# SYSTEMATICS OF THE KONEPRUSIINE TRILOBITES, WITH NEW TAXA FROM THE SILURIAN AND DEVONIAN OF LAURENTIA

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ABSTRACT—Systematics of the trilobite subfamily Koneprusiinae Vaněk and Pek, 1987 are revised on the basis of new material and a comprehensive parsimony analysis. New taxa include the genus *Nevadaprusia* (type species *N. cortezensis* n. sp.) from the Pragian of Nevada and the species *Laethoprusia graffhami* n. sp. from the Lochkovian of Oklahoma, *L. cozarti* n. sp. from the Lochkovian of Tennessee, and *Laethoprusia* n. sp. A from the Sheinwoodian of Arctic Canada and the southern Mackenzie Mountains. *Nevadaprusia insolita* (Haas) is revised on the basis of new material. *Laethoprusia* and *Nevadaprusia* are interpreted as sister taxa, and *Koneprusia* and *Isoprusia* are successive sister groups to the *Laethoprusia/Nevadaprusia* clade.

# INTRODUCTION

ESPITE THE proposal to date of more than 35 named species, the odontopleurid subfamily Koneprusiinae Vaněk and Pek (1987) remains poorly known. Ramsköld (1991a) initially considered the taxon a synonym of Selenopeltinae Hawle and Corda, 1847, but later (Ramsköld, 1991b) as a valid group. With regard to Koneprusia Prantl and Přibyl, 1949 and Isoprusia Bruton, 1966, the two genera to which most species have been assigned, Ramsköld (1991b, p. 127) considered that "Apart from the two type species, current generic assignments are ... meaningless.' A major problem has been the erection of species on the basis of single specimens, and often single sclerites. For most species, knowledge of either the cranidium or pygidium, the librigena, the hypostome, and the thorax is entirely lacking. The situation has improved little in the years since Ramsköld's review; of the nine species proposed in the past 15 yr, only one (Isoprusia kofelae Santel, 2001) is known from more than two specimens, four are known from cranidia only, one is known from a pygidium only, and none are known from codable librigenae or thoracic segments.

Koneprusiinae has been represented in Laurentia up until now by a single formally named species, "Koneprusia (new subgen.?)" insolita Haas, 1969, along with two species reported from single specimens in open nomenclature (Koneprusia sp. of Ormiston [1969] and an "odontopleurid cranidium that could be assigned to Koneprusia, Isoprusia, or Dicranurus" (Chatterton and Perry, 1983); considered Laethoprusia by Ramsköld [1991b] and assigned to Laethoprusia n. sp. A? herein). Haas's species was itself based only on one partial cranidium and a fragment of a thoracic segment. Here, we revise insolita on the basis of new topotype material, and add to the record four new Laurentian species, three of which are formally named. These newly named species are among the best known members of the subfamily thus far formally described. They represent the type species of a new genus, Nevadaprusia, as well as the first definite Laurentian occurrences of Laethoprusia Ramsköld, 1991b. We use them to revise and extend the koneprusiine parsimony analysis of Ramsköld (1991b).

# LOCALITIES AND STRATIGRAPHY

*Nevada.*—Haas (1969) studied trilobites from several localities in the Cortez Mountains and Simpson Park Range of central Nevada. Much of the silicified material in his paper came from USNM loc. 17233, on the western slope of the southern Cortez Mountains, and was derived from a single block of dark argillaceous limestone of the Wenban Limestone (Gilluly and Masursky, 1965) collected by a University of California Los Angeles student group in 1949. JMA and BDEC visited the area in 1990 and 1991

and discovered a series of distinct silicified faunas in a fairly thick though poorly exposed section in the area of Haas's sample (Fig. 1). Most of the hillside is covered with trees and brush, and in open areas by limestone talus. The section proceeds along a dip slope through this cover, and outcrop is limited and sporadic. Faunas were collected from a series of lettered localities. The relative stratigraphic position and lithology of these collections is clear, and each collection is from a narrow interval (less than 1 m) in outcrop. The absolute stratigraphic position of each is difficult to determine. Silicified collections similar in preservation and taxonomic composition to the material described by Haas (1969) were recovered from our lowest localities CR-H and CR-B, which are along strike from one another. Samples at these localities are of slabby-weathering dark gray limestone with abundant but quite poorly preserved silicified trilobites concentrated on bedding planes and in many cases compacted and distorted. All of Haas's species [Maurotarion periergum (Haas, 1969), "Decoroproetus" n. sp., "Viaphacops" claviger (Haas, 1969), Reedops sp., Kettneraspis favonia (Haas, 1969), and Nevadaprusia insolita (Haas, 1969), along with indeterminate dalmanitid specimens] are present in these collections and were not found in any of the stratigraphically higher collections. Above CR-H, an entirely new fauna occurs in medium bedded and less argillaceous black limestones at localities CR-G and CR-C, which are along strike from one another. In addition to Nevadaprusia cortezensis n. sp., this low diversity fauna includes two new species of Maurotarion G. Alberti, 1969, a new species of phacopid related to "V." claviger, and a new species of Kettneraspis Prantl and Přibyl, 1949. It is notable for the preservation of large, articulated, silicified specimens (in fact N. cortezensis is the only species not represented by at least some articulated material). Higher still stratigraphically, a third distinct fauna occurs in highly argillaceous, greenish-orange weathering limestones at locality CR-D. This fauna is not dealt with herein, but includes new species of Paciphacops Maksimova, 1972, Maurotarion, two species of Kettneraspis, Ceratocephala Warder, 1838, and a brachymetopid. Trilobites strongly numerically dominate all three of these deep subtidal faunas. Rare articulate brachiopods, rostroconch molluscs, and solitary rugosan corals are present, and a single species of lepidocoleid machaeridian is fairly abundant at CR-D. The faunas are Pragian in age, and occur within the "Lower Spinoplasia Subzone" of Johnson's (1977, fig. 2) brachiopod zonation.

*Oklahoma.*—Material of *Laethoprusia graffhami* n. sp. was derived from the Geological Enterprises quarry in the vicinity of Clarita, Coal County, Oklahoma. Full discussion of the locality along with a map (which misidentified the county as Pontotoc County) was given by Adrain and Kloc (1997, p. 703, fig. 1). The quarried horizon is from Amsden's (1960) Unit P within the



FIGURE *1*—Location of Section CR in the southern Cortez Mountains, Eureka County, central Nevada. Base map from USGS Crescent Valley  $30 \times 60$  minute quadrangle.

Cravatt Member of the Bois d'Arc Formation, Hunton Group. The horizon is Lochkovian in age. Associated trilobites were described by Campbell (1977) and Adrain and Kloc (1997).

Tennessee.--The history of study, stratigraphy, and paleoecology of the Birdsong Shale Member of the Ross Formation is detailed in papers contained in Broadhead and Gibson (1995). The unit is entirely Lochkovian in age, and contains diverse brachiopod-dominated shelly faunas from a shallow subtidal (above storm wave base) setting. The unique holotype of Laethoprusia cozarti was collected at Holladay Quarry, a well-known Birdsong Shale locality in Holladay, Benton County, Tennessee. The specimen was obtained from a pile of guarried and dumped rock within the quarry, and hence its exact position within the member is not known with certainty. However, GJK visited the quarry and was shown the rocks from which the specimen was obtained. They contain a mixture of cherty limestone from the Camden Formation, which overlies the Ross Formation, along with thinbedded bryozoan-rich limestones. The latter lithology yielded the specimen. Such rocks are typical of the upper "Bryozoan Zone" of the Birdsong Shale (e.g., Gibson, 1995, fig. 1). Hence it is very likely that the unique holotype of L. cozarti is from the upper part of the member near the contact with the Camden Formation.

*Nunavut.*—Details of localities and stratigraphy for the rich Wenlock-Ludlow silicified faunas of the Cape Phillips Formation have been given several times, with the most important references including Adrain (1997, 1998, 2003), Adrain and Edgecombe (1997), and Adrain and Ramsköld (1997). *Laethoprusia* n. sp. A is known from the middle Sheinwoodian *Struszia dimitrovi* Fauna [*Monograptus instrenuus-Cyrtograptus kolobus* Zone of Lenz and Melchin (1991)] and from the upper Sheinwoodian *Struszia petebesti* Fauna (*Cyrtograptus perneri-Monograptus opimus* Zone) of Adrain and Edgecombe (1997). Specimens of the new species were derived from in situ carbonate debris flows on the south shore of Baillie-Hamilton Island (horizons BHL 10 m, BH 1,110 m, and locality BHH-A) and from a single large boulder on an unnamed tributary of the Abbott River, northwestern Cornwallis Island.

Mackenzie Mountains .- Trilobites of the diverse deep subtidal

Llandovery-Ludlow faunas of the upper Whittaker Formation and Delorme Group in the southern Mackenzie Mountains of the Northwest Territories have been described in numerous works, including Chatterton and Perry (1983, 1984). A single new specimen tentatively assigned to *Laethoprusia* n. sp. A was collected from Section Avalanche Lake Two, 247.0 m. Based on trilobite evidence, this horizon is within the Sheinwoodian *Struszia dimitrovi* Fauna of Adrain and Edgecombe (1997).

# PARSIMONY ANALYSIS: TAXA

Ramsköld (1991b, p. 139–140) listed 28 named koneprusiine species. Three of these (*brutoni, impar, laportii*) are junior synonyms whose synonymy is accepted herein. One (*anchyses*) is rejected as a koneprusiine below. Since Ramsköld's publication, nine additional species have been proposed and three more are erected herein. Below is an expanded list of all currently accepted named ingroup koneprusiine species. Information is presented in the following order: species name and authorship; original genus assignment; provenance; alternative historical genus/subgenus assignments; sclerites figured and sources for coding; style of preservation.

- adaemona VANĚK, VOKÁČ, AND HÖRBINGER, 1992; Koneprusia (Koneprusia); Lochkov Formation, upper layers (Lochkovian), Praha 5-Lochkov, cutting of the new road to Slivenec, Prague Basin, Bohemia, Czech Republic; Koneprusia (Koneprusia): Vaněk and Valíček (2002), Hörbinger (2004; holotype refigured); single partial cranidium (Vaněk et al., 1992, pl. 2, fig. 8; refigured by Hörbinger, 2004, pl. 1, fig. 2); calcareous.
- albata VANĚK AND PEK, 1987; Koneprusia (Koneprusia); Lodénice Limestone (Pragian), Praha 5-Smíchov, quarry below Konvářka, Prague Basin, Bohemia, Czech Republic; Koneprusia: Ramsköld (1991b); Koneprusia (Koneprusia): Vaněk and Valíček (2002); single partial cranidium (Vaněk and Pek, 1987, pl. 1, fig. 3); calcareous.
- brikelos CHATTERTON, JOHNSON, AND CAMPBELL, 1979; Koneprusia (Koneprusia); locality G612, Garra Formation (Pragian), near Wellington Caves, 8 km south of Wellington, New South Wales, Australia; Koneprusia (Koneprusia): G. Alberti (1983), Vaněk and Pek (1987); Laethoprusia: Ramsköld (1991b), Santel (2001); cranidia, librigenae, thoracic segments, pygidia (Chatterton et al., 1979, pl. 111, figs. 1–17); silicified.
- bucco RICHTER AND RICHTER, 1917b; Acidaspis (Pseudomonaspis); "Crinoidenschichten mit Harpes" (Eifelian), Auburg near Gerolstein, Eifel, Germany; Koneprusia (Koneprusia): Vaněk and Pek (1987); Isoprusia (sensu lato): Ramsköld (1991b); Koneprusia: Basse (1998); Ramsköld (1991b, fig. 4) illustrated two cranidia, one of which he selected as the lectotype of bucco. The second cranidium is not conspecific with the first, differing in the size, density, and distribution of tuberculate sculpture. Ramsköld noted this but ascribed it to "intraspecific variation." No such within-sample variation in similar sized specimens is documented for any other koneprusiine (or, for that matter, any other odontopleurid) species. The less tuberculate cranidium also has a broader median glabellar lobe and relatively smaller L1; single cranidium (Ramsköld, 1991b, fig. 4a-c); calcareous.
- chynicensis VANĚK AND PEK, 1987; Koneprusia (Koneprusia); Chýnice Limestone, Zlíchov Formation (Emsian), Praha 5-Holyně, outcrop in roadcut near Opatřilka, Prague Basin, Bohemia, Czech Republic; Koneprusia (Koneprusia): Havliček and Vaněk (1996), Vaněk and Valíček (2002); Isoprusia (s.l.): Ramsköld (1991b); partial cranidium (Vaněk and Pek, 1987, pl. 1, fig. 5) and partial pygidium (Vaněk and Pek, 1987, pl. 2, fig. 1), internal molds.

- coloxyl ŠNAJDR, 1986; Selenopeltoides; Želkovice Formation (Aeronian; Monograptus sedgwicki Zone), Hýskov, near Beroun, hillside "V Jakubince," Prague Basin, Bohemia, Czech Republic; Isoprusia?: Ramsköld (1991b); Koneprusia (Isoprusia): Vaněk and Pek (1987), Vaněk and Valíček (2002) (name misspelled "caloxyl" in both works); single small pygidium (Šnajdr, 1986, pl. 1, fig. 7), internal mold.
- *convergens* FEIST, 1999; *Isoprusia*; Valentine Formation (lower Eifelian), Wolayer Lake, Carnic Alps, Austria; single small pygidium (Feist, 1999, pl. 1, fig. 20), latex from external mold.
- *cornuta* WEBER, 1932; *Acidaspis*; Middle Devonian of Turkestan and Kazakhstan; *Isoprusia*: Bruton (1966), *Koneprusia* (*Isoprusia*): Vaněk and Pek (1987); Bruton (1966, p. 340) noted that *Acidaspis cornuta* Weber, 1932, is a homonym of *Acidaspis cornuta* Beyrich, 1846 (then and currently assigned to *Miraspis* Richter and Richter, 1917a), but chose not to erect a replacement name; not seen.
- cornuticauda (ERBEN, 1952); Orphanaspis; Greifenstein Limestone (Eifelian), "Wiege," near Greifenstein, Bl. Herborn, Germany; Isoprusia: Bruton (1966), Ramsköld (1991b), G. Alberti (2000), Santel (2001); Isoprusia (Isoprusia): G. Alberti (1969); Koneprusia (Koneprusia): G. ALBERTI, 1970, Kim (1997); Koneprusia (Isoprusia): Vaněk and Pek (1987); pygidium (Erben, 1952, pl. 20, fig. 13; refigured by Bruton, 1966, pl. 56, fig. 18).
- *cortezensis* n. sp.; type species of *Nevadaprusia*; Wenban Limestone (Pragian), southern Cortez Mountains, Eureka County, Nevada; cranidia, librigenae, hypostomes, thoracic segments, and pygidia; silicified.
- *cozarti* n. sp.; *Laethoprusia*; Birdsong Shale Member, Ross Formation (Lochkovian), Holladay Quarry, Holladay, Benton County, Tennessee; single dorsal exoskeleton; calcareous.
- cyrius G. ALBERTI, 1967; type species of Isoprusia (Mauraspis); "calcaires marmoréens gris-bleu" (Eifelian), Sidi Abdallah, Rehamna, western Morocco; Isoprusia (Mauraspis): G. Alberti (1969); Koneprusia (Mauraspis): G. Alberti (1970); Koneprusia (Isoprusia): Vaněk and Pek (1987); gen indet. cyrius: Ramsköld (1991b); single partial cranidium (Termier and Termier, 1950, pl. 204, fig. 14; Gigout, 1951, pl. 7, fig. 11; refigured by G. Alberti, 1969, pl. 41, fig. 13); calcareous.
- dispersa HÖRBINGER, 2004; Koneprusia (Koneprusia); Lochkov Formation, lower layers (Lochkovian), Praha-Řeporyje, quarry "Vokounka," Prague Basin, Bohemia, Czech Republic; single partial cranidium (Hörbinger, 2004, textfig. 2, pl. 1, fig. 1); calcareous.
- dvoraki VANĚK AND PEK, 1987; Koneprusia (Koneprusia); Zlíchov Limestone, Chapel Coral Horizon (Emsian), Praha 5-Hlubočepy, abandoned quarry "U kapličky," Prague Basin, Bohemia, Czech Republic; Koneprusia: Ramsköld (1991b); cranidium (Vaněk and Pek, 1987, pl. 1, fig. 2), hypostome (Přibyl and Vaněk, 1966, pl. 7, fig. 8; Vaněk and Pek, 1987, pl. 2, fig. 4), pygidium (Přibyl and Vaněk, 1966, pl. 7, fig. 7; Vaněk and Pek, 1987, pl. 2, fig. 5); calcareous.
- *eox* BASSE, 1998; *Koneprusia*; Ohle Formation (middle Eifelian), Bl. Endorf, western Sauerland, Germany; single specimen comprising cephalon (librigenae obscured) and seven articulated thoracic segments, latex from external mold, illustrated by a small photograph in dorsal view, with the anterior part of the cephalon and posterior extension of the pleural spines cropped and omitted (Basse, 1998, pl. 12, fig. 21).
- erbeni PILLET, 1973; Orphanaspis; the Calcaire de la Grange (upper Emsian), Chalonnes, near Angers, France; gen. indet. erbeni: Ramsköld (1991b); single poorly preserved and incomplete pygidium (Pillet, 1973, pl. 61, fig. 4).

- filae VANĚK IN HAVLIČEK AND VANĚK, 1996; Koneprusia (Koneprusia); Chýnice Limestone (Emsian; Zlichovian), Bubovice, hillside "Čeřinka," Prague Basin, Bohemia, Czech Republic; single partial cranidium (Havliček and Vaněk, 1996, pl. 3, fig. 7); calcareous.
- fuscina NOVÁK, 1883; Acidaspis; Acanthopyge Limestone (Eifelian), Koněprusy area between road on Suchomasty and small abandoned quarries, Prague Basin, Bohemia, Czech Republic. The type specimen is a dorsal exoskeleton which is known only from Novák's (1883, pl. 10, fig. 19a) drawings (reprinted in Horný and Bastl, 1970, pl. 20, fig. 5). Bruton (1966, p. 342) could not trace the type specimen and it has not been reported since (Vaněk and Valíček [2002, p. 21] considered its location unknown). Vaněk and Pek (1987, pl. 1, fig. 1) assigned a partial cranidium to the species, but in the absence of existing type material or photographs the species is effectively impossible to recognize.
- *graffhami* n. sp.; *Laethoprusia*; Cravatt Member, Bois d'Arc Formation (Lochkovian), Geological Enterprises Quarry, Coal County, Oklahoma; three dorsal exoskeletons; calcareous.
- *insolita* HAAS, 1969; *Koneprusia* (subgen.?); Wenban Limestone (Pragian), USNM locality 17233, west slope of Cortez Mountains, Eureka County, Nevada; cranidia (Haas, 1969, pl. 84, fig. 12, and herein), librigenae (herein), thoracic segments (Haas, 1969, pl. 84, fig. 13, and herein); silicified.
- *kofelae* SANTEL, 2001; *Isoprusia*; Fundhorizont 1, Rauchkofel Boden section "KA 2175," base of the Othoceren-Schicten (lower Homerian), Mount Rauchkofel, Carnic Alps, Austria; cranidia and pygidium (Santel, 2001, pl. 9, figs. 2–5); calcareous.
- lanigera VANĚK, 1999; Koneprusia (Koneprusia); Vinařice Limestone (Pragian), Tobolka, near Tetín, Tobolský vrch hill, Prague Basin, Bohemia, Czech Republic; partial cranidium (Vaněk, 1999, pl. 9, fig. 4) and partial pygidium (Vaněk, 1999, pl. 9, fig. 5); calcareous.
- matutina DEAN, 1974; Isoprusia; Chair of Kildare Limestone (Ashgill), Chair of Kildare, Co. Kildare, Ireland; Isoprusia: Morris (1988), Hammann (1992), Santel (2001); Isoprusia (s.l.): Ramsköld (1991b); pygidium (Dean, 1974, pl. 43, figs. 7, 12, 15); koneprusine cranidium from same locality illustrated by Dean as "odontopleurid gen. et sp. indet." presumably belongs, as pointed out by Ramsköld (1991b, p. 139); Dean misassociated a second cranidium (1974, pl. 43, fig. 5) but it is clearly not conspecific, as well as two librigenae which belong to a pharostomatine calymenid, presumably *Prionocheilus obtusus* (M'Coy, 1846) which occurs at the same locality; calcareous.
- maura G. ALBERTI, 1970; Koneprusia (Koneprusia); Ghtira Limestone (upper Pragian), locality RT VII, Ghtira-Tal, southeast of Rabat, Morocco; Koneprusia (Koneprusia): G. Alberti (1983), Vaněk and Pek (1987); Isoprusia (s.l.): Ramsköld (1991b), Basse (1998); single pygidium (G. Alberti, 1970, pl. 19, fig. 15); calcareous; Ramsköld (1991a, p. 139) considered maura a possible junior synonym of tafilaltana G. ALBERTI, 1967.
- *mediaspina* H. ALBERTI, 1969; *Koneprusia*; lower Eifelian, Harz Mountains, Germany; gen. indet.: Ramsköld (1991b); single pygidium.
- mydlakia BRUTON, 1966; type species of *Isoprusia*; Acanthopyge Limestone (Eifelian), Zlatý Kůň, Prague Basin, Bohemia, Czech Republic; cranidia, librigena, hypostomes, thoracic segments, pygidium (Bruton, 1966, pl. 55; figs. 1– 20, pl. 56; figs. 1–16, pl. 57, fig. 13); calcareous.
- pennata LÜTKE, 1965; Koneprusia; "dunkel, tonige Kalke des

Mittleren Herzyn," (upper Emsian), Kalklinse s3, w Stöberhaifahrweb, Abt. 76, Wieda (Bl. Zorge), western Harz Mountains, Germany; *Koneprusia* (*Koneprusia*): G. Alberti (1970), Vaněk and Pek (1987); *Isoprusia*: Bruton (1966), Ramsköld (1991b); Santel (2001); *Isoprusia* (*Isoprusia*): G. Alberti (1969); cranidium (Lütke, 1965, pl. 22, fig. 12), librigena (Lütke, 1965, pl. 22, fig. 13), hypostome (Lütke, 1965, pl. 22, fig. 14); calcareous.

- pustulata VANĚK, 1999; Koneprusia (Koneprusia); Vinařice Limestone (Pragian), Vinařice, near Beroun, abandoned quarry "Homolák," Prague Basin, Bohemia, Czech Republic; two partial cranidia (Vaněk, 1999, pl. 9, figs. 6, 7); calcareous.
- salax RAMSKÖLD (1991b); type species of *Laethoprusia*; large marl pocket in biohermal limestone of the Slite Formation, unit g (Homerian), locality Solklint 1, Othem parish, Gotland, Sweden; cranidia, librigenae, thoracic segments, pygidia (Ramsköld, 1991b, figs. 6a–6b, 7a–7c); calcareous.
- sandbergeri RICHTER AND RICHTER, 1917a; Acidaspis (Ceratocephala?); Stringocephalus Limestone (lower Givetian), Villmar-Lahn, Germany; Isoprusia: Bruton (1966), Ramsköld (1991b); Isoprusia (Isoprusia): G. Alberti (1969); Koneprusia (Isoprusia): Vaněk and Pek (1987); Koneprusia (Koneprusia): G. Alberti (1970); ex Koneprusiae sandbergeri: Basse (1998); partial cranidium and left librigena (Bruton, 1966, pl. 56, fig. 17); internal mold.
- sperata BARRANDE, 1872; Acidaspis; Dvorce-Prokop Limestone (Pragian), Praha 4-Braník, Prague Basin, Bohemia, Czech Republic; Koneprusia?: Prantl and Přibyl (1949), Lütke (1965); Koneprusia: Přibyl and Vaněk (1966), Ramsköld (1991b); Koneprusia (Koneprusia): G. Alberti (1970), Vaněk and Pek (1987), Vaněk (1999), Vaněk and Valíček (2002); Koneprusia: Santel (2001); Isoprusia?: Bruton (1966); Isoprusia (Isoprusia): G. Alberti (1969); two cranidia (Přibyl and Vaněk, 1966, pl. 7, figs. 1, 2), two pygidia (Přibyl and Vaněk, 1966, pl. 7, fig. 3; Vaněk and Pek, 1987, pl. 2, fig. 3); calcareous.
- subterarmata BARRANDE, 1846; Odontopleura; Suchomasty Limestone (Emsian; Dalejan), area of Koněprusy, Prague Basin, Bohemia, Czech Republic; = Odontopleura Laportii Hawle and Corda, 1847, fide Vaněk (1962); = Odontopleura impar Hawle and Corda, 1847, fide Vaněk and Pek (1987, p. 267); Koneprusia: Vaněk (1962), Lütke (1965), Přibyl and Vaněk (1966), Ormiston (1969), Chlupáč (1969), Haas (1969), Ramsköld (1991b), Santel (2001); Koneprusia (Koneprusia): G. Alberti (1970, 1983), Přibyl and Vaněk (1973), Vaněk and Pek (1987), Havliček and Vaněk (1996), Kim (1997), Vaněk (1999), Vaněk and Valíček (2002); cranidium (lectotype of Odontopleura Laportii: Bruton, 1966, pl. 57, figs. 1, 4, 6, 7; Přibyl and Vaněk, 1966, pl. 7, fig. 5; Šnajdr, 1984, pl. 6, fig. 10), pygidia (Bruton, 1966, pl. 57, figs. 15, 17, 18; Přibyl and Vaněk, 1966, pl. 7, fig. 6); calcareous.
- tafilaltana G. ALBERTI, 1967; Isoprusia (Isoprusia); lower Hamar Laghdad Limestone (Pragian), Hamar Laghdad III (Tafilalt), east-southeast of Erfoud, southeastern Morocco; *Koneprusia (Koneprusia) brutoni* G. Alberti, 1983, from the same unit and locality, fide Ramsköld (1991b, p. 139); *Isoprusia (Isoprusia)*: G. Alberti (1969); *Koneprusia (Koneprusia)*: G. Alberti (1969); *Koneprusia (Koneprusia)*: G. Alberti, 1969, pl. 41, fig. 10), pygidium (holotype of *brutoni*: G. Alberti, 1983, pl. 2, fig. 19); calcareous.
- ursula BARRANDE, 1872; Acidaspis; Koněprusy Limestone (Pragian), Koněprusy area (probably Plešivec hill near Měňany), Prague Basin, Bohemia, Czech Republic; Koneprusia: Lütke (1965), Santel (2001); Koneprusia (Koneprusia): G. Alberti (1970); Koneprusia?: Chatterton et

al. (1979); *Isoprusia*: Bruton (1966), Ramsköld (1991b); *Isoprusia (Isoprusia*): G. Alberti (1969); *Koneprusia (Isoprusia)*: Vaněk and Pek (1987), Vaněk (1999), Vaněk and Valíček (2002); two cephala, two cranidia (Bruton, 1966, pl. 57, figs. 2, 3, 5, 8–12, 14, 16); a cranidium assigned by Vaněk (1999, pl. 9, fig. 8) is questionably conspecific.

- villosa VANĚK, 1999; Koneprusia (Isoprusia); Loděnice Limestone (Pragian), Loděnice-Branžovy, Záloženský lom quarry, Prague Basin, Bohemia, Czech Republic; partial cranidium and partial pygidium; calcareous.
- zapletali VANĚK AND PEK, 1987; Koneprusia (Koneprusia); Slivenec Limestone (Pragian), Praha 4-Podolí, swimming pool, Prague Basin, Bohemia, Czech Republic; partial cranidium (Vaněk and Pek, 1987, pl. 1, fig. 4); calcareous.

### REJECTED TAXA

Vaněk and Pek (1987) proposed Koneprusia (Isoprusia) anchyses from the Loděnice Limestone (Pragian) of the Czech Republic, with the holotype a pygidium and a partial cranidium tentatively assigned. Ramsköld (1991b, p. 139) listed it as an accepted species. The species does not appear to be a member of Koneprusiinae, but rather probably a selenopeltine. The pygidium lacks a median border spine, but its major border spines appear to have their bases set dorsally on the pleural ridge rather than in a more nearly marginal position typical of koneprusiines. If the cranidium is correctly associated, the species lacks one of the main synapomorphies of Koneprusiinae-the lack of differentiation of L3, as its L3 is prominent and transverse, and well separated from the frontal glabellar lobe by a deep S3. Again, this is a selenopeltine state. Like many of the Czech species, anchyses is so poorly described as to be all but uninterpretable, but there is scant evidence that either of the assigned sclerites represents a koneprusiine species.

Hammann (1992) erected Hispaniaspis for two species from the Upper Ordovician of Spain, classifying the genus as Koneprusiinae. Hammann recognized that the known thoracic segment count of nine [for H. morenaica (Hammann, 1976)] was at odds with the 10 segments known for and considered synapomorphic for Koneprusiinae by Ramsköld (1991b). Segment count is essentially invariant within odontopleurid subfamilies, with the sole unambiguous exception being species of the odontopleurine Kettneraspis Prantl and Přibyl, 1949 with eight versus the typical nine segments (see Ramsköld and Chatterton, 1991). This is obviously a case of fusion of the posterior thoracic segment with the pygidium, however, and is not comparable to the situation in koneprusilnes versus selenopeltines in which the tail is fully tagmatized and the number of pygidial segments similar in either subfamily. Hammann (1992) justified this by an appeal to negative evidence-the thoracic segment number is unknown in many taxa. However, it is demonstrated herein that two new species of Laethoprusia also had 10 segments. Hispaniaspis does not closely resemble koneprusiines in any cephalic features. Hammann (1992) noted that the librigena of H. dereimsi Hammann, 1992, was similar to a juvenile librigena of Laethoprusia salax Ramsköld (1991b, fig. 6l, 6m). This is true, but the morphology is also probably plesiomorphic and is widely distributed among selenopeltines. The issue of the relationship of Koneprusiinae to Selenopeltinae remains open. Hammann (1992, p. 126) suggested that *Hispaniaspis* "may represent an early, intermediate form con-necting these subfamilies," but *Hispaniaspis* does not appear to bear any of the apomorphies of Koneprusiinae and is assigned to Selenopeltinae herein.

# PARSIMONY ANALYSIS: CHARACTERS

Character analysis herein is based on that of Ramsköld (1991b) with some modifications and additions. Characters which are wholly or partly derived from Ramsköld's are denoted, e.g., "R2" for "character 2 of Ramsköld, 1991b, p. 129."

Cranidium

- L3 relative to anterolateral expansion of frontal lobe. 0 defined from it by deep S3; 1—merged, S3 weak or absent. (R1)
- 2. Longitudinal furrow opposite L3. 0—deep; 1—weak or absent. (R2)
- 3. Glabella widest across: 0—posterior part of L1; 1—anterior part of L1. (R3)
- Position of eyes. 0—opposite anterior part of L1; 1—opposite posterior part of L1. (R4)
- Occipital organ. 0—node; 1—short and slender spine running directly dorsally; 2—elongate and robust, posterodorsally directed spine. (R5, modified and recoded)
- 6. Median occipital spine developed posterior to occipital organ. 0-absent; 1-present. (R5, modified and recoded) As in other odontopleurid taxa, a distinction is apparent between two types of median occipital spines. When members of Odontopleurinae develop a median spine, it is typically a spinose extension of the occipital organ. In these cases the occipital organ is not present in front of the spine, nor is any small sagittally placed node which could possibly be the occipital organ. With exceptional preservation, the openings of the organ can be seen at the tip of the spine (e.g., Whittington, 1956, pl. 9, fig. 8; pl. 11, fig. 18). In contrast, when a median spine is developed in Acidaspidinae, it is typically more robust and with a much broader base, is posteriorly set, and is always distinguishable from the occipital organ which is either set anterior to the spine on LO or on the dorsal aspect of the spine base (e.g., Acidaspis Murchison, 1839: Chatterton and Perry, 1983, pl. 29, fig. 4; Dudleyaspis Prantl and Přibyl, 1949: Chatterton and Perry, 1983, pl. 27, figs. 1, 2, 4, 5, 7, 10, 11, 19). Ramsköld (1991b, fig. 4c) drew attention to the latter style of spine development in Isoprusia (s.l.) bucco, whereas an extension of the occipital organ appears to be present, for example, in *I. mydlakia* and is definitely present in Nevadaprusia n. gen.
- 7. Paired occipital spines. 0—present; 1—absent. (R5, modified and recoded)
- 8. Posterior band. 0—fully defined across entire rear of LO; 1 defined laterally, absent medially; 2—absent. (R6, modified and recoded) Although it can be coded from the rear of LO even in the absence of thoracic information, this character remains uncodable on many species for which cranidia have been figured. The problem is that unless the posterior band is very well expressed, a view from a somewhat posterior aspect is required to determine its presence. The species *cyrius* G. Alberti, 1967 provides a good example of how the character is hidden in dorsal view (G. Alberti, 1969, pl. 41, fig. 13a) yet clear in posterodorsal view (G. Alberti, 1969, pl. 41, fig. 13b) of the same specimen.

# Librigena

9. Eye elevated from field, with socle; 0—no; 1—yes.

## Thorax

- 10. Pleural furrows on thoracic segments. 0—distinct; 1—faint or absent. (R7)
- 11. Axial spines on anterior segments. 0—none; 1—paired; 2 single median.
- Axial spines on posterior segments. 0—none; 1—paired; 2 single median.

# Pygidium

- 13. Axial furrow along first axial ring. 0—distinct; 1—weak, ring confluent with pleural ridges. (R9)
- 14. Axial furrow along second axial ring. 0—distinctly impressed; 1—break in slope only. (R10)
- 15. Caecal sculpture on distal part of pleura (distal to pleural ridge); 0—absent; 1—present.

- Pleural area between posterior portion of axis and pleural ridge. 0—flat, level and sculpture similar to adjacent pleural area. 1—deeply recessed, irregular topography, lacking sculpture. (R13)
- 17. Pleural ridges near posterior margin. 0—well defined at least adaxially. 1—poorly defined. (R14)
- 18. Posterior border. 0—absent; 1—present. (R15; modified and recoded)
- Median border spine. 0—absent; 1—tiny; 2—long and robust. (R16; modified and recoded)
- 20. Lateral spines. 0—with base set abaxial to lateral edge of first axial ring; 1—with base adaxial to or even with lateral edge of first axial ring.
- 21. Lateral spines. 0—running almost exactly posteriorly at base; 1—posteriorly convergent at base; 2—posteriorly divergent.
- 22. Fenestrae in thorax and pygidium. 0-absent; 1-present.
- 23. Sagittal separation between rear of axis and pygidial margin. 0—little separation, border either absent or axis abuts border; 1—significant separation, rear of axis set well forward from inflated border and separated by depressed posterior area.

## PARSIMONY ANALYSIS: RESULTS

Ramsköld (1991b, table 1) coded a total of 13 ingroup species, along with outgroup codings for the genera Dicranurus Conrad, 1841, and Selenopeltoides Prantl and Přibyl, 1949. The outgroups differ in the polarity of a single character (R4, position of eyes). Dicranurus polarizes three other characters for which Selenopeltoides either lacks information (R3) or is autapomorphic (R8, R11). Ramsköld presented the full analysis with *Dicranurus* as outgroup. Ramsköld's codings for Laethoprusia salax and L. brikelos were identical and hence redundant. He carried out parsimony analysis with several sets of included taxa. All of the results (Ramsköld, 1991b, fig. 3) were consistent with one another. We reanalyzed Ramsköld's data matrix and obtained a similar result (Fig. 2), differing only in that we obtained 627 instead of 625 trees of length 21. A strict consensus with Bremer support is shown in Figure 2.1. The strict consensus resolves only nodes for Laethoprusia and Koneprusia. However, an Adams consensus (Fig. 2.2) reveals more phylogenetic structure, resolving Isoprusia matutina as sister to Laethoprusia, linking the type and another species of Isoprusia, and resolving a node within Koneprusia.

When Ramsköld (1991b, p. 130) carried out his original analysis, he noted that only five species of the 13 he included were codable for most characters. Two of these five are unpublished, and were coded from the Ph.D. thesis of Feist (1977). More information is now available, but the majority of named species are still so poorly known as to be barely interpretable. Codings are presented for 34 named species in Table 1. Codings are also present for three species described in open nomenclature. Data available for these are actually as high or higher as that for many named species. Codings are also presented for three undescribed species from the Devonian of Morocco under study by BDEC. These are species of Koneprusia from Zguilma (late Emsian), Lachana, near Jebel Oufaten (probably early Emsian), and Timarzite (late Emsian). They will be described in forthcoming works. Quality of the taxa in the matrix ranges from completely uncodable (erbeni Pillet, 1973-an uninterpretable and extremely poorly preserved pygidium) to fully coded for all 23 characters. Only four published species are fully codable, three of which are newly described herein. Ten species are codable for either 22 or 23 characters. A further 12 are known from both cranidia and pygidia but are missing librigenal and thoracic data (and in some cases cannot be coded for all cranidial and pygidial characters). Twelve named species are known from cranidia only (in one case with some librigenal and thoracic data). Six species (five formally named, including the completely uncodable erbeni) are known from pygidia only, in all cases single specimens.

All characters were unordered, and an outgroup coding was



FIGURE 2—Consensus trees from analysis of Ramsköld's (1991b) data set. *1*, Strict consensus of 627 trees of length 21 (vs. 625 trees reported by Ramsköld), c.i. = 0.810, r.c. = 0.708. Numbers beside branches are Bremer support values. *2*, Adams consensus of same 627 trees.

based on Selenopeltinae. Despite the amount of missing data and paucity of information for coding, there are no identically coded taxa in the matrix (save the uncoded *erbeni*). However, the presence of 18 species with greater than 50 percent missing data makes analyses of the entire matrix impractical. All attempts resulted in unresolved consensus trees (strict and Adams). Removing the virtually meaningless "species" based often on single poorly known cranidia or pygidia, analysis of the 22 species for which at least cranidial and pygidial data were available yielded a result similar to Ramsköld's smaller (1991b) analysis. A strict consensus was unresolved, but an Adams consensus (Fig. 3.1) retrieved nodes for Laethoprusia and for Koneprusia, with the fully known Moroccan species of Koneprusia forming a node within the genus. Laethoprusia, Nevadaprusia n. gen., and Koneprusia form a clade to the exclusion of species which have been assigned to Isoprusia and which form a basal polytomy.

Restricting the analyses to only the 10 best known species yields what we regard as the best approximation currently available of koneprusiine phylogeny, and one that is congruent with the broader 22 species result. The strict consensus (Fig. 3.2) identifies Nevadaprusia as the sister taxon of Laethoprusia, Koneprusia as sister to this clade, and *Isoprusia* as a basal taxon. *Isoprusia* is not identified as a clade in any analysis and its conventional content may represent a plesiomorphic grade group. However, most species beyond the type are so poorly known that it is difficult to be certain what the status of the genus really is. Species in the expanded analysis which join in the basal polytomy might best be referred to "Isoprusia (s.l.)" but most are known from only one or two sclerites and are virtual nomina dubia. Character support under the delayed transformation assumption is shown for one of the 33 most parsimonious trees in the 10 taxon analysis in Figure 3.3.

# SYSTEMATIC PALEONTOLOGY

*Repository.*—Figured specimens are housed in the collections of the Paleontology Repository, University of Iowa, Iowa City, with specimen number prefix SUI, the Burpee Museum of Natural History, Rockford, Illinois, with prefix BMR, the Paleontological Collections of the University of Alberta, Edmonton, with prefix UA, and the Royal Ontario Museum, Toronto, with prefix ROM.

# Family ODONTOPLEURIDAE Burmeister, 1843 Subfamily KONEPRUSIINAE Vaněk and Pek, 1987

Genera included.—Isoprusia Bruton, 1966; Koneprusia Prantl and Přibyl, 1949; Laethoprusia Ramsköld, 1991b; Nevadaprusia n. gen.

*Discussion.*—See above for exclusion of *Hispaniaspis* Hammann, 1992, from the subfamily.

### Genus NEVADAPRUSIA new genus

*Type species.—Nevadaprusia cortezensis* n. sp.

Other species.—Koneprusia (n. subgen.?) insolita Haas, 1969. Diagnosis.—Koneprusiines with large paired occipital spines set on dorsally flattened, posteriorly extended LO; median tubercle developed into short, pillar-like spine running directly dorsally; paired spines on thoracic axial rings.

Etymology.--After the state of Nevada. Gender is feminine.

Discussion.—Haas recognized that his new species insolita likely represented a new genus-group taxon, and most commentators since have agreed. No new genus has previously been erected because insolita has been known from only two fragmentary sclerites. The discovery of a slightly younger species, obviously closely related to insolita but represented by abundant well-preserved material, coupled with additional knowledge of insolita, allows the genus Nevadaprusia to be established.

Hammann (1992) suggested that *N. insolita* might be related to his new taxon *Hispaniaspis*. *Hispaniaspis* is rejected as a koneprusiine above and is instead considered a selenopeltine. Similarities with *Nevadaprusia* are few, with the main one being the presence of paired occipital spines. These spines are synapomorphic for *Nevadaprusia*, and as indicated by the phylogeny of Figure 3.3, their acquisition is probably homoplastic compared to the presence of similar spines among the selenopeltines.

# NEVADAPRUSIA CORTEZENSIS new species Figures 4, 5

*Diagnosis.*—Median glabellar lobe narrow; median occipital spine very short; paired occipital spines with robust, close-set bases; SO shallow along posterior edge; cephalic dorsal tuberculate sculpture relatively coarse; thoracic pleural spines short and relatively sparsely tuberculate.

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FIGURE 3—1, Adams consensus of 222,297 trees produced by branch and bound analysis of 22 ingroup taxa for which at least some information is available for both cranidium and pygidium. A strict consensus was unresolved. Despite the high number of MPTs due to large amounts of missing data, the Adams consensus retrieves the *Laethoprusia* and *Koneprusia* nodes. 2, Strict consensus of 33 trees produced by exhaustive search of 10 ingroup taxa for which codings are substantially complete. Numbers above branches are nonparametric bootstrap values based on 10,000 replicates using branch and bound search. Numbers below branches are Bremer support values. The Adams consensus is identical. 3, One of the 33 most parsimonious trees (selected arbitrarily) with character support for major clades mapped using delayed transformation assumption. Character numbers correspond to Table 1. Open bar denotes reversal.

 $<sup>\</sup>rightarrow$ 

FIGURE 4—Nevadaprusia cortezensis n. gen. and sp., from the Wenban Limestone (Pragian), Cortez Gold Mine Haul Road, southern Cortez Mountains, Eureka County, Nevada. 1, 4, 6, Cranidium, SUI 101456, dorsal, anterior, and left lateral views, ×6. (CR-G). 2, 5, 7, Cranidium, SUI 101457, dorsal, anterior, and left lateral views, ×7.5 (CR-G). 3, 9, 14, 15, 19, Cranidium, holotype, SUI 101458, dorsal, ventral, right lateral, anterior, and oblique views, ×10 (CR-C). 8, 11, 13, Cranidium, SUI 101459, dorsal, anterior, and right lateral views, ×7.5 (CR-G). 10, 12, 16, Cranidium, SUI 101460, dorsal, anterior, and right lateral views, ×7.5 (CR-G). 17, 20, 21, Cranidium, SUI 101461, left lateral, dorsal, and anterior views, ×7.5 (CR-G). 18, 22, 23, Cranidium, SUI 101462, dorsal, anterior, and left lateral views, ×6 (CR-G).





Description .--- Cranidium. Cited dimensions are based on the holotype (Fig. 4.3, 4.9, 4.14, 4.15, 4.19), which is intact and undistorted. Sagittal length 49 percent maximum width across posterior fixigenae; width across rear of palpebral lobes 71 percent maximum width; width across anterolateral corners of anterior border 41 percent maximum width; maximum glabellar width across approximate midlength of L1 56 percent cranidial width at rear of palpebral lobe; anterior border short and flat, slightly longer exsagittally than sagittally, anterior margin describing slightly irregular anterior arc in some specimens (Fig. 4.1-4.3), distinct, shallow, inverted "V" shape in others (Fig. 4.8, 4.10), dorsal sculpture of fine closely spaced tubercles, slightly larger at lateral extremes; anterior border furrow short, deep and well incised, partially overhung by anterior margin of glabella sagittally; anterior section of facial suture strongly laterally bowed (Fig. 4.19); eye ridge slightly wider than length of anterior border, directed anteriorly from front edge of palpebral lobe, curving adaxially subparallel with facial suture, abutting suture near palpebral lobe, separated by narrow furrow (which runs into anterior border furrow) anteriorly, with sculpture of dense tubercles; frontal area restricted to patch of smooth cuticle near confluence of lateral projection of frontal glabellar lobe, eye ridge, and interocular fixigena (Fig. 4.4, 4.5, 4.15); glabella with dorsal sculpture of dense tubercles similar to that on interocular fixigena and eye ridge; L1 elongate and variably shaped, with distinct posterior bulge in all specimens, fully isolated and independently inflated, bound on all sides by axial furrow, longitudinal furrow, SO and S1; L2 less than half length and area of L1, inflated and slightly bulging anterolaterally, tapering slightly posteromedially, isolated and inflated as for L1; L3 small and transverse, clearly distinct anteriorly with discernible S3 in some specimens (Fig. 4.4, 4.12), more or less merged with anterior lobe of glabella in others (Fig. 4.15, 4.22); median glabellar lobe slightly less inflated than L1 and L2, subtrapezoidal in shape, with longitudinal furrows anteriorly convergent, confluent with laterally expanded frontal lobe, anterior margin describing slightly more curved arc than anterior cranidial margin; interocular fixigena slightly more strongly inflated than L1 (Fig. 4.4), width greatest in front of palpebral lobe, curving without interruption into posterior fixigena that varies in sculpture from similar to interocular fixigena (Fig. 4.3) to considerably more sparsely tuberculate (Fig. 4.1); posterolateral projection with bluntly triangular shape; posterior section of facial suture short and laterally bowed; posterior border furrow nearly straight and running anterolaterally, short (exsag.) and moderately incised, deeper proximally, shallowed completely near suture in some specimens (Fig. 4.3); posterior border very short proximally, becoming steadily longer distally, tubelike in exsagittal profile, with sculpture of scattered fine tubercles mostly on posterolateral parts; SO set anteriorly, median part opposite about one third length of L1, transverse, quite strongly incised in some specimens (Fig. 4.2, 4.10), weak smooth area in others (Fig. 4.1, 4.18); LO long and broad, with sculpture generally more sparse than rear of median glabellar lobe; median spine/node set at half length, prominent, running straight dorsally (Fig. 4.5, 4.12); paired occipital spines strongly curved, with dense tubercles developed into short, thornlike, posteriorly directed spines, paired spines varying in spacing of bases and degree of posterior divergence; posterior part of LO with very weakly developed furrow and posterior band visible in some specimens (Fig. 4.1, 4.3); cranidial doublure developed only under LO.

Librigena with exsagittal length 99.8 (92.7-114.7) percent maximum width at about midlength of eye; field with width 88.0 (82.6-95.9) percent length; eye small, elevated, and turned slightly posteriorly, longer than wide/tall; eye socle of slightly inflated band elevating eye above field, with sculpture of single linear row of moderate sized tubercles; field with moderate lateral inflation, sculpture ranging from densely crowded moderate and small tubercles in smaller specimens (Fig. 5.10, 5.16) to sparse, relatively larger tubercles in largest specimens (Fig. 5.15); lateral portion of field near lateral border furrow lacking sculpture in all specimens; lateral border furrow deeper and more distinct in smaller specimens, broad and shallow in larger specimens, with distinct break in slope abutting lateral border but more shallow gradation into field, anterior part set obliquely to horizontal plane and straight, bending posteriorly opposite lobate posterior part of border, angled sharply into very poorly expressed posterior border furrow; lateral border with strong, tubelike lateral convexity, narrower anteriorly, broader and lobate posteriorly, curving without interruption into posterior border and base of genal spine, with sculpture of very dense, small tubercles anteriorly, less dense and larger tubercles

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posteriorly, posterolateral edge with row of fairly large, thornlike posteriorly directed border spines; genal spine with broad base occupying most of course of posterior border, tapering into tube-like, robust spine, curved posterolaterally, length about same as remainder of librigena, with sculpture of closely spaced coarse tubercles on dorsolateral aspect and sparse, smaller tubercles on ventral aspect; doublure with sharp, edgelike break in slope from lateral border, fringed with row of very small, closely set spines, completely flat and smooth, with adaxial extent similar to that of lateral border.

Rostral plate unknown.

Hypostome with sagittal length 53.3 (51.6–54.9) percent maximum width; anterior margin slightly anteriorly bowed; lateral margin flaring out opposite one-third length to pronounced shoulder, running posteromedially behind shoulder to form lobate posterior margin; posterior margin of two lateral lobes and median embayment; lateral and posterior borders broad, with sculpture of fine scattered tubercles on adaxial part of lateral border; lateral border furrows relatively deep and incised, slightly posteriorly convergent, merging with posteriorly bowed posterior border furrow at slight angle to define loz-enge-shaped middle body; middle body with very faint middle furrow expressed mainly as a pair of shallow dimples joined by very faint and shallow transverse furrow; middle body with sculpture of subdued tubercles, larger than those on lateral border; doublure flat and unsculptured, overlying all of lateral and posterior border, with prominent pit/perforation behind shoulder.

Thoracic segments with axial width 28.6 (26.2–31.9) percent total width of segment excluding pleural spines; articulating half ring large; ring furrow deep, anteriorly bowed; lenticular preannulus developed in front of axial ring and separated by secondary furrow slightly shallower than ring furrow; ring longer exsagittally than sagittally, with sculpture of scattered fine to moderate sized tubercles and pair of prominent, short, dorsally directed spines; axial furrow very shallow; pleura of single inflated band, bounded anteriorly and posteriorly by narrow transverse articulating edges, each separated from pleural band by very thin furrow; pleural band with sculpture of very scattered moderate sized tubercles; pleural band split distally into short downturned anterior spine running exactly ventrally (Fig. 5.5) to slightly ventrolaterally (Fig. 5.2, 5.7) with sharp, slightly out-turned tip, and sculpture of very fine and dense tubercles/spines mainly on anterior aspect, and much longer posterior spine set dorsal to this, running laterally and posterodorsally in anterior segments (Fig. 5.8, 5.9), and posteroventrally in posterior segments (Fig. 5.3).

Pygidium with sagittal length (excluding articulating half ring and posteromedian spine) 28.6 (26.2-31.9) percent maximum width; articulating half ring and ring furrow similar to those of thoracic segments; preannulus discernible on some specimens (Fig. 5.35) but others have only short ring furrow (Fig. 5.33); anterior margin of pleural region transversely straight, with narrow rim set off by fine furrow similar to structures on anterior edge of thoracic segments; main body of pygidium with more or less triangular shape, with blunt but distinct angulation at posteromedian part; margin with dense fringe consisting of linear row of spines along ventrolateral break in slope and closely packed smaller tubercles and spines on ventral aspect surrounding sharp break in slope to doublure; weak pygidial border developed, similar in dimensions to lateral spines; first axial ring longer exsagittally than sagittally, with sculpture of scattered tubercles similar to that on thoracic axial rings but lacking paired spines seen on thoracic rings; axial furrow weak (Fig. 5.32) to obscure (Fig. 5.34, 5.35); second axial ring narrower than first, set off by deep ring furrow behind first ring, weakly differentiated from subtriangular terminal piece, though ring furrow clearly present ventrally (Fig. 5.17, 5.22), with sculpture of scattered tubercles similar to that of first ring; pleural area lateral to lateral spine with slight depression bounded by anterior margin and pygidial border, sculpture of three to five tubercles sparsely scattered in area, no caecal sculpture developed; posterior area with well defined rear formed by shallowed V-shaped border furrow, rear of axis reaching nearly to border (Fig. 5.32) or terminated well in front (Fig. 5.35), pleural region concomitantly either lateral subtriangular areas (5.34) or shallow, contiguous U-shaped area (Fig. 5.35); very deep pitlike depression at junction of axial furrow and second ring furrow in some specimens (Fig. 5.32) but not evident dorsally in others (Fig. 5.35), though clearly present as small protuberance ventrally (Fig. 5.17, 5.22); lateral spines with bases set 46.0 (43.8-49.1) percent distance distally from sagittal axis, long, slightly longer than exsagittal length of pygidium in front of base, directed posterolaterally at base, curved distally to run slightly

FIGURE 5—Nevadaprusia cortezensis n. gen. and sp., from the Wenban Limestone (Pragian), Cortez Gold Mine Haul Road, southern Cortez Mountains, Eureka County, Nevada. 1–3, Thoracic segment, SUI 101463, dorsal, anterior, and right lateral views, ×7.5 (CR-G). 4, 5, 8, Thoracic segment, SUI 101464, dorsal, anterior, and left lateral views, ×7.5 (CR-G). 6, 7, 9, 11, Thoracic segment, SUI 101465, dorsal, anterior, left lateral, and ventral views, ×7.5 (CR-G). 10, Right librigena, SUI 101466, external view, ×10 (CR-G). 12, 15, Left librigena, SUI 101467, ventrolateral and external views, ×7.5 (CR-G). 13, hypostome, SUI 101468, ventral view, ×7.5 (CR-G). 14, 18, Right librigena, SUI 101469, external and internal views, ×7.5 (CR-G). 16, Left librigena, SUI 101470, external view, ×10 (CR-G). 17, 22, 26, 31, 35, Pygidium, SUI 101471, anteroventral, ventral, right lateral, posterior, and dorsal views, ×6 (CR-G). 19–21, 24, Hypostome, SUI 101472, ventral, left lateral, dorsal, and posterior views, ×10 (CR-C). 23, 27, 32, Pygidium, SUI 101473, left lateral, posterior, and dorsal views, ×6 (CR-G). 25, 30, 34, Pygidium, SUI 101474, left lateral, posterior, and dorsal views, ×6 (CR-G). 28, 29, 33, Pygidium, SUI 101475, left lateral, posterior, and dorsal views, ×7.5 (CR-G).



FIGURE 6—*Nevadaprusia insolita* (Haas, 1969), from the Wenban Limestone (Pragian), Cortez Gold Mine Haul Road, southern Cortez Mountains, Eureka County, Nevada. All from locality CR-H. *1*, *2*, *6*, Cranidium, SUI 101476, dorsal, anterior, and left lateral views, ×7.5. *3*, *10*, Thoracic segment, SUI 101477, dorsal and right lateral views, ×10. *4*, *5*, Left librigena, SUI 101478, external and ventrolateral views, ×7.5. 7, Thoracic segment, SUI 101479, dorsal view, ×10. 8, Thoracic segment, SUI 101480, dorsal view, ×7.5. 9, Right librigena, SUI 101481, external view, ×10.

posteromedially at tip, with dorsal sculpture of sparse tubercles, short spines on lateral edges less crowded than those on pygidial margin, and smaller, densely set thornlike spines on ventral aspect; median spine slightly more than half length of lateral spines, with similar sculpture; doublure with sharp break in slope from border, but sculpture somewhat gradational from small spines on border to fine granules to smooth and flat on main part of doublure, curved up to sit nearly vertically.

Etymology.—After the Cortez Mountains.

*Type and occurrence.*—Holotype, cranidium, SUI 101458, from locality CR-C, and paratypes SUI 101456, 101457, 101459–101475 from localities CR-C and CR-G, Wenban Limestone (Pragian), Cortez Gold Mine haul road, southern Cortez Mountains, Eureka County, central Nevada.

*Discussion.—Nevadaprusia cortezensis* is compared with *N. insolita* in discussion of that species below.

# NEVADAPRUSIA INSOLITA (Haas, 1969) Figure 6

Koneprusia (subgen.?) insolita HAAS, 1969, p. 655, text-fig. 6, pl. 84, figs. 12, 13.

Koneprusia insolita Haas; PERRY AND CHATTERTON, 1976, p. 1477.

Koneprusia? insolita Haas; CHATTERTON, JOHNSON, AND CAMPBELL, 1979, p. 831.

Koneprusia (Isoprusia?) insolita Haas; VANĚK AND PEK, 1987, p. 268. Koneprusia (n. subgen.?) insolita Haas; HAMMANN, 1992, p. 126. new genus? insolita Haas; RAMSKÖLD, 1991b, p. 139.

*Material and occurrence.*—Topotype specimens SUI 101476–101481 from locality CR-H, Wenban Limestone (Pragian), Cortez Gold Mine haul road, southern Cortez Mountains, Eureka County, central Nevada.

Discussion.—Haas (1969) based the species on a partial cranidium and a fragmentary thoracic segment. The taxon remains unsatisfactorily known, as topotypic material is likewise sparse and scrappily preserved. No pygidia were recovered, but a second partial cranidium amplifies knowledge of the structure across LO and the posterior fixigenae, and the first known librigenae provide additional information. Nevadaprusia insolita is distinguished from N. cortezensis in its finer tuberculate sculpture, both on the cranidium and librigena, in its relatively broader median glabellar lobe, and particularly by the structure of the occipital spines. In N. cortezensis, as in most other members of the subfamily, the median organ is small, and is only slightly extended dorsally into a stubby spine. In N. insolita, although the structure is broken in both available specimens, it is clear that the median spine was elongate and cylindrical, and must have extended dorsally for a much greater length than that of N. cortezensis. The base of the median spine is also set further forward from the posterior margin of LO in N. insolita. The paired occipital spines are set farther

apart, with a broader, much more transversely straight posterior margin of LO between their bases. Although all examples are broken, it also appears as if they have a relatively more slender base, and do not taper as rapidly distal to the base as those of *N. cortezensis*. Available thoracic segments of *N. insolita* have apparently longer, less tapering dorsal pleural spines, with a more dense sculpture of finer tubercles, than those of *N. cortezensis*.

# Genus LAETHOPRUSIA Ramsköld, 1991b

*Type species.—Laethoprusia salax* Ramsköld, 1991b, from the Slite Formation (Wenlock; Homerian), locality Solklint 1, Othem parish, Gotland, Sweden.

Other species.—Koneprusia (Koneprusia) brikelos Chatterton, Johnson, and Campbell, 1979; *L. cozarti* n. sp.; *L. graffhami* n. sp.; *Laethoprusia* n. sp. A. Ramsköld listed "*Laethoprusia* sp. of Feist (1977)" and included it in his parsimony analysis, but this species remains unpublished.

Discussion.-Ramsköld (1991a, fig. 8) demonstrated that differentiation in the exsagittal lengths of thoracic segments was consistent within taxa and important evidence supporting the monophyly of Selenopeltinae. Selenopeltines have strongly differentiated segment lengths, whereas odontopleurines and acidaspidines have segments of more or less similar lengths along the length of the thorax. Ramsköld (1991b, fig. 2) further demonstrated that a Moroccan Devonian species of Koneprusia which he illustrated (Ramsköld, 1991b, fig. 1) in open nomenclature demonstrated some length differentiation, but nowhere near as dramatic as that within Selenopeltinae, providing further evidence that Koneprusiinae was a distinct clade. Species of Laethoprusia described herein confirm this distinction (Fig. 7). Like Ramsköld's Koneprusia, segment length varies along the thorax, but over a more limited range (approximately 8 percent-12 percent) than is typical of selenopeltines (approximately 6 percent-14 percent).

# LAETHOPRUSIA GRAFFHAMI new species Figures 8–10

*Diagnosis.*—Posterior fixigena relatively broad; median glabellar lobe posteriorly broad; dorsal tuberculate sculpture subdued on all surfaces; thoracic fenestrae narrow (tr.); posterior band very strongly expressed on LO and thoracic rings.

*Description.*—Although all three type specimens are complete dorsal exoskeletons, they are somewhat crushed and distorted, and each has a different vector of deformation. Hence, numerical measurements and ratios of particular features are not appropriate and qualitative dimensions are cited.



FIGURE 7—Differentiation in thoracic segmental lengths (exsag.) in the holotype specimens of *Laethoprusia graffhami* n. sp. and *L. cozarti* n. sp. Compare with Ramsköld (1991a, fig. 8; 1991b, fig. 2).

Cranidium. Glabella with median lobe wider posteriorly than anteriorly, with sculpture of subdued and widely scattered median sized tubercles, tubercles smaller and more densely crowded on anteriormost part; longitudinal furrows broad but shallow; L1 long (exsag.), with lateral margin indented at about half length, anterolateral bulgelike projection, and sculpture of scattered tubercles smaller than those on median lobe; L2 about half area of L1, with similarly sized tubercles and small anterolateral projection; S1 and S2 angled posteromedially, very deep and nearly slotlike; L3 discernible but weakly inflated; S3 present as very shallow nearly transverse depression; LO longer sagittally than exsagittally, with sculpture of prominent median node; median node set about three quarters distance posteriorly on LO; posterior part of LO with strongly expressed posterior band similar to those of thoracic rings; SO transverse and

quite shallow medially, deep and slotlike behind L1; anterior border furrow very short (sag., exsag.) and incised; anterior border very short, lacking tuberculate sculpture; interocular fixigena narrow anteriorly but much wider posteriorly, with sculpture of densely crowded small and medium tubercles; eye ridge elevated, with single row of tubercles along its course, set off from interocular fixigena by strongly incised furrow and from frontal area by slightly less incised furrow, similar in breadth along course, bending adaxially to contact glabella opposite S3; front area small and subtriangular, with sculpture identical to that on librigenal field; palpebral lobe small and subtriangular (Fig. 9.3, right side; Fig. 10.1, right side), with very faint and small tubercles; posterior border with strong dorsal convexity, lacking dorsal sculpture, short (exsag.) and rolled proximally, much longer distally; posterior border furrow of similar length proximally and distally, shallow.

Librigena with broad field with sculpture of relatively densely scattered small and medium sized tubercles atop subdued, pinprick-like caecal pitting; field with gentle outwards inflation; eye small, about three times as long (exsag.) as tall, separated from field by faintly inflated, band-like socle with sculpture of small densely packed tubercles; lateral border furrow very broad and prominent, wider posteriorly than anteriorly, with sharper break in slope along contact with field than along contact with border; lateral border broad and dorsally flattened, narrower and more enrolled anteriorly, with dense sculpture of small and medium thorn-like tubercles/spines, border extended into lobate posterior angle beneath genal spine, with distinct row of larger spines along posteroventral edge; posterior border furrow weak opposite base of genal spine, confluent with lateral border furrow; genal spine long and robust, dorsally curved, with sculpture of small thornlike spines similar to that of posterior part of lateral border.

Rostral plate not seen; hypostome known from poorly preserved and slightly disarticulated example (Fig. 10.4, 10.7), subrectangular, considerably wider than long, otherwise not well enough known to describe.

Thorax of 10 segments; axial lobe slightly wider than pleural lobe excluding spines; axial and pleural lobes narrower posteriorly; axial portion, aside from width, with uniform morphology along thorax: ring longer (sag.) laterally than medially, divided transversely by very prominent posterior furrow which is deeper laterally than medially but is medially complete, anterior margin of ring describing very shallow "U" shape in plan view, posterior margin describing very shallow "W" shape, ring with dorsal sculpture of subdued tubercles, aligned in uneven transverse row (which may reflect only the exsagittally restricted dimensions of the ring rather than transverse alignment), ring separated from large preannulus by shallow furrow, preannulus



FIGURE 8—Laethoprusia graffhami n. sp., from the Cravatt Member, Bois d'Arc Formation (Lochkovian), Geological Enterprises quarry, near Clarita, Coal County, Oklahoma. 1–4, Dorsal exoskeleton, holotype, SUI 101482, dorsal, left dorsolateral, external view of right librigena, and dorsal pygidial views, ×4.



FIGURE 9—Laethoprusia graffhami n. sp., from the Cravatt Member, Bois d'Arc Formation (Lochkovian), Geological Enterprises quarry, near Clarita, Coal County, Oklahoma. 1-5, Dorsal exoskeleton, paratype, SUI 101483, dorsal thoracic ( $\times$ 3), oblique cephalic ( $\times$ 4), dorsal cephalic ( $\times$ 4), dorsal pygidial ( $\times$ 3), and right dorsolateral ( $\times$ 3) views.

separated from articulating half ring by sharply incised ring furrow; axial furrow shallow and weakly expressed, bowed laterally around inflated abaxial part of ring; pleural furrows very shallow, visible over entire pleural width on some segments of some specimens (e.g., Fig. 9.4, seventh segment, right hand side), discernible only proximally in others (e.g., Fig. 8.1, segments six and seven), and completely obscure in others (e.g., Fig. 10.1); pleural bands mostly conjoined and inflated into single pleural rib, with dorsal sculpture of scattered tubercles larger than those on axial ring, rib bounded anteriorly and posteriorly by very short (exsag.) strips of flat exoskeleton which abut in articulation, interrupted at midpoint of pleural lobe by relatively narrow (tr.) fenestrae; anterior pleural spines embedded in matrix in all available specimens, but clearly strongly ventrally directed; posterior pleural spines very long, curved, and dorsally produced to form splayed corona of large spines above and surrounding the thorax; spines on anterior segments narrower and shorter, on first two segments slightly anteriorly directed from base, about transverse on third segment, increasingly posteriorly directed on subsequent segments, and nearly directly posteriorly, subparallel with major pygidial spines, on tenth segment; spines with sculpture of scattered thornlike spines similar to that of major pygidial spines.

Pygidium with margin (excluding major spines) evenly posteriorly arcuate in median part, flared laterally and laterally concave abaxial to major spines; border clearly defined between major spines as broad roll, set off by shallow border furrow, best expressed medially; border poorly defined abaxial to major spines by faint subtriangular pleural depression; posteromedian spine with base confluent with border, relatively short with sagittal length about half that of pygidium excluding spine, tapered rapidly to a point, with sculpture of scattered, fine, thornlike spines; major spines long and dorsolaterally curved, with sculpture similar to that of median spine; anterior pleural margin transversely straight, with narrow articulating strip, interrupted by large fenestra; first axial ring with subdued dorsal tuberculate sculpture, bounded by weak axial furrows; pleural rib running from first axial ring very weakly expressed near ring, deflected posteriorly around large ovate fenestra, more inflated posteriorly in front of major spine, slightly wider (tr.) than spine base, with very sparse tuberculate sculpture; ring furrow between first and second rings fully incised and of similar depth medially and laterally; second ring about three quarters width of first, fully expressed and bound by axial furrow of similar expression to that opposite first ring, bound posteriorly by complete second ring furrow, with faint dorsal sculpture of two or three subdued tubercles; third axial ring not differentiated from subcrescentic terminal piece, rear of which grades into pleural area via a subtle change in slope, axial furrows not incised posteriorly; pleural area with slightly swollen crescentic area in front of border furrow and surrounding axis.

*Etymology.*—After Allen Graffham of Geological Enterprises, Ardmore, Oklahoma, who collected the holotype and one of the paratypes and made them available for study.

*Types and occurrence.*—Holotype, dorsal exoskeleton SUI 101482, and paratypes SUI 101483 and 101484, from the Cravatt Member, Bois d'Arc Formation (Lochkovian), Geological Enterprises quarry, near Clarita, Coal County, Oklahoma.

Discussion.—Laethoprusia graffhami is compared with the similar L. cozarti n. sp. in the differential diagnosis of that species below. Laethoprusia graffhami differs from L. salax in the possession of generally more subdued tuberculate sculpture on all surfaces; glabella that is broader posteriorly versus of similar width anteriorly and posteriorly; fixigena much wider posteriorly; eye set further forward; librigena with field narrower relative to exsagittal length and lateral border and genal spine with much less dense spines/tubercles; thorax with narrower fenestrae and



FIGURE 10—Laethoprusia graffhami n. sp., from the Cravatt Member, Bois d'Arc Formation (Lochkovian), Geological Enterprises quarry, near Clarita, Coal County, Oklahoma. 1–9, Dorsal exoskeleton, paratype, SUI 101484, dorsal thoracic, right dorsolateral, dorsal cephalic, oblique cephalic, right lateral, anterodorsal, anterior, posterodorsal, and posterior segments views, ×4.

longer (exsag.) and more robust pleural ribs; and pygidium with longer median spine and longer, more posteriorly directed, and much more curved major spines. *Laethoprusia graffhami* differs from *L. brikelos* in many of the ways in which it differs from *L. salax*, including a posteriorly wider median glabellar lobe, less

prominent and dense tuberculate sculpture, and much wider interocular fixigenae posteriorly. In addition, *L. graffhami* has a much longer genal spine, less prominent eye socle, smaller eye, more posterolaterally flared librigenal lateral border, shorter (sag.) LO, and a pygidium that is wider relative to its sagittal length,



FIGURE 11—Laethoprusia cozarti n. sp., from the Birdsong Shale Member, Ross Formation (Lochkovian), Holladay Quarry, Holladay, Benton County, Tennessee. 1–7, Dorsal exoskeleton, holotype, BMR P2005.1.1, dorsal thoracic, dorsal cephalic, anterior, anterodorsal oblique, detail of ventral pleural spines, right dorsolateral, and dorsal pygidial views, ×5.



FIGURE 12—1–25, Laethoprusia n. sp. A, from the Cape Phillips Formation (Wenlock; Sheinwoodian), southern Baillie-Hamilton Island and northwestern Cornwallis Island, Nunavut, Canada. 1–3, 6, Cranidium, ROM 57644, anterodorsal, dorsal, left lateral, and anterior views, ×10 (BHL 1 0 m). 4, 5, Thoracic segment, ROM 57645, right lateral and dorsal views, ×10 (ABR-TTD). 7, 12, Thoracic segment, ROM 57646, left lateral and dorsal views, ×12 (BHH-A). 8–10, Thoracic segment, ROM 57649, anterior, and left lateral views, ×15 (ABR-TTD). 11, Pygidium, ROM 57648, dorsal view, ×10 (ABR-TTD). 13–15, Thoracic segment, ROM 57649, anterior, dorsal, and right lateral views, ×12 (BHH-A). 16–18, Thoracic segment, ROM 57650, left lateral, anterior, and orsal views, ×12 (BHH-A). 16–18, Thoracic segment, ROM 57650, left lateral, anterior, and dorsal views, ×15 (BH - 10 m). 2–22, Pygidium, ROM 57651, dorsal, ventral, posterior, and left lateral views, ×10 (ABR-TTD). 23, 24, Left librigena, ROM 57652, external and ventrolateral views, ×15 (BH 1,110 m); 25, Right librigena, ROM 57653, external view, ×10 (BH 1,110 m). 26–29, Laethoprusia n. sp. A?, from the Delorme Group, Section Avalanche Lake Two, 247.0 m, near Avalanche Lake, southern Mackenzie Mountains, Northwest Territories, Canada, cranidium, UA 13525, dorsal, anterior, anterodorsal, and right lateral views, ×15 (AV 2 247.0 m).

with an obscure versus well expressed third axial ring, much larger fenestrae, and less well-expressed pleural ribs.

# LAETHOPRUSIA COZARTI new species Figure 11

*Diagnosis.*—Similar to *Laethoprusia graffhami*, but differing in the following features: cephalic tuberculate sculpture composed of slightly smaller tubercles; tubercles greater in number and much more densely packed on all dorsal surfaces; S3 impressed as a distinct transverse dimple (Fig. 11.2, right side, obscured by crack in exoskeleton on left side) versus a weak lineation (Figs. 8.1, 9.3, 10.4); L1 more ovate in plan view, lacking indentation of lateral margin at half length and slight anterolateral projection seen in *L. graffhami*; posterior band more weakly developed on thoracic segments, nearly obscure versus definitely complete medially; thoracic fenestrae considerably wider, approaching double the relative width of those of *L. graffhami* (cf. Fig. 11.1 with Figs. 8.1, 10.1); pygidium with larger fenestrae.

*Description.*—The species is so similar to the generally better known *Lae-thoprusia graffhami* that extended written description is redundant. All contrasts with the Oklahoma species are listed in the differential diagnosis above.

*Etymology.*—After Christopher Cozart, who collected the holotype and made it available for study.

*Type and occurrence.*—Holotype specimen BMR P2005.1.1, from the Birdsong Shale Member, Ross Formation (Lochkovian), Holladay Quarry, Holladay, Benton County, Tennessee.

*Discussion.*—Although the only available specimen is somewhat crushed, *L. cozarti* is clearly a distinct and diagnosable species, most similar to the approximately coeval *L. graffhami* n. sp. Both species are notable for their rarity in their respective faunas. Although both the Hunton Group and the Ross Formation have been intensively prospected and collected by both amateur and commercial collectors, the three specimens of *L. graffhami* and the unique specimen of *L. cozarti* are the only koneprusiine specimens known to have been discovered.

# LAETHOPRUSIA new species A Figure 12.1–12.25, ?12.26–12.29

?Odontopleurid sp.; CHATTERTON AND PERRY, 1983, p. 53, pl. 29, fig. 17. ?*Laethoprusia*? sp. of Chatterton and Perry; RAMSKÖLD, 1991b, p. 140.

*Material and occurrence.*—Assigned specimens from the Cape Phillips Formation (Sheinwoodian), ROM 57644, 57646, 57649, 57650, 57652, 57653 from southern Baillie-Hamilton Island and ROM 57645, 57647, 57648, 57651 from near the Abbott River, northwestern Cornwallis Island, Nunavut, Arctic Canada, and UA 13525, from the Delorme Group, Section Avalanche Lake Two, 247.0 m (Sheinwoodian), near Avalanche Lake, southern Mackenzie Mountains, Northwest Territories, Canada.

*Discussion.*—Although considerably more material is available than has typically been used to erect formally named new species of koneprusiines, the species is not sufficiently well known to name. Further, the material is from what have been recognized as separate, stratigraphically successive trilobite associations in Nunavut, the *Struszia dimitrovi* Fauna (mid-Sheinwoodian) and the *Struszia petebesti* Fauna (upper Sheinwoodian). The faunas are very similar at genus level, and often closely related but distinct species occur in each. The available cranidium and librigenae (Fig. 12.1–12.3, 12.6, 12.23–12.25) are from the *Struszia dimitrovi* Fauna but the only pygidia available (Fig. 12.11, 12.19–12.22) are from the *S. petebesti* Fauna. With no comparative material of cranidia or pygidia to study, it is hence impossible to be certain that the same species occurs in both faunas, though thoracic segments seem very similar in either fauna.

Rare cranidia of the same age from the southern Mackenzie Mountains are also difficult to compare and are assigned to *Laethoprusia* n. sp. A with question. The cranidium illustrated herein (Fig. 12.26–12.29) appears to be more densely tuberculate than the Cape Phillips Formation cranidium and also to have somewhat narrower interocular fixigenae. Difference in sculpture is partly preservational, as the Cape Phillips Formation specimen does not have most of its tubercles fully preserved. Differences in proportion and sculpture could also be attributable to ontogeny, as the Delorme Group specimen is much smaller.

It is not certain, then, that a single species is represented, and more material from all three localities would be needed to evaluate the taxonomy with confidence. Nevertheless, the material is important in extending the geographic range of the genus, and as the only Laurentian Silurian representatives known.

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