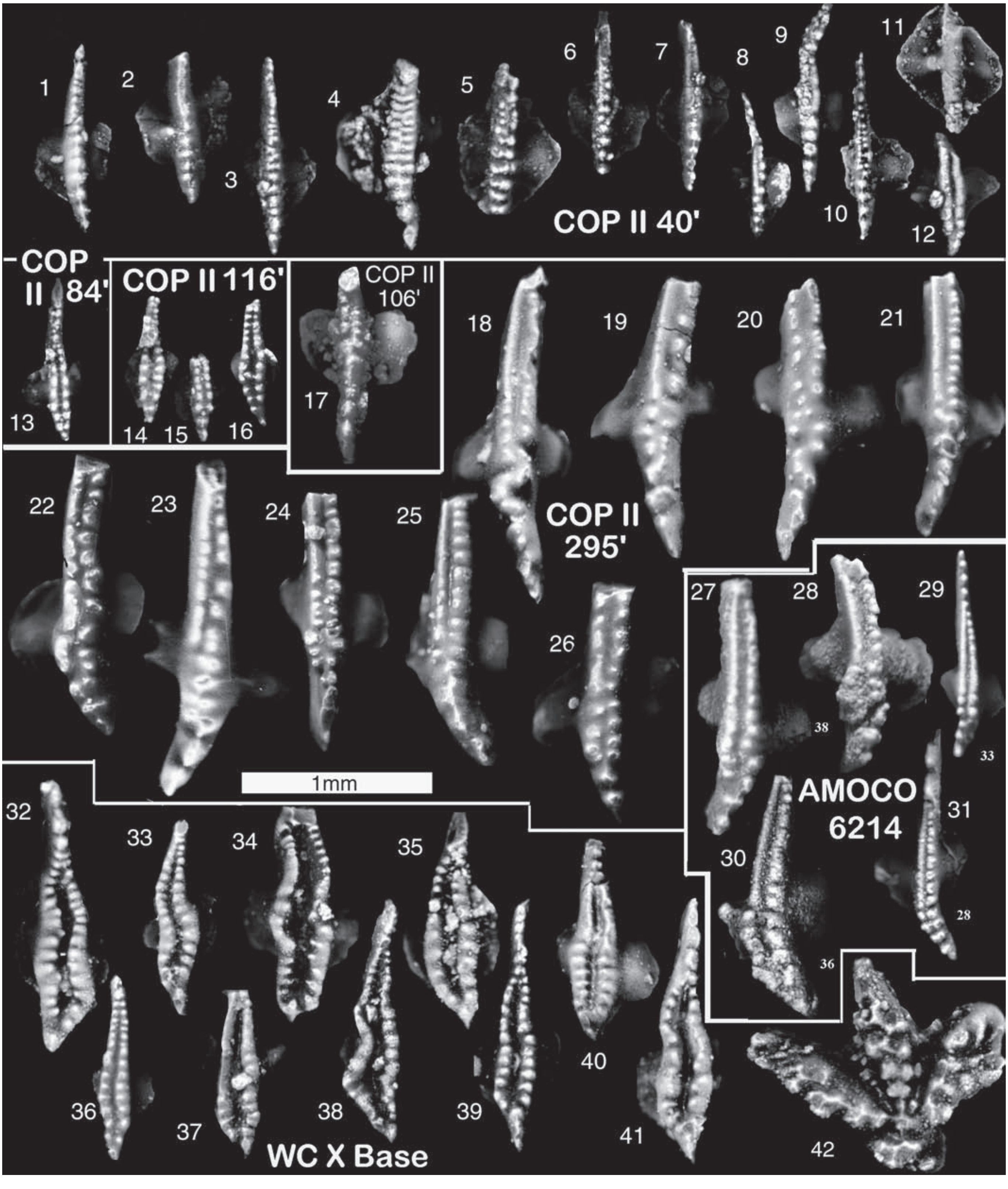
With respect to point 1, Bardashev *et al.* (2002: 383) chose *Eognathodus linearis* Philip, 1966 as the root stock of the hypothesized phylomorphogenetic development of their genus, *Gondwania*. Based on points 1-3 in their list, they assigned it to *Amydrotaxis*, a genus with a well-known and well-documented apparatus reconstruction from the Late Silurian-Early Devonian (Klapper & Murphy, 1980; Pickett, 1980; Murphy & Matti, 1983; Mawson, 1986; Uyeno, 1998). However, since *E. linearis* is an Emsian species known only from Australia Mawson *et al.* (1992: tab. 2-6) and since the *Gondwania* clade needed a late Lochkovian or early Pragian position of stratigraphic origin, they

**Figure 6.** **1**, *Masaraella pandora* (Murphy, Matti & Walliser, 1981); Pa element COP IV 120 feet. **2-18**, *Eognathodus irregularis* Druce, 1971; Pa elements, MC 20A, variation series at the base of the Pragian in the Mill Canyon section, Toquima Range, Nevada; 2-5, 9, α morph; 6, 8, 10, β morph; 11, 12, ζ morph; 13-17, η morph; 18, ε morph. **19**, *Masarella riosi* n. sp. MC 20A, Mill Canyon section, Toquima Range, Nevada. **20**, *Eognathodus irregularis* Druce, 1971; Pa element, MC 26, *irregularis-profunda* Zone, Mill Canyon section, Toquima Range. **21-31**, *Masaraella pandora* (Murphy, Matti & Walliser, 1981); MC 20, uppermost bed of the Lochkovian (*gilberti-irregularis* Zone), Mill Canyon, Toquima Range; 21-25, 27, α morph; 26, 28, 29, α–> β morph intermediate morphs; 30, β morph; 31, γ morph; to show the range of variation in the shape and position of the basal platform lobes and basal cavity.

Common taxa of the lower *profunda-brevicauda* Zone, Toquima Range (32-42, 48, 49). **32-34**, **37**, **38**, *Pedavis longicauda* n. sp., IK IV 4. 32; Pa element, holotype; 33, 34, 37, 38, M elements. **35**, **36**, **39-42**, *Eognathodus irregularis* Druce, 1971; 35, 36, 40-42 ζ morphs; 39, α morph; 48, 49, η morphs, IK IV 1A.

Common taxa of the upper *irregularis- profunda* Zone, IK IV, Toquima Range (43-47, 51-57). **43-47** *Pedavis longicauda* n. sp., IK IV 7A; 43, Pa element; 44, $M_{2A}$ element; 45, 47, undetermined M elements; 46, $S_1$ element. **51-52**, *Eognathodus irregularis* Druce, 1971, IK IV 5; 51, zeta morph, Pa element; 52, eta morph, Pa element. **53-56**, *Pedavis* sp. undetermined S and M elements, IK IV 5, possibly from the *P. longicauda* apparatus as they occur within the range of *P. longicauda*. **50**, *Pedavis gilberti* Valenzuela-Ríos, 1994, Pa element, IK IV 15, Toquima Range; zone fossil for the upper Lochkovian *gilberti-irregularis* Zone.

expanded the concept of *linearis* to include *“Ozarkodina ‘linearis’* (Philip)*”* of Klapper (1977b: fig. 3, p. 40; = Klapper & Johnson, 1980: pl. 1 figs. 13-16; = *O. pandora* ζ morph of Murphy *et al*., 1981: pl. 1 figs. 10-24; = *Masaraella pandora* ζ morph herein). This is the same taxon that Murphy *et al*. (1981) treated as part of the late Lochkovian variation among the *“O.” pandora* morphs and is the morph morphogically closest to *Eognathodus irregularis*. I know only one report citing true *linearis* as being in the same stratigraphic interval as an *Amydrotaxis* apparatus



element (Mawson *et al.,* 1992). In that case, a Pa (unfigured) and a Pb element were reported from successive samples in the range of *linearis,* bur not occurring with it. As for the misidentified *"linearis",* I know of no occurrence of *Amydrotaxis* elements with it. Thus, in assigning this taxon to *"Amydrotaxis linearis",* Bardashev *et al*. (2002) have discarded the reconstructions that have been made of the *Amydrotaxis* apparatus, which is one of the more distinctive and easily recognized apparatuses of the Lower Devonian. Also, instead of figuring the taxon that can be demonstrated to occur in stratigraphical continuity with the first *Eognathodus,* they inexplicably figure the Emsian *"Ozarkodina" linearis* as the late Lochkovian ancestor of their *Eognathodus* and *Gondwania* branches of the Eognathodontidae (Bardashev *et al*., 2002: figs. 7 and 11).

In the process they also modify the characterization of *Amydrotaxis* in their diagnosis (Bardashev *et al*., 2002: 392) as follows "completely open carminiscaphate basal cavity … anteriorly upraised, forming a semicircular 'plummage'." The emendation completely changes the diagnosis of *Amydrotaxis*, so much so that the type species would no longer qualify for assignment to the genus. Not only is the apparatus ignored, which was the main focus of the original authors (Klapper & Murphy, 1980: 492), but also the morphology of the type species is ignored (Klapper, 1969: pl. 5 figs 8-16). In none of the figures of Klapper (1969), Klapper & Murphy (1980), Pickett (1980), Mawson & Talent (1984), Murphy & Matti (1983), Murphy & Springer (1989), or Uyeno (1990) is there a "semicircular plumage" at the anterior end of the blade. In fact, *Amydrotaxis* characteristically has a single large, triangular denticle, low triangular denticles, or no development of a cockscomb at the anterior end of the blade.

Points 2 and 3. The symmetry, size, and shape of the basal platform lobes (or the basal cavity in lower view) are important discriminators in some members of the group, but the variation series shown in the plates suggests that a better interpretation of their interrelationships is that this characteristic was variable in the taxa *pandora, irregularis*, and *profunda* (at least) and cannot be used to distinguish between them (Figs. 6.1-6.15; Figs. 7.1-7.11, 7.12-7.16; Figs. 8.6-8.8 and Figs. 7.32-7.41, respectively). For example, Bardashev *et al*. (2002: figs. 11, 12) refigure two specimens from Murphy *et al*. (1981) and place them in different genera on the basis of the appressed vs. wedge-shaped posterior groove. These two specimens originally were placed in the kappa and lambda morphs of *sulcatus* (Murphy *et al*., 1981) and were found with the specimens figured here (Figs. 7.32-7.41) in the lowest bed of the Kobeh Limestone in the Willow Creek section of the northern Roberts Mountains, Nevada. This example shows that it is important to evaluate each character independently in each sample to learn which character is important for taxonomy and which is so variable that it gives spurious results.

In summary, their assignment of a species to a genus and the consequent generic nomenclature is based on their interpretation of the time of origination of the specific-rank taxon (Bardashev *et al*., 2003: fig. 11) and this in turn is based on a preconceived notion of the value of particular characters for taxonomy. As a consequence of this approach, variants from the same bed are in different genera and species from different lineages are in the same genus, and as pointed out by Prof. Walliser, *Eognathodus* is derived from two different genera, *Amydrotaxis* and *Spathognathodus* (Bardashev *et al*. 2003: Figs.11, 12)

I reject as being inapplicable the concept that one can determine *a priori* that a particular characteristic has value at a particular taxonomic level or for a particular period of time.

I regard all characters as useful for taxonomic purposes. Those that are consistently present or similar within the same stratigraphical populations or through a specific stratigraphic interval are especially important, but no particular characteristic has intrinsic value at the generic or familial level etc, nor does it necessarily have the same significance at the same rank throughout the group or during the same time interval, because we accept evolution as a guiding principle in biology and both heterochrony and convergence have been demonstrated. A character may have significance at the family, genus or species level, but the significance must be learned by experience and it must be recognized that new data may modify our interpretations.

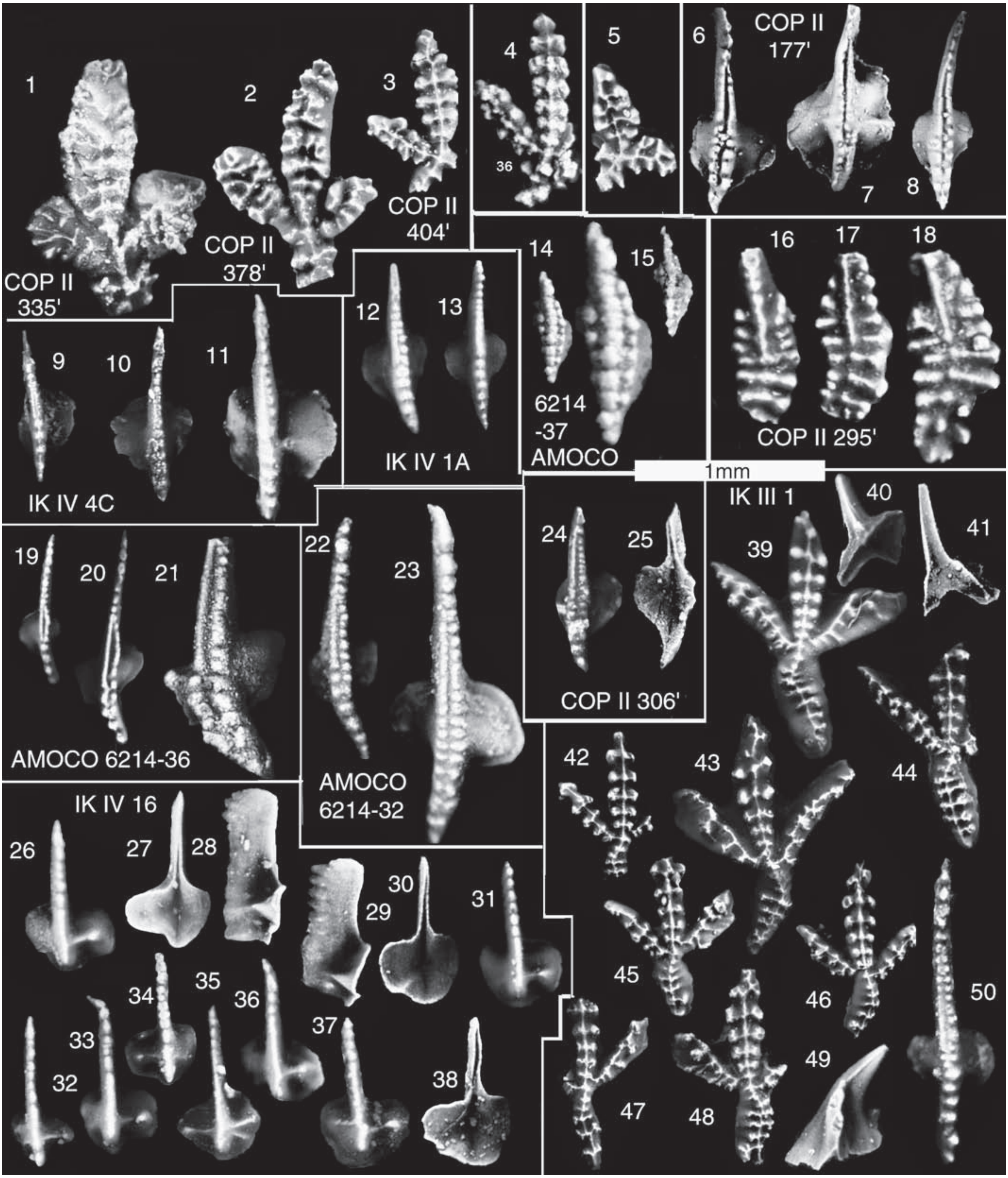
Bardashev *et al*. (2002) also listed characteristics that they believed to be important for the taxonomy of specimens normally placed in *Polygnathus,* but these are outside of the scope of this paper and will not be addressed here.

**Figure 7**. **1-11**, *Eognathodus irregularis* Druce, 1971, Pa elements, Rabbit Hill Limestone, Copenhagen Canyon, Monitor Range, Nevada, COP II 40 feet; 1, zeta morph (ζ); 2, 12, epsilon morph (ε); 3-6, eta morph (η); 7-10 theta morph (θ). Figures **11**, **13-16**, *Gondwania profunda* n. sp., chi morph (χ) new morph, Pa element, Rabbit Hill Limestone, Copenhagen Canyon, Monitor Range, Nevada; 11, COP II 40 feet; 13, COP II 84 feet; 14-16, COP II 116 feet. **17**, *Pseudogondwania kindlei* (Lane & Ormiston, 1979), sigma morph (σ), new morph, Pa element, Rabbit Hill Limestone, Copenhagen Canyon, Monitor Range, COP II 106 feet. **18-31**, *Pseudogondwania kindlei* (Lane & Ormiston, 1979), tau morph, new morph, Pa elements; 18-26, Rabbit Hill Limestone, Copenhagen Canyon, Monitor Range, Nevada, COP II 295 feet; 27-31, AMOCO 6214, Salmontrout Formation, Salmontrout River, eastern Alaska, small numbers refer to bed numbers in the Salmontrout section. **32-41**. *Gondwania profunda* n. sp., psi morph (ψ) new morph, late form, McColley Canyon Formation, northern Roberts Mountains, Willow Creek section X (WC X), Basal bed. **42**, *Pedavis brevicauda* Murphy, Matti & Walliser, 1981, Pa element, McColley Canyon Formation, northern Roberts Mountains, Nevada, Willow Creek section X (WC X), Basal bed.

## Order OZARKODINIDA Dzik, 1976
## Family **Spathognathodontidae** Hass, 1959

**Diagnosis:** Ozarkodinids that primitively have a sexmembrate or septemmembrate skeletal apparatus whose members have a carminate Pa element, angulate Pb element, dolabrate M element, and a symmetry transition series in which the Sa element normally does not develop a denticulate posterior process.

**Discussion:** Sweet (1988: 90) regarded the Spathognathodontidae as the root from which all of the other ozarkodi-



nid families were derived and believed them to be a long-ranging, plastic collection of taxa that developed their so-called platforms in a variety of ways. Some of the variations developed into clades that became the dominant elements of the later Paleozoic conodont faunas and others persisted only briefly and disappeared. It is reasonable to conclude that such a large and varied group is difficult to characterize and will be further subdivided as knowledge increases.

Bardashev *et al.* (2002) have restricted the family somewhat by separating it from the Eognathodontidae, which they erect for taxa with Pa elements whose platform develops from the ledge at the base of the denticle row at the top of the blade (see Murphy & Valenzuela-Ríos, 1999, for nomenclature of spathognathodontid Pa element). This means that the taxonomic boundary between the Spathognathodontidae and the Eognathodontidae is the same boundary as between the genera *Masaraella* n. gen. and *Eognathodus* (= boundary between *Masaraella pandora* ζ morph and *Eognathodus irregularis* η morph).

## Genus *Masaraella* new genus

**Type species:** *Ozarkodina pandora* Murphy, Matti & Walliser, 1981.

**Derivation of the name:** *masar* – New Latin (Borror, 1960), to stick out the lip, alluding to the expansion of the basal cavity in the posterior part of the blade**.**

**Diagnosis:** A spathognathodontid genus whose Pa element has a large basal cavity in the posterior part of the element, pinched posteriorly or open to the posterior end, normal in-line or suppressed denticulation without a cusp and white matter distribution restricted to the denticles and upper part of the blade. The Pb element is angulate pectiniform with both processes well developed and with numerous nearly uniform denticles.

**Discussion:** *Masaraella* new genus is established to accommodate apparatuses that developed during the late Lochkovian from the general stock that was included in "*Ozarkodina remscheidensis* Ziegler, 1960". It includes *M. pandora, M. epsilon* n. sp., and *M. riosi* n. sp. The restriction of *Ozarkodina* to forms with unique white matter distribution and erection of *Zieglerodina* for the type of *Spathognathodus remscheidensis* Ziegler (Murphy *et al.*, 2004) leaves many other taxa without a generic home. *Masaraella* partially fills this nomenclatural void.

## *Masaraella pandora*
## (Murphy, Matti & Walliser, 1981)

Figs. 6.1, 6.21-6.31

**Discussion:** The nomenclature applied to the clade that includes *Masaraella* and the eognathodontids in this paper follows that introduced by Murphy *et al.* (1981), but adds some new morphs and adjusts the ranges of some previously described morphs in the light of data accumulated since 1981. Six morphs of *M. pandora* were described by Murphy *et al.* (1981: fig. 4) and designated by the Greek letters α–>ζ. This paper modifies and clarifies the morphologic content of the *pandora* morphs as follows: All *pandora* morphs were distinguished from their ancestors

**Figure 8**. **1-5**, *Pedavis mariannae* Lane & Ormiston, 1979, Pa elements, Rabbit Hill Limestone, Copenhagen Canyon, Monitor Range, Nevada; 1, COP II 335 feet; 2, COP II 378 feet; 3, Immature Pa with broken outer lateral process, COP II 404 feet to compare with Figure 4; 4, Immature Pa, AMOCO 6214-36, type section of the Salmontrout Formation, Alaska; 5, ?S element, G-38-3, bed above the fault repeating part of the COP II section, probably equivalent approximately to the G38-2 horizon just below the fault. **6-8**. *Gondwania profunda* n. sp., omega morph (ω), new morph, Pa elements, Rabbit Hill Limestone, Copenhagen Canyon, Monitor Range, Nevada, COP II 177 feet. **9-11**, *Eognathodus irregularis* Druce, 1971, theta (θ) morph of Murphy *et al.* (1981), Pa elements, McMonnigal Limestone, Ikes Canyon, Toquima Range, Nevada, IK IV 4C. **12**, **13**, *Gondwania irregularis* (Druce, 1971), theta (θ) morph of Murphy *et al.* (1981), Pa elements, McMonnigal Limestone, Ikes Canyon, Toquima Range, Nevada, IK IV 1A showing slightly longer blade than in figures 9-11. **14-15**, *Polygnathus pireneae* Boersma, 1973, Pa elements from AMOCO 6214-37, Salmontrout Formation, Alaska; 14, juvenile Pa element at standard and double sizes to show character of juvenile platform; 15, additional juvenile specimen from sample 6214-37. **16-18**, *Polygnathus pireneae* Boersma, 1973, Rabbit Hill Limestone, Copenhagen Canyon, Monitor Range, Nevada, COP II 295 feet, mature Pa elements, to show variation in mature ornamentation of platform. **19-23**, *Pseudogondwania kindlei* (Lane & Ormiston, 1979), tau morph, Pa elements, Salmontrout Formation, Salmontrout River, eastern Alaska; 19-21, AMOCO 6214-36; 22, 23, AMOCO 6214-32. **24**, **25**, *Gondwania profunda* n. sp., chi (χ) morph, new morph, Pa element, Rabbit Hill Limestone, Copenhagen Canyon, Monitor Range, Nevada, COP II 306 feet, top and basal views, highest known occurrence of χ morph. **26-38**, *Masaraella riosi* n. sp. Pa elements, Ikes Canyon, Toquima Range, Nevada IK IV 16; 26, top view, IV 16/13C, holotype; 27, 28, basal, and lateral views, IK IV 16/14A; 29, 30,lateral and basal views IK IV 16/14C; 31, IK IV 16/13A; 32, top view IK IV 16/6B; 33, top view IK IV 16/13G; 34, top view IK IV 16/13F; 35, top view, IK IV 16/13B; 36, top view IK IV/13D; 3**7,** top view IK IV 16/13E; 38, IV 16/14B. **39-49**, *Pedavis longicauda* n. sp. Ikes Canyon, Toquima Range, Nevada; 39, I element, IK III/1; 40, 41, M element, IK III/32B; 42-48, I elements, IK III/16, IK III/2, IK III/14, IK III/20, IK III/19, IK III/5, IK III/15; 49, $S_1$ element IK III/29B. **50**. *Pseudogondwania kindlei* (Lane & Ormiston, 1979), sigma (σ) morph, new morph, McColley Canyon Formation, northern Roberts Mountains, Willow Creek section X (WC X), Basal bed.

in having 1) a basal cavity that was open to the posterior end of the Pa element as opposed to the walls of the posterior quarter of the blade being parallel or appressed, 2) a tendency for the development of a smaller cusp or lack of cusp development, and 3) a tendency to develop more robust Pa elements with larger basal cavities. 4) Morphs α, β, and γ were distinguished from one another on the basis of having the aligned, pointed denticles on a slender blade that were characteristic of the ancestral taxa and a basal platform ornamentation of none, one, or two tubercles, respectively; 5) δ, ε, and ζ were distinguished on the basis of their more robust blades and two, one, or no platform tubercles, respectively, and either a fused or suppressed denticle row or an adenticulate, smooth rounded blade crest posterior of the cockscomb. Present data suggest that the delta and epsilon morphs should be revised.

### delta morph

Two specimens were figured in Murphy *et al.* (1981: pl. 1 figs. 35, 42, 45, and 33, 40, 44) from COP IV 377 feet (UCR 6265/6) and MC 20A (UCR 8571/2). Only the former is characteristic of the morph as restricted here. The specimen from MC (Mill Canyon, Toquima Range) has a different morphology and is assigned to *M. riosi* n. sp. below.

### epsilon morph

Current data suggest that the epsilon morph of *M. pandora* starts out in the upper Lochkovian as part of the variation series of *pandora*, but survives in the Pragian as an independent lineage for which we know no intermediate varieties connecting it to the *M. pandora-Eognathodus* branch of the group. For this reason and to keep the nomenclature of Murphy *et al.* (1981) consistently applied to the group, I describe it below as *Eognathodus epsilon* n. sp. Where this morphology is part of the variation within *Masaraella pandora,* it takes the name *Masaraella pandora* epsilon morph; where it is part of the variation within *Eognathodus irregularis,* it takes the name, *Eognathodus irregularis* epsilon morph. Where it is part of the independent lineage, it takes the name *Eognathodus epsilon* n sp. and is described below under *Eognathodus*.

## *Masaraella riosi* n. sp.

Fig. 6.9, Figs. 8.26-8.38

1981. *Ozarkodina pandora*. Murphy, Matti & Walliser, pl. 1 figs. 33, 40, 44.

**Holotype:** Specimen figured on Figs. 8.26-8.28, from IK IV 16, Ikes Canyon, Toquima Range, Nevada (Locality data in Murphy, 1989: fig. 5, table 1).

**Derivation of the name:** To honor Professor José Ignacio Valenzuela-Ríos for his work in the Spanish Pyrenees.

**Diagnosis:** A *Masaraella* species based on the Pa element whose basal cavity occupies 40 to 50 percent of the posterior part of the element, extends farther posteriorly than the posterior blade and has a rounded posterior termination, with the denticles in the vicinity of the cusp and on the posterior blade partly or completely fused so that the blade is smooth.

**Description:** Pa element characterized by a straight or nearly straight, blade that has some part of the middle segment of the blade crest smooth or with low, fused denticles, posterior denticles completely fused and a low cockscomb anteriorly; basal platform lobes with a ridge alone or with a tubercle on one or both of the lobes that may be connected to the blade by a thin ridge; basal cavity large and open.

**Range:** Its first occurrence is in bed TO-I D in the *gilberti-irregularis* Zone of the late Lochkovian. It is last seen from COP II 295 feet with the first occurrence of *Pedavis mariannae* in the upper Pragian (from four beds in the TO-I section, 101.5 to 109 feet). TO-I D (3), TO I=E (4), TO-I F (1), TO-I, UCR 9460.

**Remarks:** The Pa element of *Masaraella riosi* is in some respects a homeomorph of the Silurian "*Spathognathodus*" *crispus* (Walliser, 1964).

## Family **Eognathodontidae** Bardashev, Weddige & Ziegler, 2002 [*nomen correctum,* herein]

**Diagnosis:** An ozarkodinid family characterized by Pa elements whose blades have irregularly spaced, arranged, and shaped tubercles or a longitudinal sulcus bordered by ridges or noded ridges.

**Discussion:** Bardashev *et al.* (2002) introduced the "Eognathodidae" to accommodate the taxa between the Spathognathodontidae and the Polygnathidae that have a carminiscaphate Pa element and two or three noded ridges on the platform posterior to the cockscomb. Because of their rigid adherence to the *a priori* determination that the basal cavity shape and position do not vary at the species level of taxonomy, they have excluded *kindlei* from the Eognathodontidae and have placed it in the new genus, *Pseudogondwania,* in the Spathognathodontinae (Bardashev *et al.*, 2002: 427), which they appear to classify as a subfamily of Polygnathidae, but perhaps this appearance is just a consequence of the way the text of their paper was collated. Their classification derives from the fact that *kindlei* has a restricted basal cavity in the mature stages and, therefore, cannot be in their Eognathodontidae.

I accept their restriction of *Eognathodus* to the taxa closely related morphologically to the holotype of *E. sulcatus*. I also accept their assignment of *irregularis* to *Eognathodus,* because it is close to *E. sulcatus,* type species

| | | *Masaraella* | | | | | | *Eognathodus* | | | *Pseudogondwania* | | | | | | *Gondwania* | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | TAXON / CHARACTER | *pandora α* | *pandora β* | *pandora γ* | *pandora δ* | *pandora ε* | *pandora ζ* | *irregularis* | *secus* | *sulcatus* | *profunda χ* | *profunda ψ* | *profunda ω* | ssp. A Savage | "*sulcatus*" | *nevadensis* | *kindlei λ* | *kindlei μ* | *kindlei τ* |
| | BASAL CAVITY | | | | | | | | | | | | | | | | | | |
| 1 | heart-shaped | X | | | X | X | X | X | X | | X | X | X | | X | X | | | |
| | tear-drop-shaped | X | X | X | | X | X | X | X | X | X | X | X | X | X | | | | |
| | restricted, quadrate | | | | | | | | | | | | | | | | X | X | |
| | restricted, quadrate, oblique | | | | | | | | | | | | | | | | | X | X |
| | restricted, lenticular | | | | | | | X | | | | | | | | | | | |
| 2 | BLADE ORNAMENT | | | | | | | | | | | | | | | | | | |
| | in-line palisade denticles | X | X | X | | | | | | | | | | | | | | | |
| | in-line, short denticles | | | | X | X | X | | | | | | | | | | | | |
| | irregular, linear denticles | | | | | | | X | | | | | | | | | | | |
| | irregular denticles/tubercles | | | | | | | X | X | | | | | | | | | | |
| | ridge with spurs | | | | | | | X | | | | | | | | | | | |
| | transverse pattern | | | | | | | X | | | | | | | | | | | |
| | trilineate denticles/tubercles | | | | | | | | | X | | | | | | | | | |
| | smooth or partly smooth | | | | X | X | | | | | | | | | | | | | |
| | fully sulcate | | | | | | | | | | X | X | X | X | X | | X | | X |
| | partly sulcate posterior | | | | | | | | | | | | | | | X | | | X |
| | mid-blade sulcus | | | | | | | | | | | | | | | X | | X | |
| | sulcate with tubercles | | | | | | | | | X | | | | | | | | | |
| | shallow sulcus | | | | | | | | | X | X | | | | X | X | X | X | X |
| | deep sulcus | | | | | | | | | | X | X | | X | | | | | |
| | deep narrow sulcus | | | | | | | | | | | | X | | | | | | |
| 3 | ANTERIOR PROCESS | | | | | | | | | | | | | | | | | | |
| | long | | | | | | | | | | | | | | | | X | X | X |
| | medium | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | | | |
| | short | X | X | X | X | X | X | X | | | | | | X | | | | | |
| 4 | BLADE | | | | | | | | | | | | | | | | | | |
| | straight | X | X | X | X | X | X | X | X | X | X | X | X | | X | X | X | | |
| | bent | X | | | | | | | | | | | | X | | | | X | X |
| | arched | X | X | X | X | X | X | X | | | X | X | X | | X | | | | |
| | narrow | X | X | X | | | | | | | | | | | X | | X | X | X |
| | wide | | | | X | X | X | X | | | X | X | X | | | | | | |
| | very wide | | | | | | | | X | X | | | | X | | | | | |
| | slightly sigmoidal | | X | X | | | X | X | | | | | | | | | | | |
| 5 | BASAL LOBE | | | | | | | | | | | | | | | | | | |
| | 0 tubercles | X | | | | | X | X | X | X | | X | X | X | X | X | X | X | X |
| | 1 tubercle | | X | | | X | | X | | | | | | | | | | | |
| | 2 tubercles | | | X | X | | | X | | | | | | | | | | | |

**Table 2**. Distribution of character states in the Eognathodontidae of Nevada.

The characters evaluated are the five categories in the left hand column: 1 the shape of the basal cavity; 2 – the character of the crest of the blade posterior of the cockscomb; 3 – the relative length of the anterior process (long = greater than half the length of the Pa element; medium = between 1/2 and 2/3 the length of the Pa element; short = 1/3 or less of the length of the Pa element); 4 – the character of the blade in upper view; 5 – whether or not the basal lobe bears tubercles. Examination of the table shows that basal cavity shape is not a critical feature in the discrimination of the mature stages of most taxa, however, it is useful for the discrimination of the taxa in *Pseudogondwania* from the remainder of the Eognathodontidae.

of *Eognathodus,* in morphology and sequential in age. I place *Pseudogondwania* in the Eognathodontidae because I believe it is derived from *Eognathodus* in the manner outlined above from among the variants of *E. irregularis* and does not give rise to any polygnathtid. Their derivation of *Pseudogondwania* from "*Spathognathodus" optima* (= *Pandorinellina optima*) (Bardashev, *et al.,* 2004) cannot be sustained. *P. optima* is characterized by Pa elements with a more anterior position of the basal cavity and differentiated cockscomb commonly offset to the right from the posterior blade (Klapper, 1969).

During the evolution from spathognathodontid to eognathodontid, the denticle row at the crest of the spathognathodontid blade is changed and replaced by a number of other features that are confined to the crest of the blade (see table 2). Some of these developments may still be homologous with the denticles because the initial step in the sequence of changes seems to be a simple irregular alignment of the denticle row (Murphy, 1989: figs. 1.3, 1.5, and 1.6). It is not clear how some other blade-crest patterns, such as that shown by Murphy *et al.* (1981: pl. 2 fig. 26), have developed. In the latter case, at least two scenarios should be considered: 1) that the denticle row expanded transversely and would still be homologous or 2) that this type of protuberance developed on the crest of the blade after complete fusion of the spathognathodontid denticle row and that it represents a new morphologic feature, one not homologous with the denticle row. The terms applied to these elements of the morphology should not indicate that they are the same and authors have used other terminology, such as, "nodes" or "tubercles" for these features. I use "denticles" only if the homology is apparent.

## Genus *Eognathodus* Philip, 1965

**Type species:** *Eognathodus sulcatus* Philip, 1965.

**Diagnosis:** An eognathodontid genus whose Pa element is thick walled, has a large basal cavity that may be open to the posterior end of the element, a platform at the crest of the blade that has a flat sulcus bordered by ridges that vary from smooth to transversely serrate, or irregular arrangement of nodes without a sulcus and an anterior blade that is thin and bears a cockscomb. Other elements have not been reconstructed.

**Discussion**: Philip (1965: 99) chose a large, possibly gerontic, specimen with an unusual denticulation pattern on the platform for the holotype and some smaller specimens with quite different morphology that he believed to be less mature specimens as paratypes of *Eognathodus sulcatus,* type species of *Eognathodus*. At the same time, he put two other taxa in the genus, *E. secus* and *E.* sp. [= *E. irregularis* Druce, 1971]. The two *E. sulcatus* morphologies and *E. secus* and *E.* sp. represent four rather different morphologies that were related through the possession of the large posteriorly placed basal cavity. Early papers followed Philip's (1965) diagnosis and identified all Pa elements with a well-defined sulcus as *E. sulcatus*. Later papers added a few names to the roster, but until recently a conservative taxonomic approach was adopted.

Mawson & Talent (1994) were the first to suggest that more than one evolutionary branch better represented the data. More recently Bardashev *et al.* (2002) have suggested a taxonomic hierarchy for the taxa previously included in *Eognathodus* that consists of two families: Eognathodontidae, with two genera, *Eognathodus* and *Gondwania*; Polygnathidae, in which they place *Pseudogondwania* in the subfamily Spathognathodontinae.

Some of the conclusions of Bardashev *et al.* (2002) are adopted here as is some of their nomenclature, but my phylogenetic interpretations differs in significant ways. I confine *Eognathodus* to forms with a robust Pa element, a shallow sulcus or no sulcus and scattered disorganized to partly organized tubercles between the outer rows of nodes or transversely elongated nodes; I use *Gondwania* for the robust and commonly deeply sulcate Pa elements with large basal cavities and straight relatively short blades; I include *Pseudogondwania* in the Eognathodontidae rather than in the Spathognathodontidae and include predominantly slim forms with long blades and restricted basal cavities; and I arrange the taxa in all three genera differently than they have done.

## *Eognathodus sulcatus* Philip, 1965

This taxon has not been recorded from Nevada, is rare in Australia, however, its position as the name bearer for a group of forms that dominated some environments of the Pragian has made it one of the most misunderstood taxa of the Stage. Its restriction by Bardashev *et al.* (2002) to forms with a massive Pa element with a shallow sulcus bordered by rows of transversely oriented, ridge-like denticles and with tubercles in the sulcus either scattered or arranged linearly is a necessary analytical step in determining the composition of the species. The stratigraphic positions of the holotypes of *E. sulcatus* and *E. secus* are uncertain (Murphy *et al*., 1981: 752), but the excellent data of Mawson & Talent (1994) as documented by their photos of the specimens permit us to know that the general morphologies represented by the two holotypes (1994: figs. 7D, 8I, L, M, O) occur at Boola Quarry from 5.3 to 13.1m. This is within the range of *Pedavis brevicauda* (Mawson & Talent, 1994: figs. 6A-H, 1-13.8m), which spans almost the entire Boola section. The deeply sulcate *G. profunda* n. sp. is also present in these beds and reinforces the correlation of the Boola section with the Nevada sections that uses the range of *P. brevicauda* alone. Thus, we can infer that *E. secus* and *E. sulcatus* are from the *brevicauda-mariannae* Zone and that *E. sulcatus* is, therefore, not an appropriate taxon to serve as name-bearer for a lower Pragian zone.

## *Eognathodus secus* (Philip, 1965)

This taxon has not been recorded from Nevada, is rare in Australia and does not figure prominently in either the evolutionary history of the genus or its biostratigraphy. I put it in *Eognathodus* because it is an exaggeration of the kind of morphology that occurs in the earlier *Eognathodus irregularis,* but it is much more thickly walled with a much broader platform that is ornamented by a disorganized set of pustulose tubercles.

## *Eognathodus epsilon* n. sp.

1981. *Eognathodus sulcatus* Philip, 1965, ε morph. Murphy, Matti & Walliser, 1981, pl. 2 figs. 21-23, 26; not pl. 2 fig. 24 = *Masaraella pandora* ε morph.

**Holotype:** Specimen figured in Murphy *et al.* (1981): Pl. 2 figs. 21-23 COP II 163 feet, UCR 6211/6, Monitor Range, Nevada.

**Diagnosis:** A species of *Eognathodus* based on a Pa element characterized by the combination of a row of fused denticles or smooth crest on the middle blade and a tubercle or ridge on one basal platform lobe. Basal cavity tapers to a point at the posterior end of the element.

**Description:** Pa element characterized by a straight or nearly straight, blade that has at least some part of the middle segment with smooth or with low, fused denticles, posterior denticles low and rounded and a low cockscomb anteriorly; basal platform lobes with a prominent, rounded tubercle on one of the lobes that may be connected to the blade by a thin ridge; basal cavity large and open, and tapering to a point at the posterior end of the element.

**Discussion:** The epsilon morph was one of the taxa included exclusively in *M. pandora* by Murphy *et al.* (1981). At the time, only a few specimens were known and it was thought to be an extreme variant of *M. pandora*. Now with more material available, it can be shown to maintain a discrete identity without intermediate forms in the higher early Pragian. Even with the basal-Pragian boundary correlated with a position lower in the section than in 1981, its lowest occurrence is still in the uppermost Lochkovian zone; the highest occurrence is in the lower part of the *brevicauda-mariannae* Zone.

## *Eognathodus irregularis* Druce, 1971

Figs. 6.2-6.18, 6.35, 6.36, 6.39-6.42, 6.48, 6.49, 6.51, 6.52; Figs. 7.1-7.11

1965. *Eognathodus* sp. Philip, 102, pl. 10 fig. 19.
1971. *Eognathodus irregularis*. Druce, 33, text-fig. 2, pl. 4 figs. 4-7.
1971. *Eognathodus sulcatus* Philip, 1965. Druce, pl. 1 fig. 6.
1980. *Eognathodus irregularis* Druce. Pickett, 77, fig. 7D-F.
1981. *Eognathodus sulcatus* Philip, 1965, eta morph. Murphy, Matti & Walliser, pl. 2 figs. 17-19, 25.
1987. *Eognathodus sulcatus* Philip. Weddige, 481, figs. 3-5.
1989. *Eognathodus sulcatus eosulcatus*. Murphy, figs. 1.2, 1.4-1.9
2002. *Eognathodus drucei*. Bardashev, Weddige & Ziegler, text-fig. 11.4.
2002. *Eognathodus grahami*. Bardashev, Weddige & Ziegler, text-fig. 11.3.

**Holotype:** Australia, Bureau of Mineral Resources, Geology and Geophysics CPC 10122, Canberra, Australia.

**Original Diagnosis:** "An eognathodid with irregular linear dentition on the platform."

**Diagnosis:** An *Eognathodus* based on a Pa element with robust blade and irregular dentition or tuberculation of the middle and posterior blade, but without development of a sulcus; basal cavity large, tapering to the posterior end of the element.

**Discussion:** Many morphs participate in the variation of the taxon in the early Pragian. Every large sample that contains *E. irregularis* shows intermediate morphologies between all of the morphs of *Masaraella pandora* and *E. irregularis* and also shows that the size and shape of the basal cavity, the relative length and thickness of the blade, and the pattern of protuberances on the crest of the blade are extremely variable. Nevertheless, the combination of medium- to large-sized basal cavity and a pattern that has blunt, irregularly sized, shaped and arranged denticles or tubercles, but no development of a sulcus is characteristic of the lowest interval of the Pragian.

## Genus *Gondwania* Bardashev, Weddige & Ziegler, 2002

**Type species:** *Spathognathodus bipennatus nevadensis* Clark & Ethington, 1966

**Emended Diagnosis:** An eognathodontid genus whose Pa element is thick walled, has a large basal cavity open to the posterior end of the element, a platform at the crest of the blade that is characterized by a sulcus bordered on each side by a ridge or noded ridge or combination thereof. The anterior blade is thin and bears a cockscomb. The other elements have not been reconstructed.

## *Gondwania profunda* n. sp.

Figs. 7.12-7.16, 7.32-7.41; Figures 8.6-8.8, 8.24, 8.25.

1965. *Eognathodus sulcatus*. Philip, 101, fig. 1a-c, pl. 10 figs. 17, 18.

1981. *Eognathodus sulcatus* Philip, lambda morph. Murphy, Matti & Walliser, pl. 3 figs. 1, 2, 11.
1981. *Eognathodus sulcatus* Philip, kappa morph. Murphy, Matti & Walliser, pl. 3 figs. 9, 10.
2002. *Gondwania juliae* (Lane & Ormiston). Bardashev, Weddige & Ziegler, 396, text-fig. 11.10, 11.11.
2002. *Pseudogondwania kindlei* (Lane & Ormiston). Bardashev, Weddige & Ziegler, text-fig. 12.13.

**Holotype:** Specimen UCR 7343/4 figured in Murphy *et al.* (1981): pl. 3 figs. 9 and 10 from the basal 6 inches of the Kobeh Member of the McColley Canyon Formation, Willow Creek X section, northern Roberts Mountains, Nevada.

**Derivation of the name:** *Profund*, Latin meaning deep, alluding to the deep sulcus characteristic of the taxon.

**Diagnosis:** A *Gondwania* species based on the Pa element that has two denticulate or partially denticulate ridges separated by a deep sulcus that is present from the posterior edge of the cockscomb to the posterior tip of the element.

**Description:** A species of *Gondwania* based on a robust Pa element with anterior single row of denticles in a high-standing cockscomb followed by two denticulate or partially denticulate ridges reaching to the posterior tip of the element and with a deep sulcus between them; blade straight, arched, or bent; sulcus straight or sigmoidal; shape of the basal cavity variable from heart shaped and open to the posterior tip to subquadrate and restricted to the quartile behind the midpoint.

**Morphs:** I recognize three morphs of *G. profunda* as follows:
chi morph (χ) - for morphs with a straight blade, moderately deep, almost parallel-sided sulcus that is bordered on each side by denticulate ridges that are almost the same width as the sulcus (Figs. 7.12-7.16; Figs. 8.24, 8.25);
psi morph (ψ) – for morphs with a straight blade, deep sulcus of variable width because the bordering ridges bulge out on one or both sides of the blade (Figs. 7.32-7.41);
omega morph (ω) – for morphs with a straight or gently bowed blade, deep, narrow, parallel-sided sulcus with bordering ridges on which the denticles are longitudinally elongate (Figs. 8.6-8.8).

**Discussion:** Bardashev *et al.* (2002: figs. 11, 12) classify the ψ morph in two different phylogenetic series depending on the shape of the basal cavity. In the series *Gondwania,* it is identified as *G. juliae;* in the other series, *Pseudogondwania,* it is identified as *P. kindlei*. The two specimens cited by Bardashev *et al.* (2002) and the specimens figured here (Figs. 7.32-7.41) come from a single sample at the base of the WC X section at Willow Creek in the northern Roberts Mountains. This sample yielded more than 35 specimens whose basal cavities show a wide range of shapes that includes specimens with shapes intermediate between the cited specimens. It is obvious from this sample that basal cavity shape cannot be used as a means of distinguishing generic-level differences in forms with a very deep sulcus. At Willow Creek, these forms occur with *Pedavis brevicauda* (Fig. 7.42). However, Bardashev *et al.* (2002: fig. 12) have put the specimens at different levels in their diagrams. In other words, they have put two specimens from the same sample at different stratigraphic levels in their summaries. The reverse case is true with *G. nevadensis* and *Pseudogondwania juliae,* the holotypes of which they figure at the same level, but which must be stratigraphically half of the stage apart. *G. nevadensis* occurs low in the COP II section in the lower part of the *profunda-brevicauda* Zone. The holotype of *P. juliae* occurs in a bed that probably correlates with beds over 100 feet higher in the COP II section than *G. nevadensis*.

## Genus *Pseudogondwania* Bardashev, Weddige & Ziegler, 2002

**Type species:** *Eognathodus kindlei* Lane & Ormiston, 1979.

**Diagnosis:** An eognathodontid genus whose Pa element has a restricted basal cavity, long anterior process (>50% of the length of the element), and partially sulcate blade.

## *Pseudogondwania kindlei* Lane & Ormiston, 1979

Figs. 7.17-7.31, Figs. 8.19-8.23, 8.50

1969. *Eognathodus sulcatus* Philip, 1965. Klapper, pl. 3 figs. 16-21.
1977a. *Eognathodus sulcatus* Philip, 1965. Klapper, *Eognathodus* Pl. 1 fig. 2.
1979. *Eognathodus sulcatus kindlei*. Lane & Ormiston, pl. 4 figs. 1-5.
1979. *Eognathodus sulcatus juliae*. Lane & Ormiston, pl. 4 figs. 6-8, 9.
1980. *Eognathodus sulcatus kindlei*. Lane & Ormiston. Johnson, Klapper & Trojan, pl. 3 fig. 26.
1981. *Eognathodus sulcatus* Philip, lambda morph. Murphy, Matti & Walliser, pl. 2 fig. 29.
1990. *Eognathodus sulcatus kindlei* Lane & Ormiston. Uyeno, pl. 20 figs. 35-37.
2002. *Pseudogondwania clarki*. Bardashev, Weddige & Ziegler, 428, text-fig. 12.9 (=τ morph herein).
2002. *Pseudogondwania ethingtoni*. Bardashev, Weddige & Ziegler, 428, text-fig. 12.11 (=τ morph herein).
2002. *Pseudogondwania klapperi*. Bardashev, Weddige & Ziegler, 429, text-figs. 12.3, 12.4 (=σ morph herein)
2002. *Pseudogondwania murphyi*. Bardashev, Weddige & Ziegler, 430, text-fig. 12.5, 12.7 (=σ morph herein).

**Holotype:** Specimen figured in Lane and Ormiston (1979), pl. 4 figs. 1, 4, and 5; USNM 249800.

**Diagnosis:** A species of *Pseudogondwania* in which the basal cavity expansion of the Pa element is restricted to the anterior half of the posterior half of the platform and the free blade is long.

**Morphs:** I recognize four morphs of *P. kindlei* as follows:

sigma (σ) –for morphs with a straight blade, a single row of stout denticles on the posterior process, sulcus confined to the middle part of the blade; moderate-sized basal cavity (*profunda-mariannae* Zone; Fig. 8.50);

tau (τ) – for morphs with slightly arched or bent blade, on which the sulcus extends posterior of the cusp position; the posterior blade has either a double row of nodes Figs. 8.19-8.21) or disorganized denticles (Figs. 7.20, 7.21, 7.23) or a distorted ridge (Figs. 7.18, 7.25); basal cavity moderate-sized, slightly asymmetrical (*mariannae-lenzi* Zone);

upsilon (υ) - for morphs with slightly arched or bent blade, a single row of denticles on the posterior process, moderate-sized or small basal cavity, and with the single row of posterior denticles in line with the outer ridge or row of nodes of the middle blade (Murphy *et al.*, 1981: pl. 2 figs. 27, 28, 30-32; *mariannae-lenzi* Zone);

phi (φ) - for morphs with slightly arched or bent blade, a single row of denticles on the posterior process not in line with the rows of nodes or ridges of the middle blade, moderate-sized or small basal cavity (Murphy *et al.*, 1981: pl. 2 figs. 10-12, pl. 3 figs. 19-21; *mariannae-lenzi* Zone).

**Range.** Lane and Ormiston's unfigured material was re-examined during this study in order to get a better understanding of the range of variation in the various samples. Examination of the specimens from their sample 28 revealed a specimen of *P. kindlei* that does not appear on their range chart (Lane & Ormiston, 1979: tab. 1a). This addition increases the overlap to include all beds after the first bed in which *P. juliae* occurs and suggests that the two subspecies might be ontogenetic variants. Observations on specimen size throughout their combined ranges indicate that where *P. juliae* occurs alone, the specimens are small; where *P. kindlei* occurs alone the specimens are large.

**Discussion:** I prefer to explain the observations discussed in the preceding paragraph with the hypothesis that *E. sulcatus juliae* Lane & Ormiston (1979) represents an early ontogenetic stage of *E. sulcatus kindlei* rather than that they are genetically distinct and temporally overlapping taxa. I grant that the observations do not preclude Lane and Ormiston' hypothesis, but they give an alternative.

Bardashev *et al.* (2002: text-fig. 11.9, 11.10) have shown *P. juliae* as an independent species that occupies a very low stratigraphic position in the Pragian in the same range as the holotype of *G. nevadensis*. This would put its occurrence far below the range of *Pedavis brevicauda* with which it occurs in Nevada and Australia. Current evidence suggests that even if *kindlei* and *juliae* are separate taxa, the stratigraphic position of *juliae* is not as low as *nevadensis*.

### Order PRIONIODONTIDA Bassler, 1925
### Family **Icriodellidae** Sweet, 1988

Confirmation of the derivation of *Pedavis* from *Icriodella* or perhaps *Distomodus* as shown by Sweet (1988: 65, fig. 5.17) still suffers from a large gap in our knowledge of middle Silurian faunas bearing these faunal elements. However, it should be recognized that any new data could shift the balance in favor of the Distomodontidae.

## Genus *Pedavis* Klapper & Philip, 1972

**Type species:** *Icriodus pesavis* Bischoff & Sannemann, 1958.

**Discussion:** Sweet (1988: 65) has suggested that *Pedavis* is most closely related to *Icriodella* Rhodes, 1953 and that it has a quinquemembrate apparatus in which the Pa element is stelliscaphate, the Pb element is pyramidal pastiniscaphate, and the M elements bipennate or pastinate. *Pedavis* species with which I am acquainted seem to have pyramidal pastiniscaphate elements in both the Pb (or $S_1$) and M (or $M_{2a}$) positions. The Pb position is occupied by an element that has a differentiated cusp and an outer lateral process that is denticulate, whereas the M element is a simple keeled and adenticulate pyramidal cone that flares out at the base and that may have some costae on one or more faces of the pyramid. Of the remaining two elements Sweet assigns a costate dolabrate element to the Sa position. However, these elements in the *Pedavis longicauda* n. sp. apparatus are asymmetrical and are accompanied by simple conical elements that have symmetry of both form and costation, so the dolabrate element does not seem to be homologous with the Sa element in the Sweet & Schönlaub (1975) notation. In addition, other elements are present that are neither dolabrate nor symmetrical. This leads me to suppose, given the variety of elements that accompany rather uniform Pa elements, that the apparatus has six or more members as previously suggested in Murphy & Matti (1983: 45). Sweet's notation for the transition series elements presumably would be Sa and Sb. If there were more than the number he envisioned, presumably the S series could be expanded indefinitely.

Notations for the transition series elements, if they are indeed transition series elements, have been suggested by Klapper & Philip (1971), Murphy & Matti (1983), Sweet (1988), and by Simpson *et al.* (1993). Although Sweet's is in general use at present, the above example illustrates that its use for the *Pedavis* apparatus is not entirely satisfactory because we do not have a reconstruction of the apparatus as yet and the homologies are far from certain. For that reason, I have used the notation invented by Klapper & Philip (1971) and expanded by Murphy & Matti (1983) with the acknowledgment that it too may not be satisfactory when we have a better reconstruction of the *Pedavis* apparatus.

## *Pedavis mariannae* Lane & Ormiston, 1979
Figs. 8.1-8.5

1979. *Pedavis mariannae*. Lane & Ormiston, 59, pl. 4 figs. 14-20, 23-25, 27, pl. 5 figs. 1, 7, 8, 11-14, 17-22.

1983. *Pedavis mariannae* Lane & Ormiston. Murphy & Matti, 54, pl. 8 figs. 1, 2, 4-6, 9, 11, 12.

**Original Diagnosis:** "A species of *Pedavis* in which the Pa element has a short but straight posterior process. Lateral processes diverge at acute angles from the long anterior process. The unit is gently curved from the anterior to the posterior and fully excavated on the lower side. The fully developed $S_1$ element is shaped like the Greek letter lambda and the $M_2$ element is a reclined to recurved multicostate cone with very coarse costation around its base."

This taxon was described early in the studies of the genus *Pedavis* but the main elements of the diagnosis, shape and relative proportions of the processes still apply. In addition, the ornamentation of the upper surface of the I element changes ontogenetically from icriodontid-style ornamentation with individual transverse rows of denticles to an ornamentation of branching and normally interconnecting ridges in which the outer rounded denticles of the transverse rows are replaced by a ridge that bifurcates distally. This additional discussion also is based on too few specimens and so the limits of variability will probably need further adjusting.

**Discussion:** I recognize two morphs of *P. mariannae*:
tau morph (τ) - for the holotype and similar forms;
alpha morph (α) -for the specimens figured in Murphy & Matti (1983: figs. 1, 5, 6, 9, 11).
The α morph differs from the τ morph in having a relatively shorter main process.
The τ morph ranges from COP II 335 feet to the top of the COP II section; the α morph is known only from COP II 295 and 378 feet.

*Pedavis mariannae* was reported from the Emsian by Yolkin *et al.,* (1989) and this report has been accepted by other writers (Mawson *et al.,* 1992). However, these reported occurrences have not been documented by figured specimens from the Zinzilban section in the Zeravshan Mountains from whence they came and so I continue to regrard the range of *P. mariannae* as being restricted to the upper Pragian.

*Pedavis mariannae* is an important taxon in the upper Pragian by virtue of reports of its occurrence on a global scale. Although I have dealt almost exclusively with its North American occurrences above, it has been reported with *Polygnathus pireneae* also in Spain and western Siberia. The Spanish occurrence has been documented by a juvenile specimen (Valenzuela-Ríos, 1994: pl. 7 fig. 20), but one that is virtually identical to the juvenile specimens reported from Nevada (Fig. 8.3) and Alaska (Fig. 8.4). The Siberian specimen is as yet undocumented by figured specimens (Yolkin *et al.*, 1989).

## *Pedavis brevicauda* Murphy & Matti, 1983

Fig. 7.42

1969. *Icriodus* n. sp. A. Klapper, 10, pl. 1 figs. 15-18.
1971. *Icriodus* n. sp. A Klapper. Klapper *et al.*, 290, text-fig. 1.
1977b. *Pedavis* n. sp. A (Klapper). Klapper, 52, no. 20.
1980. *Pedavis* n. sp. A (Klapper). Klapper & Johnson, 451, pl. 2 fig. 10.
1983. *Pedavis brevicauda* Murphy & Matti, 50, pl. 6 figs. 14-17.

**Discussion:** *P. brevicauda* has a relatively short range in the middle Pragian of Nevada. Mawson & Talent (1994: 47) have suggested that its range extends into the Emsian based on a specimen that Uyeno (1991: pl. 2 fig. 18) identified as *Pedavis* sp. cf. *P. sherryae* Lane and Ormiston, which appears to have a short posterior process and which they re-identified as *P. brevicauda*. T. T. Uyeno (Letter, January 13, 2004) kindly reexamined the specimen in question and reports that the posterior process is broken and, thus, looks shorter than it would be if complete and, as originally stated, that the specimen more closely resembles *P. sherryae* than *P. brevicauda*. Therefore, to date no data support a range extension into the Emsian for *P. brevicauda*. Also, Mawson & Talent (1994) have accepted the synonymy of Klapper (1991: 101), which lists a broken specimen figured by Fåhraeus (1971) as *P. brevicauda*. This specimen has a broken main process and the posterior process is obscured in basal view, but permissibly it may be identified as *P. brevicauda*. This would give the species a range possibly as high as 300 feet in the COP II section in figure 2.

The taxon was originally recognized by Klapper (1969) from a sample that included material from the stratigraphic interval 466-492' in the Royal Creek I section of Lenz in Yukon Territory, Canada. This sample includes occurrences of *Pandorinellina philipi* Klapper, 1969, *Pand. optima* Moskalenko, 1966, *Pand.? boucoti* (Klapper, 1967) and *Eognathodus "sulcatus"*. As it does in Australia, *Pedavis brevicauda* occurs in Nevada with *Gondwania profunda*, and in three sections with the overlapping ranges of *Icriodus steinachensis* Al-rawi, 1977, and *I. claudiae* Klapper, 1980, but no co-occurrences with *Pandorinellina* are known. Because the Royal Creek sample represents a considerable thickness of strata, the ranges of *Pedavis brevicauda*, *Pandorinellina philipi,* and *Pandorinellina? boucoti* cannot be considered as overlapping.

## *Pedavis longicauda* n. sp.

Figs. 6.32-6.34, 6.37, 6.38, 6.43-6.47, ?6.53-6.56,
Figs. 8.39-8.49

**Holotype:** Specimen figured on Plate 1, Figure 32, IK IV 4/1.

**Derivation of the name:** Long, Latin, meaning long, alluding to the very long posterior process of the I element that characterizes the taxon.

**Diagnosis:** A *Pedavis* based on a platform element with a long, slightly bent posterior process, straight anterior process, and almost equal lateral processes oriented at 45 degrees to the anterior process.

**Description:** Stelliscaphate element (Pa): Anterior process of nearly straight, with 5 or 6 straight or slightly chevron-shaped transverse rows, central denticle formed by the intersection of prominent longitudinal ridge and ridge of transverse row with outer denticles of various shapes; outer lateral process nearly straight, ornamented by a narrow longitudinal ridge oriented at 45 degrees to the anterior process that connects single tubercles along the crest of the process and that may branch and may form transverse rows of denticles or remain a simple ridge; inner lateral process nearly straight, ornamented by a narrow longitudinal ridge as in the outer lateral process but with greater development of transverse rows and rounded outer tubercles; posterior process bent slightly inward from the junction of the processes for about one third of its length and then bent outward, ornamented by a strong narrow longitudinal ridge with transverse ridges and tubercles developed laterally.

**Comparison:** *P. longicauda* Pa element differs from *P. pesavis* and *P. striatus* in having a straighter and longer posterior process and the anterior process is relatively longer and narrower than in *P. pesavis;* from *P. brevicauda* it differs in having more transverse rows of denticles, longer lateral processes and much longer posterior process; from *P. gilberti* it differs in having the posterior process in line with the anterior process instead of the lateral process; *P. robertoi* has a shorter and more curved posterior process and lateral processes are of unequal lengths in *robertoi*, sub-equal in *longicauda*; transverse denticle rows on the main process in *robertoi* are strongly chevron shaped.

**Discussion:** Many kinds of simple conical elements are present in the residues from which *P. longicauda* has been identified. Some of these have been figured with the Pa elements on Plate 1, but several more are present and indicate that the apparatus is either more complex than the five or six kinds of elements that make up other apparatuses of the genus or that more than one taxon is represented.

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