The late Cambrian (Furongian; Steptoean) trilobite genus *Xenocheilos* Wilson, 1949: systematics and biostratigraphic significance

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The affinities of the poorly known Laurentian trilobite genus *Xenocheilos* Wilson, 1949, have been the subject of much discussion in the literature. Here, we revise the genus through study of type material as well as new collections from Oklahoma and Utah. There are probably at least five distinct species but only two of these, *X. minutum* Wilson, the type species, and *X. spineum* Wilson, are named formally at present; '*X.*' *granulosum* Palmer and '*X*'. *orthos* Kurtz are assigned incorrectly to the genus. All species are limited to a narrow stratigraphic interval within the late Steptoean *Elvinia* Zone. *Xenocheilos* shares traits, including a very long frontal area, long, backwardly deflected posterolateral projections of the fixigenae, and bacculae opposite L1 glabellar lobes, with the Gondwanan family Nepeidae Whitehouse. Parsimony analysis provides support for a relationship between these taxa.

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THE GENUS *Xenocheilos* Wilson, 1949, is an exceedingly rare member of upper Steptoean trilobite faunas of Laurentian North America, and its affinities are poorly understood. Wilson (1949) left the genus unassigned and made only general comparisons with the pterocephaliid *Pterocephalia* Roemer, 1849; subsequent work in Pennsylvania (Wilson 1951) offered no further insight on relationships. In a similar vein, Bell *et al*. (1952) and Deland & Shaw (1956) simply ignored the question of affinities, whereas Stitt (1971) followed Lochman (in Moore 1959) in assigning the genus to the polyphyletic family Avonidae Lochman, 1936. Palmer (1965) made a case for a relationship with the family Menomoniidae Walcott, 1916, and his view was endorsed by Kurtz (1975). Westrop (1986) later suggested that *Xenocheilos* might be an opisthoparian member of the family Norwoodidae Walcott, 1916, and this was followed without comment by Hohensee & Stitt (1989) and Jell (in Jell & Adrain 2003). However, Westrop (1986, p. 32) also compared the genus to cranidia from the Pomegranate Limestone that were identified by Shergold (1980, pl. 14, figs 6B, 8) as "ptychopariacean genus et species undetermined E", and went so far as to suggest that the latter may be a species of *Xenocheilos*.

In this paper, we revise *Xenocheilos* with restudy of type material and new specimens from the Honey Creek Limestone of Oklahoma and the Orr Formation of Utah, and explore the relationship between the genus and the Gondwanan family Nepeidae Whitehouse, 1939. New and published data on the stratigraphic occurrence of the genus suggest that it occurs through a narrow interval within the *Elvinia* Zone.

BIOSTRATIGRAPHY OF *XENOCHEILOS*

Xenocheilos is confined to the *Elvinia* Zone, a Furongian (Steptoean) biostratigraphic unit that is recognised widely across Laurentian North America. Many workers have noted that this zone could be subdivided to provide more resolution (e.g., Wilson 1951; Stitt 1971; Westrop 1986) and is in need of revision. For the purposes of this discussion, we will follow recent practice of dividing the *Elvinia* Zone into two informal 'subzones' or divisions (e.g., Westrop *et al*. 2007).

Texas, Oklahoma, Arkansas

The original description of *Xenocheilos minutum* Wilson, 1949, was based upon two cranidia from the Morgan Creek Member of the Wilberns Formation at different localities (Baldy Mountain and Threadgill Creek; Wilson 1949). The associated fauna includes species of *Dokimocephalus* Walcott, 1924, *Elvinia* Walcott, 1924; *Irvingella* Ulrich & Resser, in Walcott, 1924, *Kindbladia* Frederickson, 1949, and *Plataspella* Wilson, 1949. This fauna correlates with the lower division of the *Elvinia* Zone in the Honey Creek Formation of Oklahoma (Westrop *et al*. 2007). In the latter area, sclerites that are assigned questionably to *X. minutum* occur in the Royer Ranch section described by Stitt (1971; collections RR 126, RR127; see systematic palaeontology section for discussion).

A similar species, *X.* cf. *X. minutum*, occurs through a stratigraphic interval of about five metres in the Honey Creek Formation in the sections measured on the slopes of Ring Top Mountain on the Kimball Ranch, Comanche County, Oklahoma (see Westrop *et al*. 2007), where it straddles the boundary between the lower and upper divisions of the *Elvinia* Zone. At section KRI (Westrop *et al*. 2007, fig. 2), this species occurs in a sparsely fossiliferous interval between 12.7 and 14 m above the base of the section in association with *Dokimocephalus lingulus* Resser, 1942. This interval is 3.45 m above the occurrence (9.25 m) of a lower *Elvinia* Zone fauna that includes *Plataspella alpersensis* (Resser, 1942) and *Camaraspis parabola* Frederickson, 1948. *Xenocheilos* cf. *X. minutum* is also present in a new section, KR3, that was measured 450 m southeast of the KR2 section of Westrop *et al*. (2007, fig. 2). Here, it occurs at a single horizon, 20.5 m above the base of the section, with *P. alpersensis*, *C. parabola*, *Burnetiella exilis* (Resser, 1942), and *Dokimocephalus* cf. *D. extensus* (Resser, 1942), together with *Kindbladia*. This fauna lies within the lower division of the *Elvinia* Zone, and correlates with an interval approximately nine to eleven metres above the base of section KR1. Finally, *X.* cf. *X. minutum* is also part of a diverse, lower *Elvinia* Zone fauna in a collection made 5.75 m above the base of the Dotson Ranch section, Murray County, Oklahoma (Westrop & Adrain 2007, fig. 1c).

Xenocheilos minutum has also been reported from the Collier Shale of Arkansas by Hohensee & Stitt (1989, fig. 5.21-5.24), although the single cranidium they illustrated probably does not belong to this species (see below). The association with *Kindbladia* indicates an occurrence within the lower division of the *Elvinia* Zone.

Missouri

An indeterminate species allied with *Xenocheilos spineum* Wilson, 1951, occurs as small, somewhat flattened specimens preserved in shale in the lower half of unit C of the type section of the Davis Formation (section 9 of Kurtz 1975; collection 977.67-5), St. Francois County, Missouri. The associated fauna includes species of *Cliffia* Wilson, 1951, *Pseudosaratogia* Wilson, 1951, *Housia* Walcott, 1916, and *Irvingella*. It appears to be somewhat younger than the lower interval of the *Elvinia* Zone in Texas and Oklahoma as it occurs about six metres above the highest local occurrence of *Kindbladia*.

Pennsylvania

The holotype of *Xenocheilos spineum* Wilson, 1951, is from the Ore Hill Member of the Gatesburg Formation at Drab-Beaverton, Pennsylvania. Wilson (1951) indicated this species occurred through a seven metre interval of the Drab section between about 15 and 22 m above the base of the Member, where it is associated with species of *Plataspella* and *Kindbladia* among others. The Loch & Taylor (2004, fig. 2) range chart for the same section records *X. spineum* from a single collection (DB 22) that also includes species of *Kindbladia*, *Buttsia*, *Bynumina*, *Cliffia*, '*Deadwoodia*', *Deckera*, *Dellea*, *Elvinia* and *Kindbladia*; *Plataspella* (identified as *Iddingsia anatina*) enters the succession about two metres higher (collection DB 29). These assemblages correlate into the lower division of the *Elvinia* Zone in Oklahoma and Texas.

Utah

Previous records of *Xenocheilos* in the Great Basin were restricted to a single occurrence of *X. granulosum* Palmer, 1965 from the Corset Spring Shale (*Elvinia* Zone) at Shingle Pass, Nevada, but this species is assigned incorrectly to the genus (see following discussion of *Xenocheilos* in the Systematic Palaeontology section). However, silicified sclerites of the genus have been isolated from collections in the Corset Spring Shale-Sneakover Member transition of the Orr Formation at Orr Ridge, Millard County, Utah (Hintze & Palmer 1976; Westrop & Adrain 2007). These talus collections (ORR 29T/B; ORR 30T/A) were made 29-30 m above the top of the Johns Wash Member and are a metre above the highest occurrence of *Kindbladia* (also a talus collection, ORR 28T; *Kindbladia* occurs in situ 2.5 m lower in the section, at ORR 26.5). As such, this occurrence of *Xenocheilos* is probably coeval with the upper part of the range of *X.* cf. *X. minutum* at Ring Top Mountain, Oklahoma.

Rocky Mountains (Alberta and Wyoming)

In the basal few metres of the Bison Creek Formation, Banff and Jasper national parks, Alberta, *Xenocheilos* is part of an assemblage that includes *Kindbladia* and *Plataspella*, and which correlates with the lower division of the *Elvinia* Zone of Oklahoma and Texas (Westrop 1986). The material was identified originally (Westrop 1986) as *Xenocheilos* cf. *X. spineum* Wilson, 1951, but, as discussed below, it almost certainly represents a new species.

Deland & Shaw (1956) assigned a single cranidium from the basal 45 centimetres of the Open Door Limestone, Sweetwater Canyon, Wyoming, to *Xenocheilos spineum*. It is impossible to identify this specimen with any confidence, and its position within the *Elvinia* Zone is equally uncertain.

Minnesota

A single incomplete cranidium that Bell *et al*. (1952, pl. 30, fig. 2) identified as *Xenocheilos* cf. *X. minutum* Wilson was collected from exposures of the Wonowoc Formation along U.S. Highway 61 near Reads Landing, Wabasha County, Minnesota (see Grant 1962, fig. 1 for a locality map). The associated fauna of *Camaraspis*, *Cliffia*, *Elvinia* and *Irvingella* probably correlates into the upper division of the *Elvinia* Zone.

Correlation

The data from the various regions suggest that *Xenocheilos* is confined to a narrow stratigraphic interval in the mid-*Elvinia* Zone. Most occurrences are within the lower division of the zone, but the upper part of the range of *X*. cf. *X. minutum* extends into the lower part of the upper division in Oklahoma. *Xenocheilos* sp. 1 from Utah is known only from the lower part of the upper division, as is the indeterminate species from Missouri.

PHYLOGENETIC ANALYSIS

In an attempt to explore the affinities of *Xenocheilos*, we performed parsimony analysis with PAUP* 4.0b10 (Swofford 2000) and TNT v.1.1 (Goloboff *et al*. 2008; sponsored by the Willi Hennig Society); character optimisation was performed in PAUP* and Winclada v. 1.00.08 (Nixon 2002). The ingroup for the analysis included representatives of taxa with which the genus has been allied in the past (see above). Four species of *Xenocheilos* were coded from images published herein, with the exception of *X*. cf. *spineum* Wilson, 1951, from Alberta, which is based on photographs from Westrop (1986, pl. 29, figs 11-14). The type species, *Xenocheilos minutum* Wilson, 1949, was not included because neither of the types (Fig. 2A-F) preserve the palpebral lobes and it does not differ in coding of observable traits from *X*. cf. *X. minutum* from Oklahoma, which also provides data on the librigena. We also selected two species from the family Menomoniidae, *Menomonia semele* (Walcott, 1916) [coding source: Pratt 1992, pl. 29, figs1-6, 8, 11-12], and *Dresbachia amata* Walcott, 1916 [coding source: Rasetti 1965, pl. 8, figs 1-4], and two species from the Family Norwoodiidae, '*Hardyoides*' *mimicus* Palmer, 1965 and *Holcacephalus praecursor* Rasetti, 1965. "Ptychopariacean genus et species undetermined E" was coded from illustrations in Shergold (1980).

Three species of nepeid trilobites were included in the matrix, *Nepea narinosa* Whitehouse, 1939, *Penarosa retifera* Öpik, 1970 and *Ferenepea hispida* Öpik, 1967, all of which were coded from images published recently by Paterson (2005). *Biaverta biverta* Öpik, 1967 and *B. reineri* Öpik, 1967 are also part of the ingroup. Öpik (1967) assigned *Biaverta* to the family Menomoniidae, but glabellar structure is identical to *Ferenepea* (compare Öpik 1967, pl. 37, fig. 6 and pl. 38, figs 1-4 with pl. 39, figs 7, 8) and clearly differs from such menomoniids as *Menomonia* (e.g., Rasetti 1965, pl. 2, figs 19, 25, pl. 5, fig. 14; Pratt 1992, pl. 29, figs 1-4). *Biaverta* lacks a median boss on the preglabellar field, but does display long, backwardly deflected posterolateral projections of the fixigenae and appears to possess bacculae (described by Öpik 1967, as "alae" but their apparent depression seems to be a result of their location between convex L1 lobes and more inflated regions of the fixigenae). Öpik (1967, p. 367) described *Biaverta* as "without eyes", but also noted (p. 369) the presence of a "rudiment" of the palpebral lobe just in front of the glabella on one specimen (Öpik 1967, pl. 38, figs 1a, b). For this reason, we coded the palpebral lobes as "minute", rather than "absent", and we also note that *Ferenepea* also shows sharp reduction of the palpebral lobe (e.g., see Öpik 1967, p. 363).

Palmer (2005) compared *Eldoradia* Resser, 1935 to *Nepea*, and it is possible that this genus will prove to be a member of the ingroup. *Eldoradia* is in need of revision and is too poorly known to include in the phylogenetic analysis. The best available illustrations (Palmer 1954, pl. 16, figs 8-10) indicate that the genus has a long frontal area with a median preglabellar boss. However, there is no evidence of bacculae, and the posterolateral projection of the fixigena apparently lacks the strong posterior deflection characteristic of nepeids.

We selected *Bolaspidella housensis* (Walcott, 1886) as the outgroup, and coded it from images from Robison (1964) and Lee & Chatterton

Characters	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
Xenocheilos cf. *X. minutum*	1	0	1	1	0	0	1	1	1	1	0	1	0	0	0	1	0	1	0	0
X. sp. 1	1	0	1	1	0	0	1	1	1	1	0	1	0	0	0	1	3	1	0	0
X. spineum	1	1	1	2	0	0	1	1	1	1	0	1	0	0	0	1	3	?	0	?
X. cf. *X. spineum*	1	1	1	1	0	0	1	1	1	1	0	1	0	0	0	1	3	1	0	?
Nepea narinosa	1	0	0	0	1	1	1	2	1	2	1	1	0	1	0	0	1	0	0	0
Penarosa retifera	1	1	1	2	1	1	1	2	1	2	1	1	0	1	0	0	1	0	0	0
Ferenepea hispida	1	0	0	0	1	0	1	1	1	2	1	0	1	1	0	1	2	0	0	0
Biaverta biaverta	2	0	1	3	0	1	1	2	1	2	2	?	1	?	1	1	2	0	0	0
B. reineri	2	?	?	4	0	1	?	?	1	2	?	?	?	?	1	1	2	?	0	?
”gen. indet. E”	1	1	1	1	0	1	0	?	1	0	1	1	0	0	0	1	0	0	0	?
Holcacephalus praecursor	1	0	0	1	0	0	0	?	0	0	1	0	0	0	0	0	0	0	1	0
“*Hardyoides*” *mimicus*	0	0	0	1	0	0	1	1	0	0	1	0	1	0	0	0	0	0	1	0
Menomonia semele	0	0	1	3	0	2	0	?	0	0	1	0	0	?	2	1	0	0	0	1
Dresbachia amata	2	?	?	4	0	2	0	?	0	0	2	0	1	?	2	1	0	0	0	1
Bolaspidella housensis	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0

Table 1. Data matrix for parsimony analysis (Fig. 1). “gen. indet. E” = “Ptychopariacean genus et species undetermined E” of Shergold (1980).

(2005). Various authors (e.g. Robison 1964; Pratt 1992; Westrop & Ludvigsen 2000) have assigned *Bolaspidella* to the Menomoniidae. However, the family has yet to be defined phylogenetically, and the absence of several potential synapomorphies of *Menomonia* and *Dresbachia*, including the loss of genal spines, course of the posterior facial sutures, morphology of the librigena, and the anterior palpebral lobe position, indicate that *Bolaspidella* is, at best, a basal member of this clade. Although divergent opinions have been expressed on the relationship between the Nepeidae and Menomoniidae (see Paterson 2005 for summary), *Bolaspidella* is not unreasonable as a choice for the outgroup.

The majority of the species lack information on sclerites other than cranidia and this is a significant constraint on the analysis. The matrix (Table 1) included 14 ingroup taxa, 13 binary characters and seven multistate characters (Appendix); reductive coding (Strong & Lipscomb 1999) was used for inapplicable states. Searches with PAUP* (branch and bound) and TNT (implicit enumeration) yielded a single tree of length 50 (CI = 0.60; RI =0.71; RC = 0.43) that is shown in Figure 1A. Although the cladogram is fully resolved, support for individual branches is relatively low and no node has Bremer support >2. The optimised character distributions are shown in Figure 1B.

The results support monophyly of *Xenocheilos*, which emerges as the sister group of the Nepeidae *sensu* Paterson (2005), although *Biaverta* is nested within the latter. “Ptychopariacean genus et species undetermined E” of Shergold (1980) joins at the node immediately below. At the current state of knowledge, with pygidia and librigenae unknown for many species, these results are clearly of a preliminary nature. They do suggest that restriction of the Nepeidae to species with a median boss on the preglabellar field may leave a paraphyletic group that includes *Xenocheilos* and “Ptychopariacean genus et species undetermined E”. A more inclusive approach would expand the family to incorporate these taxa that possess some, but not all, of the apomorphies of the Nepeidae *sensu* Paterson (2005). These apomorphies include a long frontal area and long, posteriorly curved posterolateral projections of the fixigenae.

SYSTEMATIC PALAEONTOLOGY

Figured material is housed at the National Museum of Natural History (USNM), Peabody Museum of Natural History, Yale University (YPM), Oklahoma Museum of Natural History, University of Oklahoma (OU), and the Paleontology Repository, Department of Geoscience, University of Iowa (SUI). Collection numbers indicate metres above the base of sections at the following localities: DR, Dotson Ranch, Oklahoma; KR1 and KR3, Kimbell Ranch, Oklahoma; ORR, Orr Ridge, House Range, Utah. Collection numbers with the designation “T” were made from talus.

In order to maximise depth of field, images in Figures 2-5 were rendered from stacks of images focused at 200 micron intervals using Helicon Focus 4.0 for the Macintosh <http://www.heliconsoft.com>.

Proportions expressed in percentages in descriptions and diagnoses are means, with numbers in parentheses indicating the range of values. All measurements were made on digital images to the nearest tenth of a millimetre using the Measure Tool of Adobe Photoshop ™.

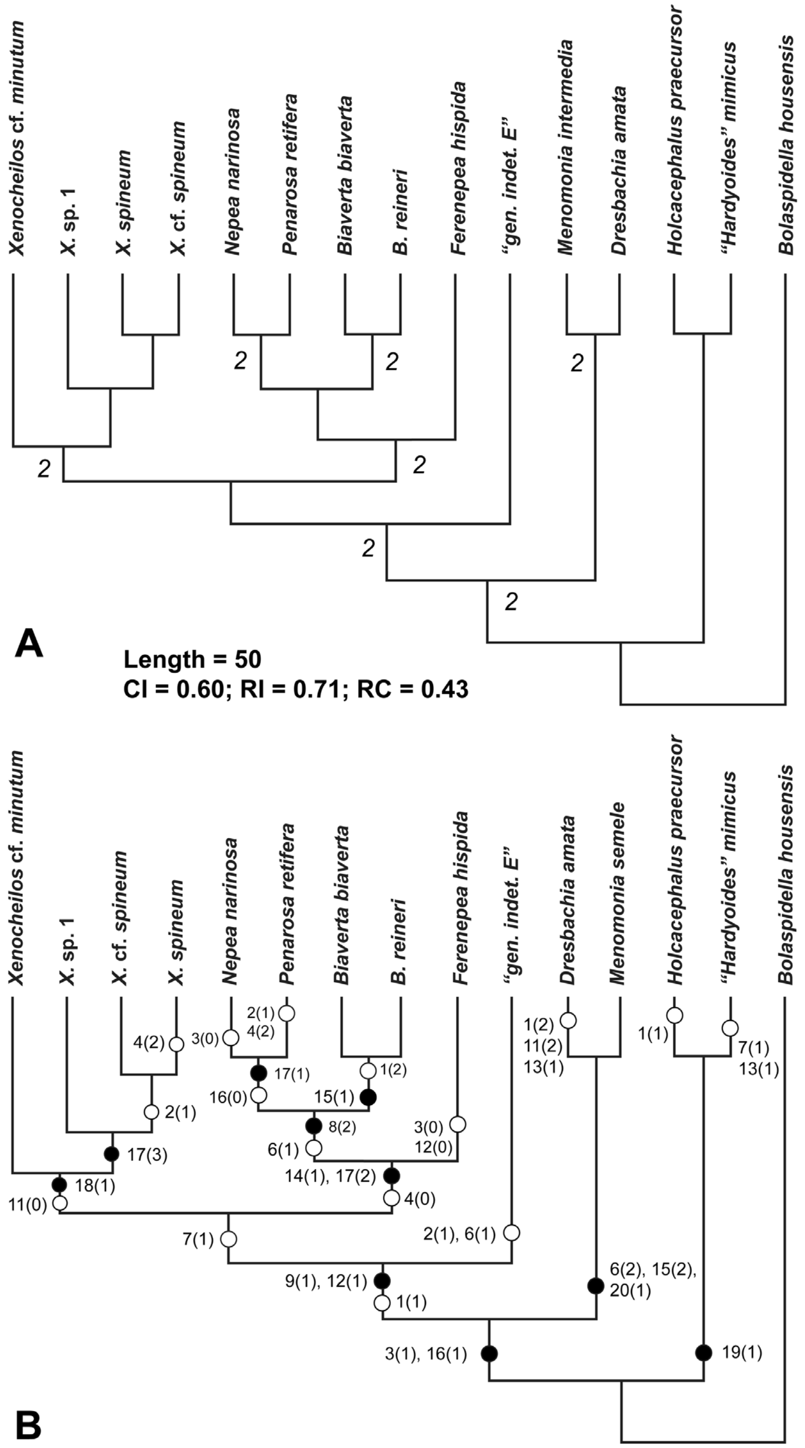


Fig. 1. Cladogram generated by parsimony analysis of matrix (Table 1). **A**, Single tree discovered by branch-and-bound search (implicit enumeration). Bremer support of nodes > 1 is indicated by numbers in italics. **B**, Optimised character distribution showing only those states that are unambiguous (i.e., occur at the same node under both ACCTRAN and DELTRAN optimisation). Closed circles indicate character states confined to a single node; open circles indicate those that occur at more than one node. "gen. indet. E" = "Ptychopariacean genus et species undetermined E" of Shergold (1980).

Family NEPEIDAE Whitehouse, 1939

Discussion. Although *Xenocheilos* lacks the most conspicuous apomorphy of the Nepeidae, the median boss on the preglabellar field, it does share several other characters with this family. The posterolateral projection of the fixigena is swept back well beyond the posterior tip of the glabella. *Xenocheilos* is bacculate, albeit weakly so in larger individuals. Finally, the very long frontal area of nepeids is matched in *Xenocheilos*.

"Ptychopariacean genus et species undetermined E" of Shergold (1980) also shares some of these characters with *Xenocheilos*, but it lacks bacculae and has anteriorly positioned palpebral lobes comparable to such nepeids as *Nepea* and *Penarosa*. Although this study is not intended as a comprehensive evaluation of scope and content of the Nepeidae, we suggest that "Ptychopariacean genus et species undetermined E", which may represent a new genus, be treated as a basal member of the family. As such, the Nepeidae can be diagnosed by the frontal area proportions and the configuration of the posterolateral projection.

Inclusion of *Xenocheilos* and "Ptychopariacean genus et species undetermined E" in the Nepeidae results in a significant range extension for the family. Both are Furongian in age, whereas other nepeids are from strata correlative with the older Guzhangian and Drumian stages (Paterson 2005, text-fig. 2; Peng & Babcock 2008, fig. 4.5). In more detail, "Ptychopariacean genus et species undetermined E" occurs in the *Stigmatoa diloma* Zone at the top of the Australian Idamean Stage (Shergold 1980). *Xenocheilos* is slightly younger, occurring in Late Steptoean strata that correlate into the overlying Iverian Stage of Australia (Peng & Babcock 2008, fig. 4.5).

Xenocheilos Wilson, 1949

Type species. *Xenocheilos minutum* Wilson, 1949 from the Morgan Creek Member, Wilberns Formation, central Texas (by original designation).

Diagnosis. Nepeidae that lack an inflated median boss on preglabellar field. Downsloping anterior border that may flatten anteriorly. Bacculae ill-defined except in smaller cranidia, and may be little more than weakly inflated area that interrupts axial furrow at L1 and constricts posterior border furrow. Narrow (exsag.), well incised slit-like posterior border furrow that extends along entire width of posterolateral projection. External surfaces with anastomosing terrace ridges.

Assigned species. *Xenocheilos minutum* Wilson, 1949; *X. spineum* Wilson, 1951. Material placed in open nomenclature, *X.* cf. *X. minutum* Wilson from Oklahoma, *X.* cf. *X. spineum* Wilson from Alberta (Westrop 1986), and *Xenocheilos* sp. 1 from Utah, likely represent new species but will not be formally named herein.

Discussion. The most striking difference between *Xenocheilos* and Gondwanan nepeid trilobites is the absence of a preglabellar boss on the frontal area in the former. However, the absence of a boss is, by both outgroup comparison and ontogenetic criteria (e.g., Öpik 1970, p. 43), retention of a plesiomorphic condition. Apomorphic states of *Xenocheilos* include morphology of the anterior border, expression of the bacculae, and the narrow, slit-like posterior border furrow. Some species show effacement of the lateral glabellar furrows (e.g., Fig. 5B) but others have at least shallow S1 and S2 furrows (e.g., Fig. 2E) that resemble those of the outgroup species, *Bolaspidella housensis*. The anterior border is differentiated largely from the preglabellar field by a change in slope (e.g., Figs 2D, 3B, O, 4B, F).

Our new images of the holotype cranidium (Fig. 5I-L) of *Xenocheilos granulosum* Palmer, 1965, from the Corset Spring Shale, Shingle Pass, Nevada, show that it is incorrectly assigned to the genus. Palmer's (1965, pl. 7, fig. 7) photograph is heavily shadowed and gives a misleading impression of the width of the glabella and the depth of the axial furrows. The frontal area occupies slightly more than 25 percent of cranidial length and slopes steeply forward to a convex anterior border that accounts for nearly 40 percent of frontal area length; the border furrow is firmly impressed. The fixigenae slope upward from the border furrow and the small palpebral lobe, which is centred opposite the L2 glabellar lobe is elevated; the palpebral furrow is obsolete. Anterior branches of the facial suture are gently convergent between the palpebral lobe and anterior border furrow. The convex glabella tapers conspicuously forward, so that width at S3 is less than two-thirds of the width at LO; three pairs of short lateral furrows are present, with S1 and S2 well incised and S3 faint. The occipital spine is long and well tapered, equal to about half of preoccipital glabellar length; it curves upward and backward, flattening near the tip. The rear edge of the posterolateral projection curves gently forward and more steeply downward at the fulcrum. The posterior area of the fixigena and the anterior border carry scattered coarse granules that were mentioned by Palmer (1965, p. 91) but are not evident in his photograph. Although clearly unrelated to *Xenocheilos*, the affinities of this

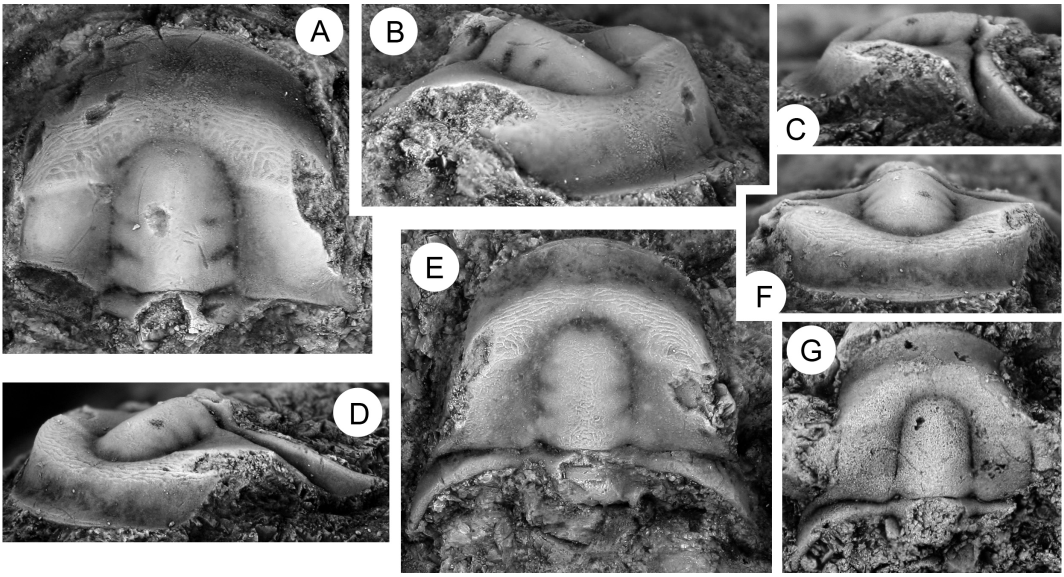


Fig. 2. *Xenocheilus minutum* Wilson, 1949. Morgan Creek Formation, Texas, except G (Royer Ranch section, Arbuckle Mountains, Oklahoma, collection RR 126). All x12. All testate except G. **A, B**, cranidium, dorsal and anterior-oblique views, USNM 185742 (paratype); **C-F,** cranidium, lateral, anterior-oblique, dorsal and anterior views, USNM 185741 (holotype); **G**, cranidium (assigned questionably), dorsal view, OU 12407.

unique specimen are obscure. We have resampled Palmer's (1965) Shingle Pass section, but no additional material of "*X*". *granulosum* has been discovered. For the foreseeable future, the status of this species is likely to remain unresolved.

Similarly, *Xenocheilos orthos* Kurtz, 1975, (Fig. 6E, F) is excluded from the genus. It differs from *X. minutum* and all other members of the genus in having shorter (tr.) posterolateral projections of the fixigena that are not swept backwards. This configuration also rules out a relationship with the Nepeidae. We are uncertain about the affinities of '*X.*' *orthos*, although the well defined border furrow, upturned border, conspicuous bacculae (Fig. 5E) and unfurrowed glabella invite comparisons with liostracinids such as *Liostracina volens* Öpik, 1967 (pl. 35, figs 1-3) and *L. nolens* Öpik, 1967 (pl. 35, figs 6). A detailed evaluation of relationships is difficult because the only known specimens of '*X*'. *orthos* (Fig. 5E, F) are small, somewhat flattened internal moulds preserved in calcareous shale. '*Xenocheilos*' *orthos* lacks the median preglabellar furrow of *Liostracina*, and the palpebral ridges are ill defined; the occipital ring is prominent on the most completely preserved specimen (Fig. 5E), accounting about one-third of glabellar length. The librigena (Fig. 6G) attributed to '*X*'. *orthos* by Kurtz (1975) is substantially larger than either cranidium (Fig. 5E, F) and is clearly misassigned.

Xenocheilos minutum Wilson, 1949 (Fig. 2A-F, ?2G)

1949 *Xenocheilos minutum*; Wilson, p. 44, pl. 9, figs 11-13.
?1971 *Xenocheilos minutum*; Stitt, p. 15, pl. 1, fig. 15.
non 1989 *Xenocheilos minutum*; Hohensee & Stitt, p. 871, fig. 5.21-5.24 [= *Xenocheilos* sp. indet.].

Diagnosis. *Xenocheilos* with long anterior border equal to 31 percent (29-35; highest value in largest cranidium) of preoccipital glabellar length; border is nearly flat anteriorly. Long posterior projection curved evenly backward; extends backward for distance equal to 33 percent of glabellar length.

Holotype. A cranidium (USNM 185741) from the Morgan Creek Member, Wilberns Formation, Threadgill Creek, Mason County, central Texas (Wilson's [1949] collection 42-12w, 7.92 m above the base of the Wilberns Formation) (Fig. 2C-F).

Occurrence. Morgan Creek Member, Wilberns Formation, Baldy Mountain, Burnet County, and Threadgill Creek, Mason County, central Texas (Wilson 1949); ?Honey Creek Formation, Murray County, southern Oklahoma (Stitt 1971).

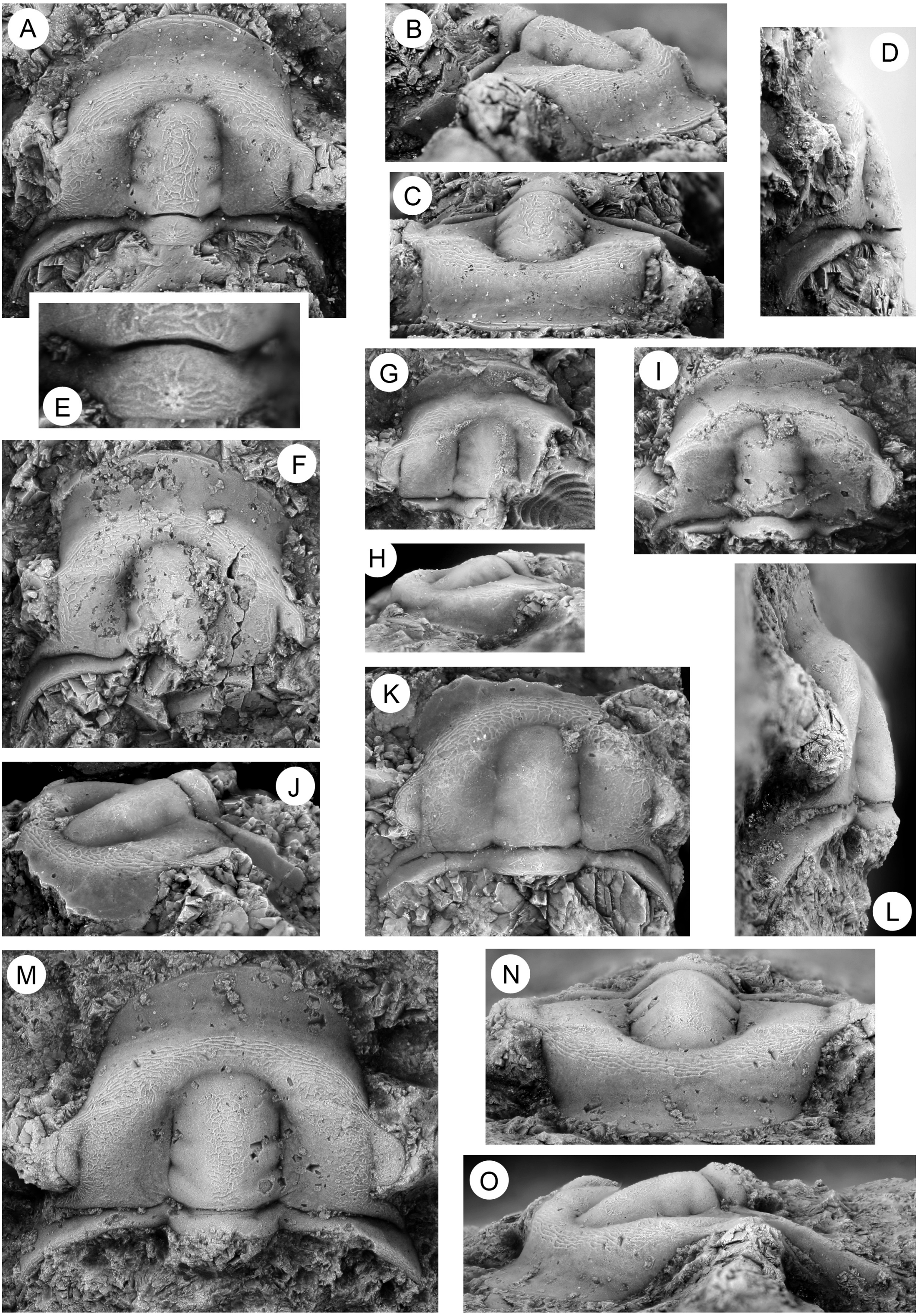
Description. Cranidium strongly arched in anterior and lateral views, and sub-semielliptical in outline with well rounded anterior margin. Axial and preglabellar furrows very shallow. Glabella convex, nearly parallel-sided between LO and S3, but becomes rounded anteriorly; upper surface slopes gently forward towards preglabellar furrow; glabella width at LO equal to 76 percent (72-79) of glabellar length; occupies 65 percent (63-67) of cranidial length. LO accounts for 21 percent (19-23) of glabellar length; SO finely etched and nearly transverse medially, but curves forward and deepens abaxially. S1 and S2 furrows shallow but clearly defined, extend obliquely inward for short distance from axial furrow; holotype (Fig. 2C-F) has barely perceptible S3. Internal mould assigned questionably to species lacks glabellar furrows. Postocular area of fixgena with small, weakly inflated baccula opposite L1 that interrupts axial furrow and constricts posterior border furrow. Frontal area equal to 68 percent (62-74) of preoccipital glabellar length. Preglabellar field gently inflated posteriorly and rises above preglabellar furrow before sloping steeply forward. Border differentiated largely by change in slope and is initially forward sloping, becoming flatter anteriorly; occupies 46 percent (44-47) of frontal area length and equal to 31 percent (29-35; highest value in largest cranidium) of preoccipital glabellar length. Palpebral area of fixigena gently inflated, rising above axial furrows, and broad, with width a little less than glabellar width at SO. Palpebral lobes are broken on both the holotype (Fig. 2E) and paratype (Fig. 2A) but appear to be centered near S1.

A cranidium assigned questionably to this species (Fig. 2G) possesses palpebral lobe whose length equals about 40 percent of preoccipital glabellar length. Palpebral furrow well defined posteriorly but terminates abruptly at intersection with palpebral ridge. Palpebral ridge curves very gently inward and forward across fixigena, reaching axial furrow immediately in front of S3. Anterior branches of facial suture incompletely preserved but apparently converge slightly forward between palpebral lobe and anterior border, before converging more rapidly along anterior cranidial margin; posterior branches diverge backward along strongly curved path. Long posterior projection curved evenly backward; extends backward for distance equal to 33 percent of glabellar length. Posterior border curves evenly backward, extending along backwardly deflected posterolateral projection, and expands in length (exsag.) abaxially. Posterior border furrow is a narrow (exsag.) slit that widens somewhat abaxially and extends to sutural margin of posterolateral projection. Inflated posterior portions of preglabellar and preocular fields with sculpture of terrace ridges; terraces ridges also present on crest of glabella; internal moulds smooth.

Discussion. *Xenocheilos minutum* differs most obviously from *X. spineum* Wilson, 1951 in the proportions of the frontal area and in the lateral profile of the anterior border. The border of *X. minutum* occupies about 45 percent of the frontal area. It slopes forward initially but flattens towards the anterior margin (Fig. 2B-D). The border of *X. spineum* (Fig. 5A-D) is relatively shorter, accounting for about 30 percent of frontal area length, and slopes evenly forward; a short (sag.) plectrum is present. The fixigenae are relatively narrower in *X. minutum* with the distance between axial and palpebral furrows equal to only about two-thirds of glabellar width, but equal to about 90 percent in *X. spineum*. Also, the posterolateral projection is relatively longer in *X. spineum*, extending backward for a distance equal to about 75 percent of glabellar length, versus about 33 percent of glabellar length in *X. minutum*. Finally, the lateral glabellar furrows are barely perceptible on *X. spineum* (e.g., Fig. 5C), but are well defined on *X. minutum*, particularly on larger cranidia.

Xenocheilos minutum is known with certainty only from the type area in Texas. Cranidia attributed to this species by Stitt (1971, pl. 1, fig. 15; Fig. 2G) have similar frontal area proportions to the holotype and may record the presence of this species in the Honey Creek Formation of Oklahoma. Hohensee & Stitt (1989, fig. 5.21, 5.24) illustrated a single cranidium from the Collier Shale of Arkansas that they identified as *X. minutum*. Unfortunately, this sclerite is almost certainly misidentified. It has a very short anterior border and the orientation of the posterior cranidial margin differs from the evenly curved margin of *X. minutum* (e.g., Fig. 2E). The margin of their specimen is transverse along the postocular area, but swings abruptly backward along the posterolateral projection. Of the other

Fig. 3. *Xenocheilos* cf. *X. minutum* Wilson, 1949. Honey Creek Formation, Oklahoma. All from collection KR3 20.5 except where indicated. All x12 except E (x 30); all cranidia; all testate. **A-E**, dorsal, anterior-oblique, anterior, lateral and enlargement of occipital ring, OU 12398; **F**, dorsal view, OU 12399; **G, H**, dorsal and anterior-oblique views, collection KR1 12.7-14, OU 12400; **I**, dorsal view, OU 12401; **J, K**, anterior-oblique and dorsal views, OU 12402; **L-O**, lateral, dorsal, anterior and anterior-oblique views, collection DR 5.75, OU 12403.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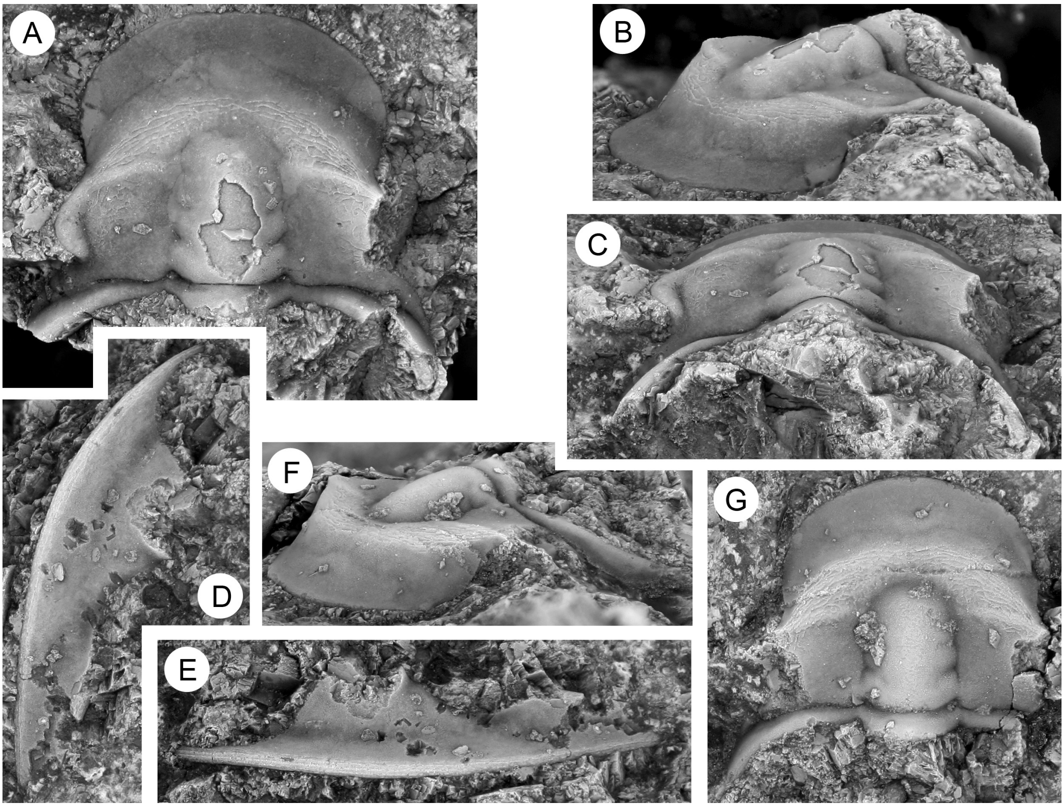


Fig. 4. *Xenocheilos* cf. *X. minutum* Wilson, 1949. Honey Creek Formation, Oklahoma. All from collection DR 5.75. All x12. **A-C**, cranidium, dorsal, anterior-oblique and posterior views, OU 12404; **D, E**, librigena, dorsal and lateral views, OU 12405; **F, G**, cranidium, anterior-oblique and dorsal views, OU 12406.

sclerites illustrated from Arkansas, the librigena (Hohensee & Stitt 1989, fig. 5.23) is probably assigned correctly as it resembles librigenae associated with *X.* cf. *X. minutum* in Oklahoma (Fig. 4D, E) and with *Xenocheilos* sp. 1 in Utah (Fig. 7Q-V); we cannot corroborate the pygidial association (Hohensee & Stitt 1989, fig. 5.22).

Xenocheilos cf. X. minutum Wilson, 1949 (Figs 3, 4)

cf. 1949 *Xenocheilos minutum*; Wilson, p. 44, pl. 9, figs 11-13.
non 1952 *Xenocheilos* cf. *X. minutum*; Bell, Feniak & Kurtz, p. 185, pl. 30, fig. 2.
cf. 1971 *Xenocheilos minutum*; Stitt, p. 15, pl. 1, fig. 15.

Occurrence. Honey Creek Formation, collections KR1 12.7-14; KR 3 20.5; DR 5.75.

Discussion. *Xenocheilos* cf. *X. minutum* is sufficiently similar to the type species that a full description is unnecessary. Cranidia from Oklahoma differ from the types of *X. minutum* is possessing a relatively longer anterior border. Our material encompasses a larger size range than the types, and there is evidence to indicate that the anterior border becomes proportionally longer during the ontogeny of *Xenocheilos* (see following discussion of *X.* sp. 1). Nonetheless, when similarly sized specimens are compared, differences in the relative length of the border are striking (compare Figs 2E and 4G). In other respects, including expression of the glabellar furrows and bacculae, relative width and degree of inflation of the palpebral area of the fixigena, length and orientation of the posterolateral projection of the fixigena, and sculpture of terrace ridges, cranidia from Texas and Oklahoma do not differ appreciably. The material from Oklahoma may well represent a new species but, in view of the limited number of specimens of *X. minutum* available from Texas for comparison, it will be left in open nomenclature.

Our specimens provide information on aspects of the cranidial anatomy that are not preserved on the types of *X. minutum*. In particular, the palpebral lobes (Figs 3A, I, K, M, 4A) are relatively large, equal to 42 percent (38-43) of glabellar length,

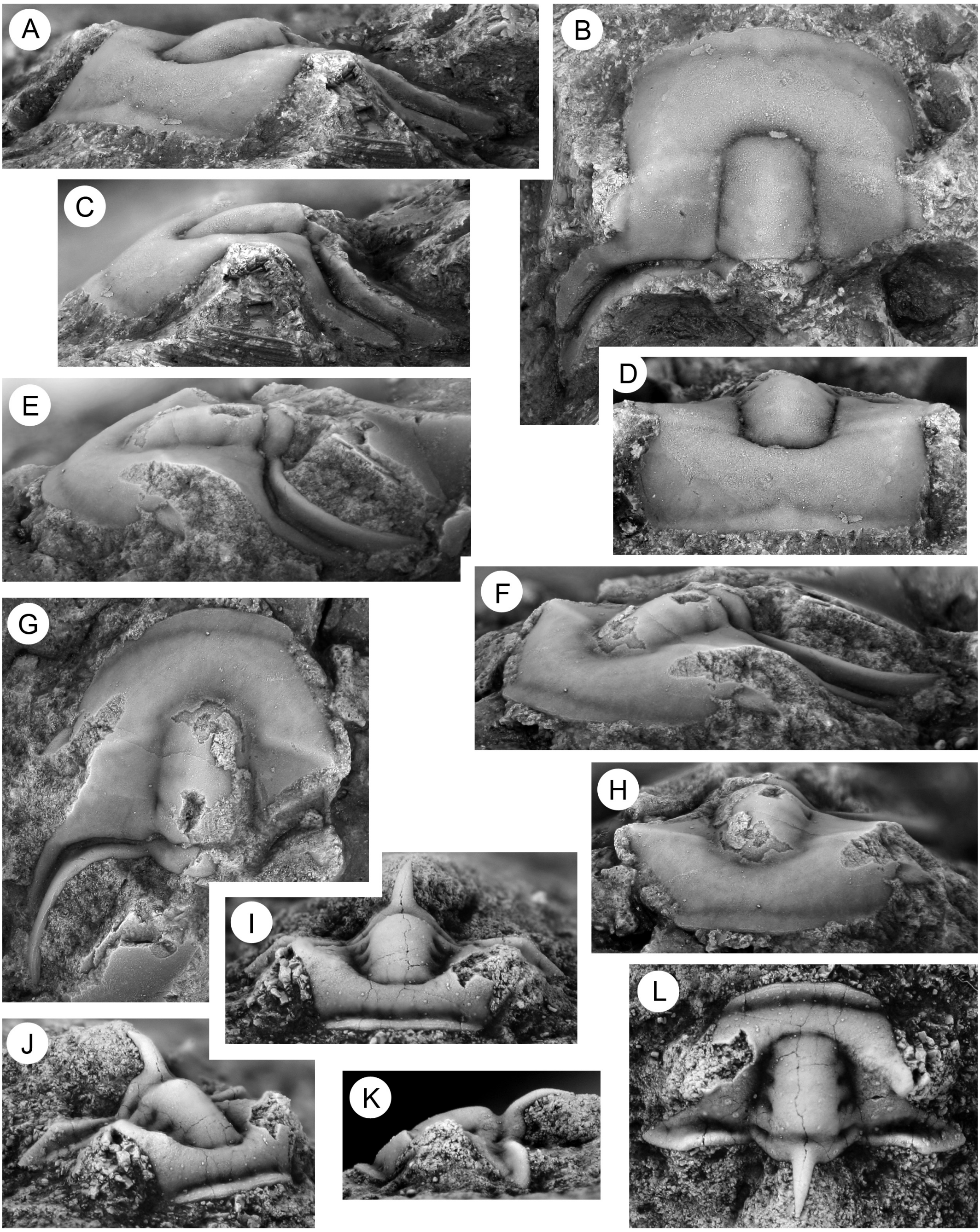


Fig. 5. **A-D**, *Xenocheilos spineum* Wilson, 1951, Ore Hill Member, Gatesburg Formation, Pennsylvania, x12, cranidium (exfoliated), anterior-oblique, dorsal, lateral and anterior views, YPM 18509 (holotype). **E-H**, *Xenocheilos* sp. indet., Ore Hill Member, Gatesburg Formation, Pennsylvania, x12, cranidium (testate), lateral, anterior-oblique, dorsal and anterior views, YPM 18512 (paratype of *X. spineum*). **I-L**, "*Xenocheilos*" *granulosum* Palmer, 1965, Corset Spring Shale, Shingle Pass, Lincoln County, Nevada, x16, cranidium (testate), anterior, anterior-oblique, lateral and dorsal views, USNM 141601 (holotype).

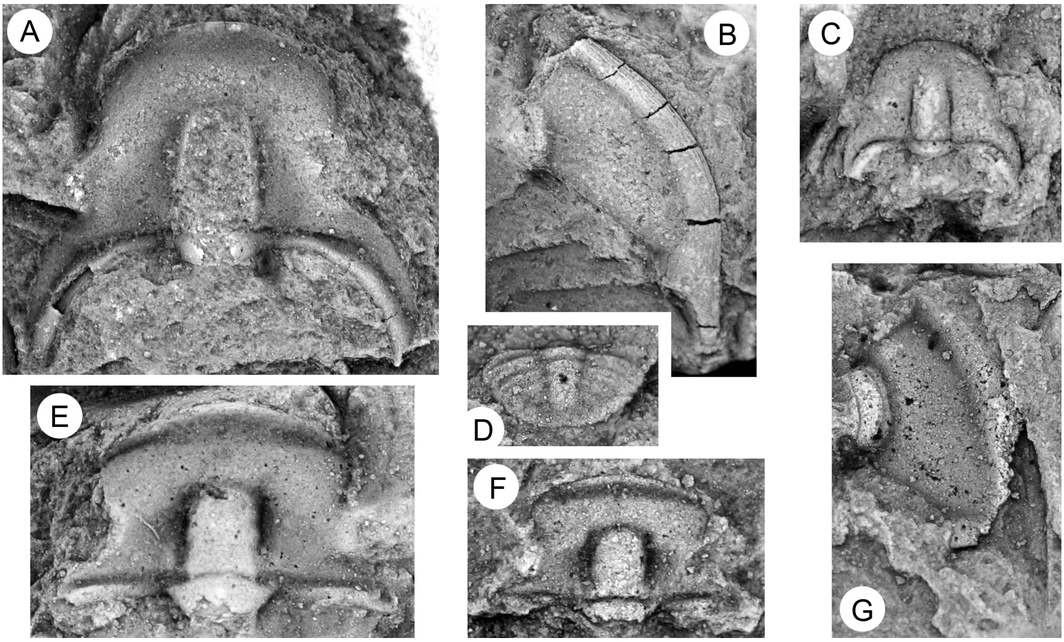


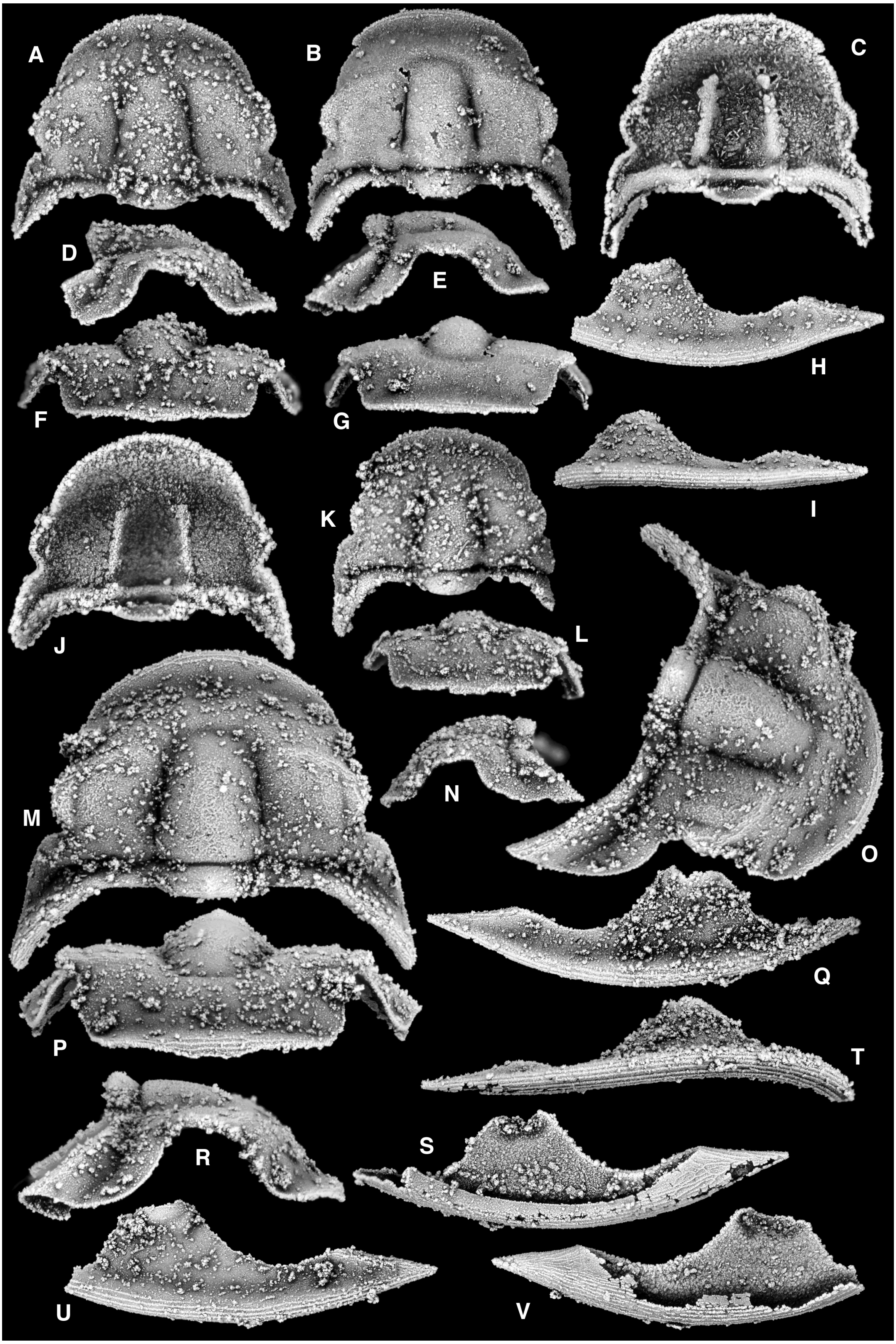
Fig. 6. **A, C**, *Xenocheilos* sp. indet., Unit C, Davis Formation, Missouri. **A**, cranidium, dorsal view, OU 3493a (previously figured by Kurtz 1975), x12; **C**, cranidium, dorsal view, OU 3493b (previously unfigured), x16. **B**, *Cliffia* sp. indet., Unit C, Davis Formation, Missouri, librigena, dorsal view, OU 3493c (previously figured by Kurtz, 1975, as *X. spineum*), x12. **D**, Gen. et sp. indet., Unit C, Davis Formation, Missouri, transitory pygidium, dorsal view, OU 3493d (previously figured by Kurtz 1975, as *X. spineum*), x21. **E, F**, "*Xenocheilos*"*orthos* Kurtz, 1975, Unit C, Davis Formation, Missouri, x16. **E**, cranidium, dorsal view, OU 3491 (holotype). **F**, cranidium, dorsal view, OU 3492 (paratype). **G**., Gen. et sp. indet., Unit C, Davis Formation, Missouri, librigena, dorsal view, OU 8104 (previously figured by Kurtz 1975, as "*X.*" *orthos*), x10.

and centered just in front of S1. Palpebral lobes of *X. spineum* (Fig. 5B) are relatively short, equal to about 30 percent of glabellar length. The palpebral furrow of *X.* cf. *X. minutum* is variable in depth. It is well incised over the posterior half of its length but shallows abruptly anteriorly. This contrasts with the shallower but evenly impressed palpebral furrows of *X. spineum*. Several well preserved specimens show that *X.* cf. *X. minutum* possessed an occipital organ (“cephalic median organ” of Lerosey-Aubril & McNamara 2008) on the highest point of the occipital ring (Fig. 3A, E, K); terrace ridges radiate out from the margins of the organ. We have not been able to establish the presence of an organ in any other species of *Xenocheilos*. The sculpture of terrace ridges is well expressed on several cranidia (e.g., Figs 3A, 4A) and is present along the margin of the anterior border, the posterior, inflated portions of the preglabellar and preoccular fields, palpebral ridge, palpebral lobe, abaxial portions of the palpebral area, and the edge of the posterior border along the posterolateral projection.

An incomplete librigena (Fig. 4D, E) shows a broad, relatively flat lateral border that is separated from a steeply upsloping librigenal field by a very shallow border furrow. It likely had a short genal spine similar to that of *X.* sp. 1 (Fig. 7Q, S, U).

Xenocheilos cf. *X. minutum* of Bell *et al*. (1952, pl. 30, fig. 2) from the Wonowoc Formation of Minnesota is incomplete and cannot be evaluated

Fig. 7 (opposite). *Xenocheilos* sp. 1, Corset Spring Shale Member, Orr Formation, Orr Ridge, northern House Range, Millard County, western Utah, from section ORR, collections ORR 29T-B and ORR30T-A. All sclerites are silicified. **A, D, F, J**, cranidium, dorsal, left lateral, anterior, and ventral views, ORR 30T-A, SUI 110492, x25. **B, C, E, G**, cranidium, dorsal, ventral, right lateral, and anterior views, ORR 30T-A, SUI 110493, x25. **H, I**, left librigena, external and ventrolateral views, ORR 30T-A, SUI 110494, x15. **K, L, N**, cranidium, dorsal, anterior, and left lateral views, ORR 30T-A, SUI 110495, x25. **M, O, P, R**, cranidium, dorsal, oblique, anterior, and right lateral views, ORR 29T-B, SUI 110496, x20. **Q, S, T**, right librigena, external, internal, and ventrolateral views, ORR 30T-A, SUI 110497, x15. **U, V,** left librigena, external and internal views, ORR 30T-A, SUI 110498, x15.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fully. It resembles cranidia from Oklahoma in having clearly defined lateral glabellar furrows, but has a much shorter anterior border, so there is little doubt that it represents a different species.

Xenocheilos spineum Wilson, 1951 (Fig. 5A-D)

1951 *Xenocheilos spineum*; Wilson, p. 649, pl. 95, figs 15-16 [only; fig. 17 = *Xenocheilos* sp. indet.]
non 1956 *Xenocheilos spineum*; Deland & Shaw, p. 560, pl. 65, figs 4, 6, 13 [= *Xenocheilos* sp. indet.].
non 1975 *Xenocheilos spineum*; Kurtz, p. 1033, pl. 4, figs 27-29 [fig. 27 = *Xenocheilos* sp. indet.; fig. 28 = gen indet.; fig. 29 = *Cliffia* sp.].

Diagnosis. *Xenocheilos* with short anterior border equal to 25 percent of preoccipital glabellar length; border slopes evenly forward; short plectrum present. Palpebral lobe small, equal to about 30 percent of glabellar length. Very long posterior projection curved strongly backward; extends backward for distance equal to about 75 percent of glabellar length.

Holotype. A cranidium (YPM 18509) from the Ore Hill Member, Gatesburg Formation, Drab, Pennsylvania, 14.9 metres above the base of the member (Fig. 5A-D).

Occurrence. As for holotype.

Description. Cranidium (excluding posterolateral projection) subrectangular in outline with gently rounded anterior margin, length about 80 percent of width across palpebral lobes; strongly arched in anterior and lateral views. Glabella rectangular, width nearly 80 percent of length, and outlined by shallow but clearly defined axial and preglabellar furrows; gently convex, with longitudinal profile that slopes forward in front of midlength; occupies 60 percent of cranidial length and 30 percent of cranidial width across palpebral lobes. LO incompletely preserved but appears to have occupied no more than 20 percent of glabellar length. SO a finely etched groove, nearly transverse medially but curved forward abaxially. S1 very shallow, short and oblique; remainder of glabella unfurrowed. Low baccula present next to L1 (Fig. 5C); axial furrow shallows between baccula and L1. Frontal area long, equal to about 80 percent of preoccipital glabellar length, gently inflated in front of preglabellar furrow, then slopes steeply forward. Anterior border defined by change in slope and very shallow border furrow; short, equal to about 25 percent of preoccipital glabellar length; maximum length at short plectrum but narrows abaxially. Palpebral area of fixigena broad, width (excluding palpebral lobe) slightly less than glabellar width at SO, and nearly flat. Palpebral lobe small, length equal to about one-third of glabellar length, semielliptical in outline, and centered just in front of S1. Palpebral ridge weak, oblique, and extends forward from palpebral lobe to reach axial furrow near anterior corner of glabella. Anterior branches of facial sutures subparallel before swinging inward along anterior margin of glabella; posterior branches diverge sharply near palpebral lobe, but curve backward to become nearly parallel at posterior corner of cranidium.

Posterolateral projection broad (exsag.) and swept back well beyond level of posterior tip of glabella; posterior extent equal to about 75 percent of glabellar length. Posterior border is firmly impressed, narrow and slit-like; posterior border short near axial furrow but expands abaxially. Holotype is exfoliated; internal mould is smooth.

Discussion. In establishing *Xenocheilus spineum*, Wilson (1951) illustrated only two cranidia. These specimens are similar in size but are from different localities and do not appear to be conspecific. The paratype (Fig. 5E-H) is from Potter Creek, which is about 20 km south of the Drab section that yielded the holotype (Fig. 5A-D). It differs from the holotype in a number of respects. For example, the posterolateral projection of the holotype is broader (exsag.) and is less strongly curved backward than in the paratype. The paratype lacks the plectrum present on the anterior border of the holotype and the anterior cranidial margin, although incomplete, appears to be more rounded. Other differences in the paratype include a somewhat narrower (tr.) palpebral area of the fixigena, a more convex glabella with S1 and S2 lateral furrows, and a less inflated baccula. Under the present state of knowledge, *X. spineum* is best restricted to the holotype.

The single cranidium of Deland & Shaw (1956, pl. 65, figs 4, 6, 13) from the Open Door Limestone of Wyoming has narrower interocular fixigenae and a more rounded anterior margin than *X. spineum*. We regard it as an indeterminate species of *Xenocheilos*. Material from the Davis Formation of Missouri that was identified by Kurtz (1975, pl. 4, figs 27-29) as *X. spineum* is also of uncertain identity. Although it shares the very long posterior projection of *X. spineum*, the larger cranidium (Fig. 6A) is relatively narrower (tr.) with an ill defined anterior border. The glabella of this specimen is incomplete, but the smaller specimen illustrated by Kurtz (Fig. 6C)

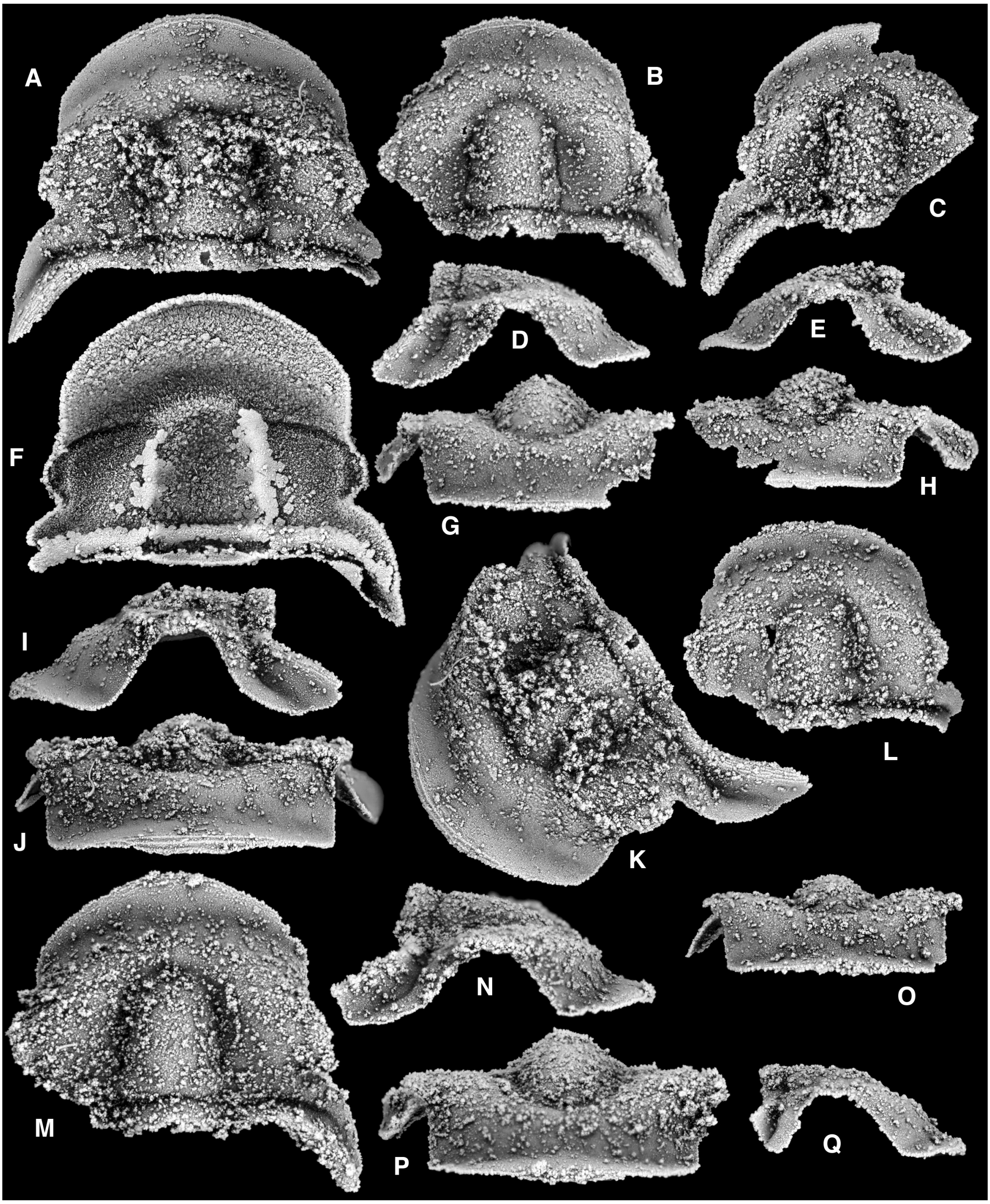

Fig. 8. *Xenocheilos* sp. 1, Corset Spring Shale Member, Orr Formation, Orr Ridge, northern House Range, Millard County, western Utah, from section ORR, collections ORR 29T-B and ORR30T-A. All sclerites are silicified. All are x15. **A, F, I-K**, cranidium, dorsal, ventral, left lateral, anterior, and oblique views, ORR 30T-A, SUI 110499. **B, D, G**, cranidium, dorsal, right lateral, and anterior views, ORR 29T-B, SUI 110500. **C, E, H**, cranidium, dorsal, left lateral, and anterior views, ORR 30T-A, SUI 110501. **L, O, Q**, cranidium, dorsal, anterior, and right lateral views, ORR 30T-A, SUI 110502. **M, N, P**, cranidium, dorsal, right lateral, and anterior views, ORR 29T-B, SUI 110503.

lacks glabellar furrows. The associated librigena (Fig. 6B) is misassigned. Compared to silicified librigenae of *Xenocheilos* sp. 1, it has a more convex lateral border and broader librigenal field. The genal spine is incomplete but, unlike the simple, short, triangular spine of *Xenocheilos* sp. 1, it tapers abruptly and appears to be relatively long. Overall, this sclerite is identical to librigenae of *Cliffia* Wilson, 1949, that occur in silicified collections at Orr Ridge (Adrain & Westrop, unpublished) and it is hence reassigned to this genus. The tail assigned by Kurtz (Fig. 6D) is a transitory pygidium, the identification of which, is questionable.

Cranidia from the Bison Creek Formation of Alberta, identified as *Xenocheilos* cf. *X. spineum* by Westrop (1986, pl. 29, figs 11-14), resemble the holotype of *X. spineum* in having relatively narrow, subrectangular glabellae that are weakly furrowed. However, none of these possess a plectrum and the anterior borders are relatively flatter than in *X. spineum* and maintain an even length along the anterior cranidial margins. Also, the palpebral lobes are larger and, like *Xenocheilos* cf. *X. minutum* (Fig. 3A, F, G, I, K, M), the palpebral furrows are well incised posteriorly but terminate abruptly at the palpebral ridge. In contrast, the palpebral furrow of *X. spineum* is shallow and evenly impressed. Finally, the posterolateral projection, although curved backward at a similar angle and distance, is relatively narrower (exsag.) in *X.* cf. *X. spineum*. *Xenocheilos* cf. *X. spineum* likely represents a new species and was coded separately in the phylogenetic analysis (Fig. 1).

Xenocheilos sp. 1 (Figs 7, 8)

Occurrence. Transition interval between Corset Spring and Sneakover members of the Orr Formation, Orr Ridge, Millard County, Utah, in talus collections 29-30 metres above the base of the Corset Spring Member.

Discussion. *Xenocheilos* sp. 1 is most similar to *X. minutum* from Texas (Fig. 2A-F) and *X.* cf. *X. minutum* from Oklahoma (Figs 3, 4), although comparisons are limited by the small sizes of most of the available cranidia of the former. They share the configuration of the frontal area, in which the anterior border is differentiated from the preglabellar field largely by a change in slope. The length of the anterior border increases during the ontogeny of *Xenocheilos* sp. 1 (compare Figs 7B, K, and 8A). If similarly sized cranidia are considered, the anterior border of *Xenocheilos* sp. 1 is comparable to that of *X. minutum* but is relatively shorter than in *X.* cf. *X. minutum*.

The external surfaces of variously sized cranidia of both *X. minutum* and *X.* cf. *X. minutum* display clearly defined glabellar furrows, particularly S1, but these are not expressed in *Xenocheilos* sp. 1. The posterolateral projection of *Xenocheilos* sp. 1 is deflected sharply backward at the fulcrum and the cranidial margin at the postocular area is nearly transverse (e.g., Fig. 8A, B, M). In contrast, the posterior margin of the fixigenae is evenly curved in both *X. minutum* (e.g., Fig. 2E) and *X.* cf. *X. minutum* (e.g., Figs 3A, F, M, 4A, C, G).

Several well preserved librigenae are available from collection ORR 30T-A (Fig. 7 H, I, Q-V). The genal spine is short, evenly tapered and triangular in shape. The lateral border is defined largely by a change in slope at the base of the librigenal field and is relatively narrow (tr.). It extends to the tip of the genal spine, where it joins the short (exsag.), gently convex posterior border. The librigenal field is tall, raised well above the border, relatively short (exsag.) and subtrapezoidal in outline; some specimens preserve the visual surface of a small eye. Both borders carry sculpture of terrace ridges which extends onto the doublure. A librigena of *X.* cf. *X. minutum* from collection DR 5.75 in Oklahoma (Fig. 4D, E) has a proportionately wider (tr.), flatter lateral border than that of *Xenocheilos* sp. 1 but is otherwise similar.

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APPENDIX: CHARACTER STATES

1. Frontal length. 0, short (>33%, <50% of preoccipital glabellar length); 1, long (>60% of preoccipital glabellar length); 2, very short (< 33% of preoccipital glabellar length).
2. Anterior border length. 0, long (>40% of frontal area length); 1, short (no more than 30% of frontal area length).
3. Anterior border furrow. 0, well defined (e.g., Paterson 2005, pl. 7, figs 8, 9); 1, weakly defined, so that border is differentiated largely by change in slope (e.g., Fig. 3B, O; Paterson 2005, fig. 10A, B, D).
4. Anterior border. 0, gently convex (e.g., Lee & Chatterton 2005, fig. 11p, r, t; Paterson, 2005, fig. 9b, c); 1, downsloping at least posteriorly, may flatten anteriorly (e.g., Figs 3A, O, 5C); 2, concave, upturned anteriorly (e.g., Paterson 2005, pl. 3, figs 2, 3); 3, convex, strongly upturned rim (e.g., Öpik 1967, pl. 38, figs 2a, 3, 4; Pratt 1992, pl. 29, figs 1-5); 4, frontal area undivided (e.g., Öpik 1967, pl. 39, fig. 1a).
5. Median boss on preglabellar field. 0, absent; 1, present.
6. Palpebral area of fixigena. 0, gently inflated or gently upsloping (e.g., Fig. 3C, 4D); 1, moderately to strongly inflated or upsloping (e.g., Paterson 2005, pl. 1, fig. 6, 7); 2, steeply upsloping, forms part of eye stalk (e.g., Pratt 1992, pl. 29, figs 1-2).
7. Bacculae. 0, absent; 1, present.
8. Bacculae size and shape. 1, small, ill-defined and weakly inflated (e.g., Figs 2E, 5C, 6E); large, conspicuous (e.g., Paterson, 2005, pl. 1, figs 8, 11, text-fig. 9A, fig. 10D).
9. Posterolateral projection. 0, transverse to weakly deflected backwards (e.g., Fig. 6E; Lee & Chatterton, 2005, fig. 11p, r, u); 1, strongly deflected backwards (e.g., Fig. 2E, 5B; Paterson, 2005, pl. 1, figs 8, 11, pl. 3, figs 1-3; Öpik, 1967, pl. 38, figs 3, 4, pl. 39, fig. 1a).
10. Posterior border furrow. 0, relatively wide, well defined (e.g., Pratt, 1992, pl. 29, fig. 1; Rasetti 1965, pl. 3, fig. 10); 1, narrow, firmly impressed, slit-like; extends along entire width of posterolateral projection (Figs 3A, F, 4A, 5B); 2, deep abaxially but shallows abruptly at fulcrum (e.g., Paterson 2005, pl. 3, fig. 3, pl. 6, figs 1-2, pl. 7, fig. 9).
11. Palpebral lobe position (for *Biaverta*, location of inflexion of suture). 0, centered opposite posterior part of L2 (e.g., Figs 3A, K, M, 5B); 1, centered opposite or in front of L3 (e.g., Paterson 2005, pl. 3, fig. 1, pl. 7, figs 1, 7); 2, entirely in front of glabella (e.g., Rasetti 1965, pl. 8, figs 1-2).
12. Palpebral lobe orientation. 0, strongly upsloping and elevated well above level of fixigena (e.g., Lee & Chatterton 2005, fig. 11 t, v); 1, nearly flat and not elevated appreciably above level of fixigena (e.g., Figs 3N, 5D; Paterson 2005, pl. 3, fig. 4).
13. Palpebral lobe size. 0, large, equal to 30% or more of glabellar length; 1, minute (no more than 15 percent of glabellar length) or absent (e.g., Paterson 2005, pl. 7, figs 1, 7, 11; Öpik 1967, pl. 38, figs 3, 4).
14. Palpebral ridge. 0, simple; 1, bifurcate (see Paterson 2005).
15. Glabellar outline. 0, parallel-sided to gently tapered; 1, tapered from SO to S2, then parallel-sided (e.g., Paterson 2005, pl. 7, figs 1, 7, 11; Öpik 1967, pl. 37, fig. 6); 2, conical (e.g., Pratt 1992, pl. 29, fig. 1; Rasetti 1965, pl. 8, figs 1-2).
16. Occipital spine. 0, present; 1, absent.
17. Lateral glabellar furrows. 0, shallow S1 and S2 (with or without faint S3) (e.g., Fig. 3A, M; Lee & Chatterton 2007, fig. 11i, p, r); 1, deep S1-S3 (e.g., Paterson 2005, pl. 3, fig. 6); 2, deep S1, S2, faint S3 (e.g., Paterson 2005, pl. 7, figs 1, 7, 11; Öpik 1967, pl. 37, fig. 6); 3, lateral furrows largely effaced (Figs 5A-D, 6E, F, 7M, O, P, R).
18. Sculpture of external surface. 0, granulose or tuberculate (e.g., Robison 1964, pl. 89, fig. 1; Paterson 2005, pl. 3, fig. 6, pl. 7, figs 1, 7); 1, anastomosing terrace ridges (Figs 2E, 3A).
19. Sutures. 0, opisthoparian; 1, proparian.
20. Genal spine. 0, present (e.g., Lee & Chatterton 2005, fig. 11s; Paterson 2005, pl. 3, fig. 7: Fig. 7H, Q, U); 1, absent (e.g., Pratt 1992, pl. 29, figs 4, 6).