Trilobites from the Al Rose Formation (Lower Ordovician, Inyo Mountains, California)—faunas marginal to the Great Basin

Richard A. Fortey,[1] Ernesto E. Vargas-Parra,[2,3]* and Mary L. Droser[3]

[1]Department of Earth Sciences, The Natural History Museum, London SW7 5BD, UK <raf@nhm.ac.uk>
[2]Division of Paleontology, American Museum of Natural History, New York, New York 10024, USA <evargas-parra@amnh.org>
[3]Department of Earth and Planetary Sciences, University of California, Riverside, California 92521, USA <mary.droser@ucr.edu>

Non-technical Summary.—During the Early Ordovician, much of the Laurentian paleocontinent was flooded by shallow, warm seas in which a great variety of endemic trilobites evolved, particularly those belonging to the family Bathyuridae. These have been collected and well studied from many localities across the Great Basin and adjacent areas. Deeper-water trilobites belonging to biofacies in peripheral sites around the carbonate-rich platform have a much poorer fossil record, largely because later tectonics have erased the appropriate sites. We describe here a rare example of a relatively low-diversity trilobite fauna of this kind recovered from the Al Rose Formation in the Inyo Mountains, California. Trilobites of the families Metagnostidae, Olenidae, and Raphiophoridae are well represented in this fauna, although they are rare or unknown from contemporary platform carbonates.

Abstract.—The Lower Ordovician (Floian) Al Rose Formation from the Inyo Mountains, California, is a deeper-water, graptolitic equivalent of the well-known and richly fossiliferous successions described from Utah and Nevada. It is considered to have been originally marginal to the Laurentian paleocontinent. It has yielded a low-diversity trilobite fauna that differs strikingly from contemporary faunas to the east in its abundance of raphiophorid, nileid, olenid, and agnostoid trilobites, resembling that of the Nileid Biofacies known from scattered locations marginal to Laurentia. Two new trilobite species are described: *Globampyx sexsegmentatus* (Raphiophoridae) and *Protopresbynileus divergens* (Nileidae). *Carolinites genacinaca* Ross, 1951 is a link with the Great Basin. Other trilobites include the olenid *Cloacaspis* cf. *C. ceryx anataphra* Fortey, 1974, metagnostid *Geragnostus* cf. *G. (Novoagnostus) longicollis* Raymond, 1925, and pliomerid *Hintzeia* sp.

UUID: https://zoobank.org/19a679ce-968d-4ce1-a590-f7f55bf9d62d

Introduction

The Lower Ordovician Al Rose Formation is exposed in the White Inyo Mountains of California in Mazourka Canyon (Fig. 1). However, extensive studies on the development of the carbonate platform in the Great Basin have rather neglected the Al Rose Formation, possibly because there are not extensive well-exposed outcrops and the preservation of fossils is not equal to that of the shelf limestones farther east, in Utah, where the standard reference sections for the Ibexian Series are located (Ross et al., 1997). Some of the trilobites from the Al Rose were briefly noted in a regional correlation chart by Ross (1967, plate 11), but none has ever been described. However, the Al Rose Formation provides an autochthonous occurrence of deeper-shelf faunas over this major area of the Ordovician Laurentian continent that is missing elsewhere. This paper assesses the significance of the fauna and proves its age, and then describes some of the taxa that have been collected in the past 15 years.

Geological setting

Field characteristics.—At Badger Flat, the Al Rose Formation is approximately 100 meters thick but consists of poor outcrop (Fig. 1). The unit varies in thickness throughout the region and has been thinned structurally through the area (Stevens, 1986). The Al Rose is composed of splintery, siliceous shales with interbedded thin limestones, 2–7 cm thick. Limestones and shales, where cropping out, are laminated. Fossils were collected largely from float.

Ross (1967, plate 11, left-hand column) showed the lowest prolific fauna on his stratigraphic column—including "ampyxinid, aff. *Parabolinella* sp., *Phyllograptus anna, Didymograptus protobifidus,* and *D. artus*"—at the base of the Badger Flat Limestone rather than at the top of the Al Rose Formation. We believe that this is probably not a correct interpretation since the black limestones of the basal Badger Flat Limestone are

*Corresponding author
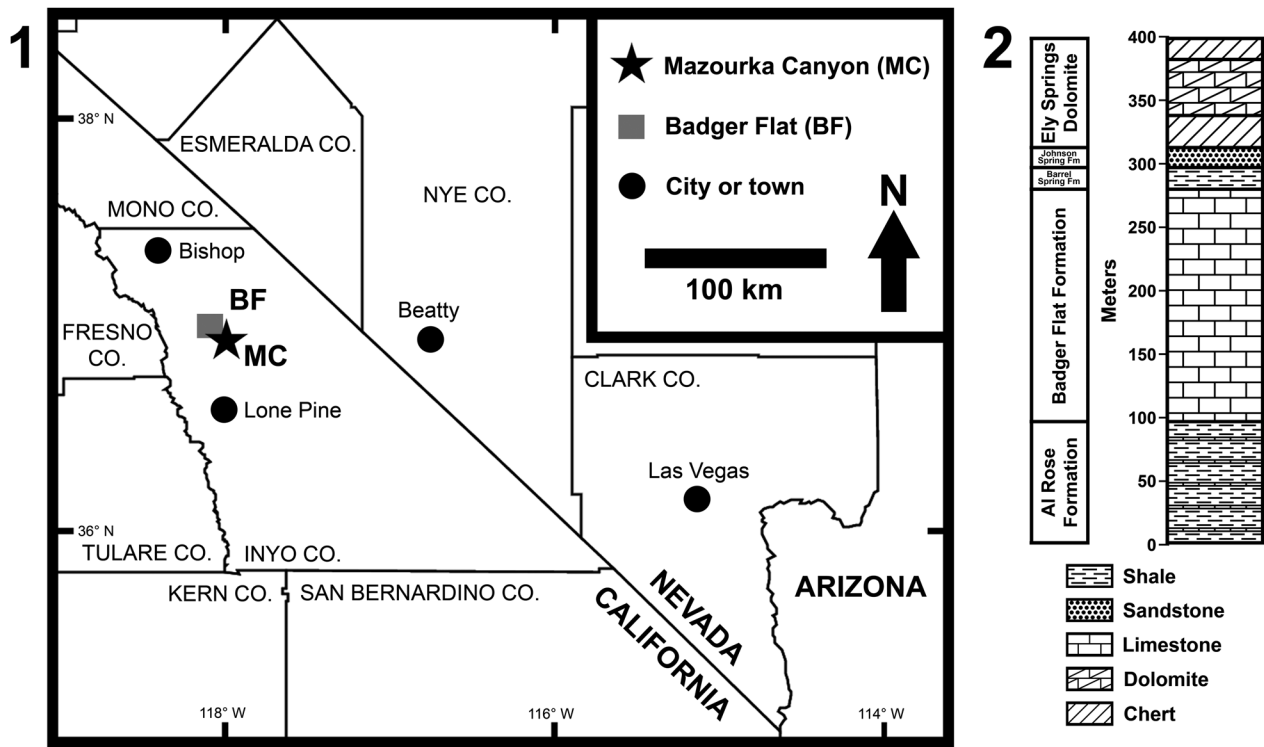
Figure 1. (**1**) Map of southeastern California showing general locations of localities in the White Inyo Mountains, Inyo County. (**2**) Stratigraphic section at Badger Flat locality modified from Stevens (1986).

apparently without fossils. This interval is underlain by a seam of splintery shales that do indeed yield pendent didymograptid graptolites along with *Globampyx sexsegmentatus* n. sp., which is likely what Ross listed as an ampyxinid and is the most abundant macrofossil of the Al Rose Formation below that level. It seems more likely to us that the collections referred to by Ross should actually belong to the topmost bed of the Al Rose Formation. The obvious lithological boundary between the Al Rose Formation and the overlying Badger Flat Limestone Formation is at the first robust black limestone bed that lies just above this shale interval.

Age and correlation of the Al Rose Formation.—Graptolites from the Al Rose Formation are quite numerous. They represent a typical open-shelf biotope for the Early Ordovician, dominated by pendent didymograptids and phyllograptids. Oceanic elements such as sigmagraptines and isograptines are absent. Because much of the material is derived from local float, it is not possible to determine stratigraphic ranges of species. However, in situ material excavated from small pits in the fissile shales do not show any significant differences between the lower part of the formation and near the top, and it is likely that only one biozone is represented in the collections. The specimens are flattened in shales but are otherwise not greatly distorted.

The following species have been identified: *Didymograptellus kremastus* Vandenberg, 2017 (= *Didymograptus (Didymograptellus) protobifidus* Elles, 1933, of North American usage, e.g., Berry, 1960, see also comments in Cooper and Fortey, 1982); *Didymograptus (Expansograptus) similis* Hall, 1865; *Phyllograptus typus* Hall, 1858; *Tetragraptus amii* Elles and Wood, 1902; *T. serra* Brongniart, 1828; *T. quadribrachiatus* Hall, 1858. The specimens of *Phyllograptus typus* are well-enough preserved to observe the characteristic virgellar spine that distinguishes the species from superficially similar specimens of *Pseudophyllograptus*. Although several of the species have long ranges, comparison with other Lower Ordovician graptolite faunas from measured sections around the Laurentian platform (Berry, 1960; Braithwaite, 1976; Cooper and Fortey, 1982; Williams and Stevens, 1988) locates the overlap of these species within the equivalents of the Chewtonian and early Castlemainian of the Australian graptolitic standard. This equates with the Blackhillsian Stage of the Ibexian Series in North American terminology (Ross et al., 1997), the later part of the earlier half of the Arenigian Stage in terms of the classical European usage (Fortey and Owens, 1987), which is Floian in terms of the new standard ratified by the International Union of Geological Sciences.

The shelly faunas are abundant, but the trilobites constitute mostly new species, and some of the material is not adequate to permit formal nomenclature. However, the pelagic trilobite *Carolinites genacinaca* Ross, 1951 is typical of the *Pseudocybele nasuta* (J) Zone in Utah, Idaho, and Nevada, and the Al Rose Formation is therefore likely to be the equivalent of the appropriate part of the Wahwah Formation and Garden City Formation in those sections (Ross, 1951; Hintze, 1953, 1973). The occurrence of the trilobite genera *Lachnostoma* and *Protopresbynileus* is consistent with this, even though they are represented by different species to the east.

The basal part of the overlying Badger Flat Limestone Formation comprises well-laminated black limestones that are singularly devoid of macrofossils. It seems likely that they represent anoxic conditions. Four meters above the base, we recovered the pelagic trilobite species *Carolinites angustagena* Ross, 1967, which has been identified from early Whiterockian strata in Nevada (Fortey and Droser, 1999).

Biofacies of the Al Rose Formation.—The benthic fauna of the Al Rose Formation is different from its contemporaries that have been studied in detail in the western United States. Shallow-shelf trilobite faunas in the Lower to Middle Ordovician formations across the Great Basin are dominated by faunas including prolific asaphids (in the Blackhillsian), bathyurids, and pliomerids with many additional dimeropgyids, cheirurids, and illaenids (Adrain et al., 2009); the last two families are often more significant in "mound" or bioherm faunas, such as that at Meiklejohn Peak, Nevada (Ross, 1972). Fortey and Droser (1996, fig. 4) indicated that a deeper-water Nileid Biofacies was present in collections from Ike's Canyon, Nevada, while the most off-shelf biofacies dominated by olenid trilobites has yet to be found in the western United States. The fauna described in the following is also typical of the Nileid Biofacies, and as in its typical development in the Valhallfonna Formation of northern Spitsbergen (Fortey, 1975a), it also has abundant raphiophorids and some agnostids as well as the eponymous family (note that we assign *Protopresbynileus* to Nileidae). In the systematic part that follows, close species comparisons are made with trilobites from the Al Rose and those of *Lachnostoma*, *Globampyx*, *Cloacaspis*, and *Rhombampyx* from Spitsbergen. Pliomeridae are rare although the family is extraordinarily diverse in the Great Basin as currently documented by J.M. Adrain and his colleagues (2009). Further, no example of a bathyurid was collected. Pelagic trilobites of the genus *Carolinites* provide the most conspicuous common element linking with the shallower-water faunas to the east. A total count of sclerites from the Al Rose Formation is only meaningful in the most general way as collections from individual beds have not been made. A sample of 100 sclerites taken at random from the collections breaks down as follows: Raphiophoridae 50%, Nileidae 30%, Agnostidae 8%, Asaphidae 5%, Telephinidae 2%, Olenidae 3%, Pliomeridae 1%, Indeterminate 1%. Lingulate brachiopods are numerous, as are plumulitid machaeridians. It is remarkable how agnostids and raphiophorids are apparently absent from contemporary strata in the Pogonip Group, despite the fact that many hundreds of specimens have been recovered by acid solution there. Olenid trilobites are rather rare in the Al Rose Formation, suggesting only that an olenid-dominated environment may have lain further offshore.

As far as the habitat of the Al Rose Formation is concerned, numerous flat bedding planes covered with graptolites such as *Phyllograptus* provide evidence that the seafloor may have been depleted in oxygen at times. However, the abundance of the blind benthic trilobite *Globampyx* on other bedding planes demonstrates that at other times there was enough bottom oxygenation to support large populations of what were probably particle feeders from suspension (Fortey and Owens, 1999).

However, most of the other species of trilobites (agnostids excepted) were not blind and had well-developed eyes. The olenid has the longest eyes of any described species. It therefore does not seem likely that the habitat was below the photic zone, where atheloptic trilobites dominate. The fact that articulated trilobites are rather common compared with more inshore environments does suggest that the bottom sediments were not disturbed by strong currents. Many of the articulated specimens are likely to have been molts, and these remain unreworked, which makes the same point.

The Nileid Biofacies was probably widely distributed along the western paleocontinental margin of Laurentia in the earlier Ordovician, although it has not been preserved in many places. For example, Norford and Ross (1978) described a small fauna undoubtedly of this kind from British Columbia. Raphiophorid-bearing strata advance toward the cratonic interior later in the Ordovician. Possibly, some relatively marginal sites were overridden by allochthonous terranes (e.g., Vinini Formation in Nevada) that may serve to conceal the former extent of the deeper shelf biofacies. However, Ketner and Alpha (1992) dispute some of the geological evidence relating to the emplacement of the Vinini Formation. The Al Rose Formation is important in providing an accessible locality to examine this relatively marginal trilobite biofacies and its associated faunas, and it proves the presence of an onshore–offshore sequence of biofacies east of the Great Basin similar to those elsewhere on the flanks of Ordovician Laurentia.

Materials

Repository and institutional abbreviation.—All specimens are deposited in the Natural History Museum of Los Angeles County's Invertebrate Paleontology collections (LACMIP) and are assigned to LACMIP locality 42370.

Systematic paleontology

Family Metagnostidae Jaekel, 1909
Genus *Geragnostus* Howell, 1935

Type species.—*Agnostus sidenbladhi* Linnarsson, 1869, late Tremadocian of Sweden (see Ahlberg, 1989).

Subgenus *Novoagnostus* Nielsen, 1997

Type species.—*Arthrorhachis longicollis* Raymond, 1925, middle Table Head Formation, western Newfoundland.

Remarks.—Nielsen (1997) noted that nearly 100 taxa of Ordovician age had been assigned to *Geragnostus*. He opted to partition this large number of taxa into a number of subgenera, although the basis for placing a particular form into one of these rather than another was acknowledged to be somewhat arbitrary. Since the species from the Al Rose Formation is very similar to the type species of the subgenus *Novoagnostus*, we are obliged to use this name if we use any at all. However, it is clear that even within the type species, *N. longicollis* Raymond, 1925, there is variation in the length

of the pygidial axis. For example, Whittington's (1965, pl. 1, fig. 7) type series includes a specimen with an axis that occupies almost 70% of the pygidial length. This is more than the proportion taken up on the type species of *Geragnostus* (*Geragnostus*), *G. sidenbladhi* (Linnarsson, 1869); for example, the pygidium illustrated by Ahlberg (1989, fig. 3F) has an axis only 62% pygidial length. Therefore, it cannot be true that species of *Geragnostus* (*Novoagnostus*) are characterized by "a shorter pygidial axis, although the axis still accounts for 60% of the pygidial length or more" as Nielsen (1997, p. 486) states. Nielsen also assigns *Geragnostus clusus* Whittington, 1963 to *Novoagnostus* even though one of Whittington's (1963, pl. 1, fig. 10) specimens has an axis nearly 80% pygidial length, in what is presumably a highly variable species. Comparative pygidial axial length is clearly not a satisfactory character to delineate a subgenus. Possibly the pygidial terminal piece being well defined posteriorly and with a tendency to be wider (tr.) than the axial ring in front of it may be of use in distinguishing a species group within *Geragnostus*, but it is clear that no current revision is yet satisfactory. It also is likely that revision of the whole group will result in synonymizing of species since agnostid species are generally widespread, and this is not reflected in the current taxonomy of *Geragnostus*.

Geragnostus cf. *G. (Novoagnostus) longicollis* Raymond, 1925
Figure 2.1–2.3

cf. 1925 *Agnostus longicollis*; Raymond p. 12, pl. 1, fig. 5
cf. 1965 *Geragnostus longicollis* (Raymond, 1925); Whittington p. 301, pl. 1, figs. 1–12,14,16,17.

Material.—External mold of exoskeletons LACMIP 42370.1, LACMIP Type 14950; LACMIP 42370.2, LACMIP Type 14951; LACMIP 42370.36, LACMIP Type 14985; cephalon LACMIP 42370.37, LACMIP Type 14986; pygidium LACMIP 42370.3, LACMIP Type 14952; LACMIP 42370.38, LACMIP Type 14987.

Remarks.—*Geragnostus longicollis* was fully described from good material from western Newfoundland by Whittington (1965), and rather poor material from the Al Rose Formation adds nothing to our understanding of the species. One obvious difference from the holotype (Whittington, 1965, pl. 1, fig. 1) is the relatively shallow furrows on the pygidial axis of our material, but different preservation may account for this. The most important shared character between our best specimen illustrated on Figure 2.2 herein and the type material is that the pygidial axis tapers backward before slightly expanding at the terminal piece, which is as long (sag.) as the axis in front of it. This is not so clear on a second specimen (Fig. 2.3) with a more effaced pygidial axis, and it is possible that this represents a second agnostid species; the preservation is imperfect for systematic treatment, and it is referred with reservation to *Geragnostus* cf. *G. longicollis*.

Family Raphiophoridae Angelin, 1854
Genus *Globampyx* Fortey, 1975

Type species.—*Globampyx trinucleoides* Fortey, 1975 (Fortey, 1975b), early Whiterockian, Valhallfonna Formation, Spitsbergen.

Remarks.—The inclusion of the new species described in *Globampyx* requires that the original diagnosis of the genus be emended to include species with six, as well as five, thoracic segments. Raphiophorids are unusual among post-Cambrian trilobites in being variable in the number of free segments in the thorax, which can be as few as two in *Taklamakania* but five, six, or seven in other taxa. If it is accepted that the larger number is more likely to be the primitive condition, then the presence of six segments in *G. sexsegmentatus* n. sp. is not an apomorphy and thus not a possible basis for separating the taxon from *Globampyx*.

Globampyx sexsegmentatus new species
Figure 3

Holotype.—Axial shield, LACMIP 42370.8, LACMIP Type 14957 (Fig. 3.2).

Diagnosis.—A *Globampyx* species distinguished from others by having six, rather than five, thoracic segments and an anteriorly comparatively less-inflated glabella.

Description.—A common small species, entire exoskeletons 1 cm long or less, of which much is accounted for by the genal spines, so that the main body of the animal is not much more than 5 mm long. The length of the latter (sag.) is close to its width at the midpoint of the thorax. Much of the convexity is on the cephalon, the thorax being nearly horizontal away from the axis. The cephalon lacks an anterior median spine and is just under half total axial length. The cranidium is twice as wide as long, and at its widest, close to its anterior margin, the glabella is slightly more than one quarter cranidial width. Our material is mostly slightly crushed, so it is not possible to be certain of the original convexity of glabella; however, a well-preserved external mold shows a relatively gradual increase in width and height anteriorly before an almost semicircular frontal lobe. There is a suggestion of a median tubercle at the high point of the glabella, as in *G. trinucleoides*, but no trace of the muscle impressions on the glabella are preserved. Occipital ring narrow and curved slightly backward. Posterior border furrow fades out toward glabella, the border being widest at about two-thirds its length. Facial sutures run around the edge of the cranidium, and the yoked free cheeks probably comprised a strip of doublure separating the very long needle like genal spines, which double the length of the whole animal and seem to curve inward slightly posteriorly.

Thorax widens backward to third segment and thereafter narrows; thoracic axis follows a similar pattern, but even at its widest is not wider than the adjacent thoracic pleura. Thoracic segments are all similar to one another, in touch along their whole length, with sharply truncate pleural tips, which are downturned. Pygidial margin continues this near-vertical peripheral wall, which gradually widens before a posterior notch. Length of pygidium less than half that of thorax, and pygidium more than three times as wide as long. Axis tapers noticeably
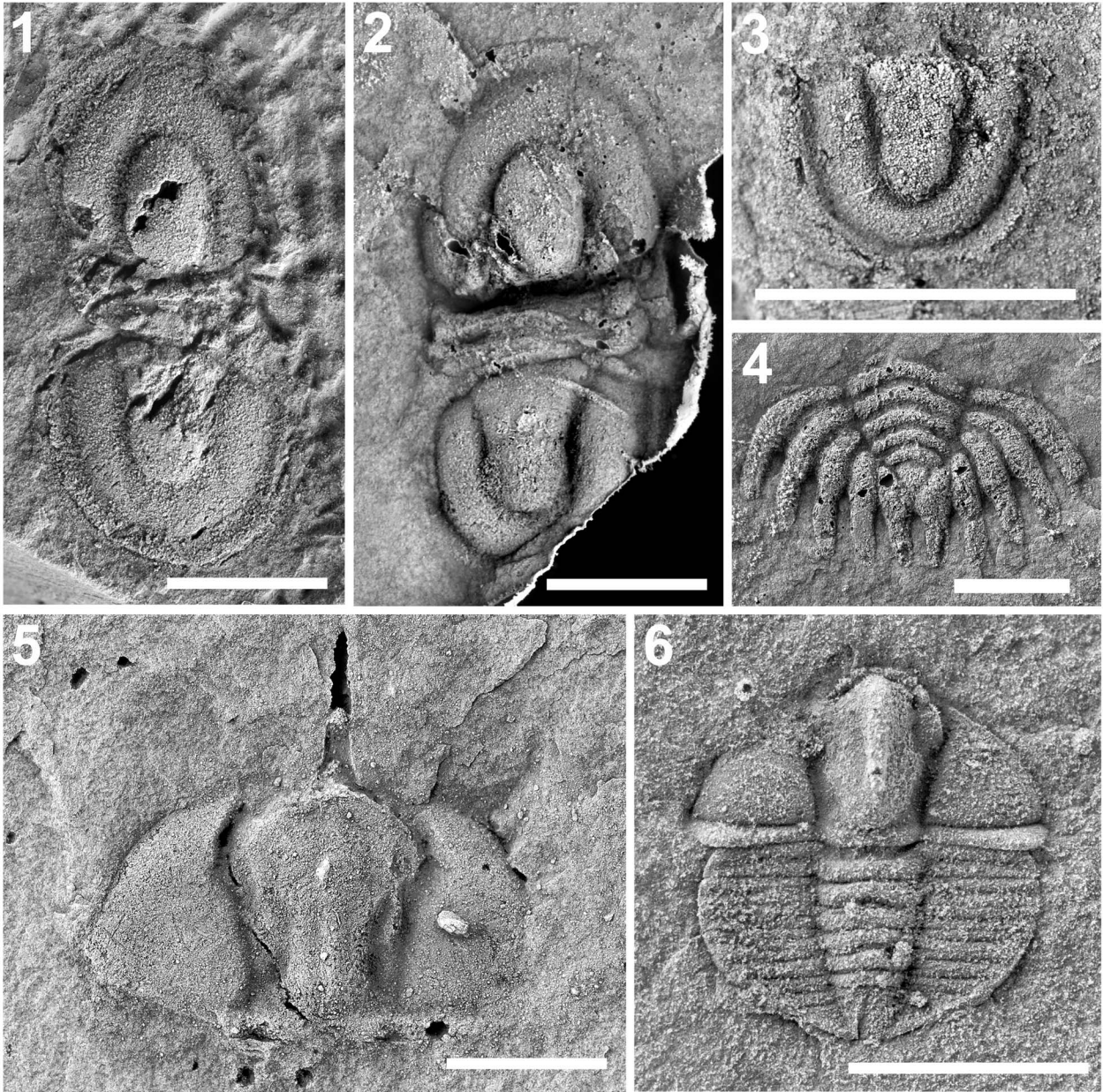
Figure 2. (**1–3**) *Geragnostus* cf. *G. (Novoagnostus) longicollis* Raymond, 1925: (**1**) dorsal exoskeleton, LACMIP 42370.1, LACMIP Type 14950; (**2**) latex cast from dorsal exoskeleton, LACMIP 42370.2, LACMIP Type 14951; (**3**) pygidium, LACMIP 42370.3, LACMIP Type 14952, referred with caution to this species. (**4**) *Hintzeia* sp. pygidium, LACMIP 42370.6, LACMIP Type 14955. (**5, 6**) *Rhombampyx* sp.: (**5**) cranidium, LACMIP 42370.4, LACMIP Type 14953; (**6**) axial shield, LACMIP 42370.5, LACMIP Type 14954. Scale bars = 3 mm.

posteriorly and reaches border. Most specimens show little in the way of pygidial pleural furrows, but this feature is variable, as it is in *G. trinucleoides*, and up to three pygidial axial rings and an equivalent number of more-or-less transverse pleural furrows may be visible. There is no indication of surface sculpture on the exoskeleton.

Etymology.—Referring to six thoracic segments.

Material.—Holotype, axial shield, LACMIP 42370.8, LACMIP Type 14957; other paratypic material includes axial shield, LACMIP 42370.7, LACMIP Type 14956; dorsal exoskeletons, LACMIP 42370.9, LACMIP Type 14958;

LACMIP 42370.10, LACMIP Type 14959; LACMIP 42370.12, LACMIP Type 14961; LACMIP 42370.13, LACMIP Type 14962 (slab); LACMIP 42370.39, LACMIP Type 14988; LACMIP 42370.40, LACMIP Type 14989; cranidium, LACMIP 42370.11, LACMIP Type 14960; fused free cheeks, LACMIP 42370.41, LACMIP Type 14990.

Remarks.—Two species of *Globampyx* are known previously, both from early Middle Ordovician (Whiterockian) strata. The type species, *G. trinucleoides* from the Valhallfonna Formation, Spitsbergen, is similar to *G. sexsegmentatus* in size and, like it, can be abundant on certain bedding planes. It differs in having a distinctly pyriform glabella and in having
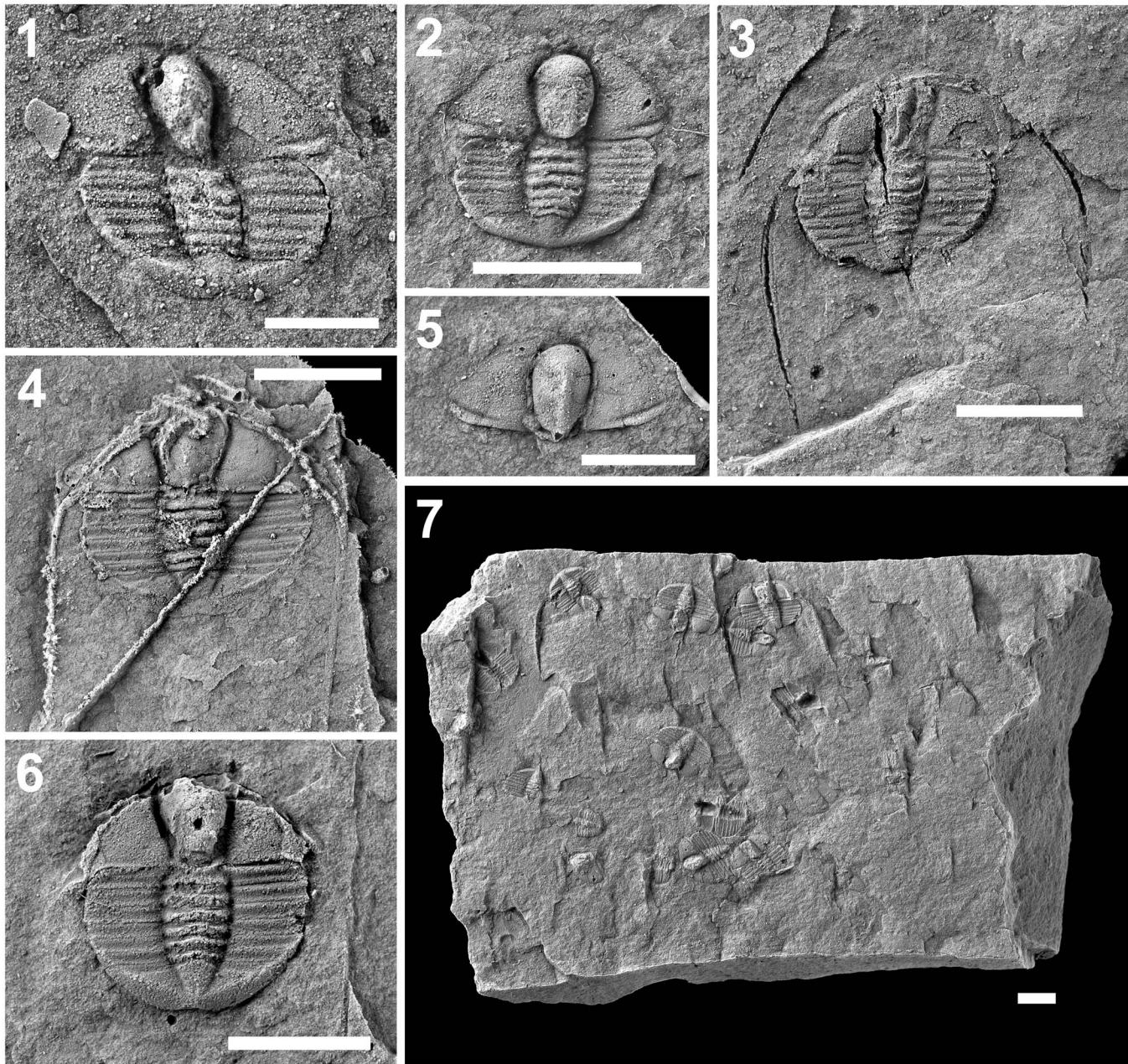
Figure 3. *Globampyx sexsegmentatus* n. sp.: (**1**) axial shield, LACMIP 42370.7, LACMIP Type 14956; (**2**) holotype, axial shield, LACMIP 42370.8, LACMIP Type 14957; (**3**) dorsal exoskeleton, LACMIP 42370.9, LACMIP Type 14958; (**4**) latex cast from imperfect dorsal exoskeleton, LACMIP 42370.10, LACMIP Type 14959; (**5**) well-preserved cranidium, LACMIP 42370.11, LACMIP Type 14960; (**6**) latex cast from complete exoskeleton, LACMIP 42370.12, LACMIP Type 14961; (**7**) limestone block showing abundance of this species in the Al Rose Formation, LACMIP 42370.13, LACMIP Type 14962. Scale bars = 3 mm.

only five thoracic segments (Fortey, 1975b, pl. 29, fig. 4). The other species from the Glenogle Shales of British Columbia, *G. sinalae* Norford and Ross, 1978, is more like *G. sexsegmentatus* in general proportions but like *G. trinucleoides* has only five thoracic segments. *G. sinalae* carries a surface sculpture of fine rugae on the fixed cheeks, unlike the other two species. *G. trinucleoides* has a sculpture of fine punctae, and *G. sexsegmentatus* appears to be smooth. Since *G. sexsegmentatus* is older than either of these species, it is not unreasonable to suppose that the shorter thoraces of the younger species were achieved by failure of release of one thoracic segment from the front of the pygidium. Some

support for this is given by the fact that the pygidium of *G. trinucleoides* accounts for 25% of the exoskeletal length, and this proportion is the same as the length of the pygidium plus sixth thoracic segment on *G. sexsegmentatus*. The preservation of most specimens of the latter species leaves something to be desired, and so it would be difficult to put this observation on a more quantified footing.

Genus *Rhombampyx* Fortey, 1975

Type species.—*Rhombampyx rhombos* Fortey, 1975 (Fortey, 1975b), Valhallfonna Formation, Spitsbergen.

Rhombampyx sp.
Figure 2.5, 2.6

Material.—Axial shield, LACMIP 42370.5, LACMIP Type 14954; cranidium, LACMIP 42370.4, LACMIP Type 14953.

Remarks.—One raphiophorid shield (exoskeleton lacking free cheeks) and cranidium among dozens of *Globampyx* differ from that genus in possessing a stout anterior spine carried on a relatively wide glabella and a small pygidium with pleural furrows. The overall small size and short, wide, furrowed pygidium, together with details of the occipital structure, are different from *Ampyx*, in which the pygidia are typically longer (sag.) than the thorax. The Al Rose material is closely similar to the type species of *Rhombampyx*, *R. rhombos* Fortey, 1975, but the material available is not sufficient to characterize a new species. Nonetheless, it differs from *R. rhombos* in a less anteriorly protruding glabella, narrower (tr.) cheeks, with narrow posterior border furrows, and much longer (tr.) pleurae on the anterior thoracic segment. *Ampyx* and its relatives were already widespread in the Floian across Baltica and marginal Gondwana, but raphiophorids in general appear widely in Laurentia only at the Middle Ordovician (Whiterockian) (Ross, 1967; Fortey and Droser, 1999). The Al Rose species of *Rhombampyx* is older than the earliest Whiterockian species from Spitsbergen and clearly different from it.

Family Telephinidae Marek, 1952
Genus *Carolinites* Kobayashi, 1940

Type species.—*Carolinites bulbosus* Kobayashi, 1940 from Middle Ordovician of Caroline Creek, Tasmania.

Carolinites genacinaca subsp. indet.
Figure 4

Synonymy.—See discussion in McCormick and Fortey, 1999.

Material.—Cranidia, LACMIP 42370.14, LACMIP Type 14963; LACMIP 42370.15, LACMIP Type 14964; and with eye attached, LACMIP 42370.42, LACMIP Type 14991; partial thorax and pygidium, LACMIP 42370.16, LACMIP Type 14965; articulated exoskeleton? LACMIP 42370.43, LACMIP Type 14992; thorax, LACMIP 42370.44, LACMIP Type 14993; pygidium, LACMIP 42370.17, LACMIP Type 14966.

Remarks.—This pelagic species has been claimed by McCormick and Fortey (1999) as the most widely distributed Ordovician trilobite. It has been described several times from paleoequatorial localities, mostly from better-preserved material than that from the Al Rose Formation, for example, by Ross (1951), Hintze (1953), Fortey (1975b), and McCormick and Fortey (1999). Further description would be superfluous here. Critical features in determining *Carolinites* species include the relative size of the bacculae on the cranidium. A large cranidium from the Al Rose Formation has been slightly flattened and is identical to a similarly preserved specimen from Spitsbergen figured by Fortey (1975b, pl. 38,
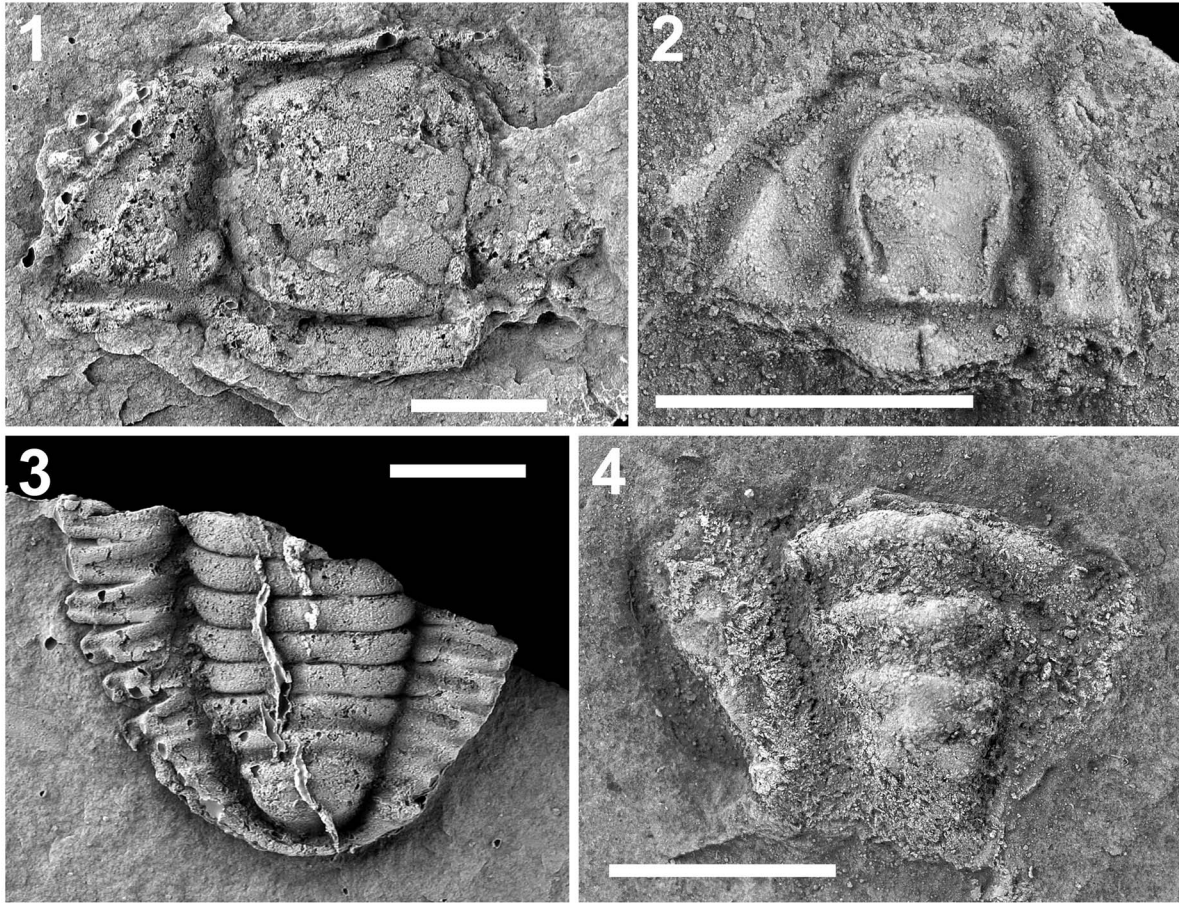
fig. 1). Pygidia of *Carolinites genacinaca genacinaca* Ross, 1951 taper more posteriorly than do those of other species of the genus, and the posterior axial ring tends toward effacement—both features seen on the specimen with the posterior part of the thorax figured here in Figure 4.3. *C. genacinaca genacinaca* has a range through the J Zone (*Pseudocybele nasuta*) of the platform sequences in Utah and Nevada and has been distinguished from *C. genacinaca utahensis* Hintze, 1953, the status of which is not finalized. Perfectly preserved silicified material from the Great Basin should clarify these taxa, but the Al Rose material is closer to *C. genacinaca genacinaca* in the proportions of its bacculae.

Family Nileidae Angelin, 1854
Genus *Protopresbynileus* Hintze, 1954

Type species.—*Pseudonileus willdeni* Hintze, 1953.

Remarks.—Classification of effaced asaphoids is notoriously difficult, and the species considered in the following is no exception. The type species of *Protopresbynileus* was described from the zone G fauna of Ibex, Utah, by Hintze (1953). It was originally regarded as close to *Presbynileus* (Asaphidae), and to reflect this assumed relationship, Fortey (1975b) included *Protopresbynileus* within it as a subgenus. This is now regarded as implausible. Hypostomes are very important in asaphoid classification (Fortey et al., 2022, p. 318), and the hypostomes of the type species of *Presbynileus*, *P. ibexensis* Hintze, 1953, and that of *Protopresbynileus* are fundamentally different. This is a far more important feature than general dorsal effacement, which is manifestly polyphyletic in Asaphida. The hypostome of *Presbynileus* is deeply forked, as it is in the subfamily Isotelinae of Asaphidae, whereas that of *Protopresbynileus* has wide (tr.) rounded borders, a tapering middle body interrupted by prominent smooth maculae, and a markedly shallow fork with a median tooth. It is, in fact, identical to the hypostome regarded typical of the family Nileidae and that of *Nileus* itself (see, e.g., Schrank, 1972). The hypostome associated with a new species of *Protopresbynileus* from the Al Rose Formation is nearly identical to that of the type species of the genus illustrated by Hintze (1953, pl. 15, fig. 16). Hence, we believe that the true affinities of *Protopresbynileus* lie within Nileidae rather than within Asaphidae. *Presybnileus* is certainly a member of Asaphidae, and the three species named by Hintze (1953) all share common hypostomal characters. It might be objected that *P. willdeni* and *P. divergens* n. sp. show a ventral median cephalic suture, whereas Nileidae have yoked cheeks. However, Owens et al. (1982) noted that the early nileid *Platypeltoides* had a median suture, and the same feature has now been recognized in early cyclopygids, so it is a plesiomorphic character for Cyclopygoidea (sensu Fortey and Chatterton, 1988) and hence not relevant to classification at the family level.

If this is correct, a species from Spitsbergen attributed with question to *Protopresbynileus*, *P.? glaber* Fortey, 1975 (Fortey, 1975b), should rather be attributed to *Presbynileus* sensu stricto because, although its hypostome is not known, it does show good panderian openings on the thoracic doublure, which is a

Figure 4. *Carolinites genacinaca* subsp. indet. Ross, 1951: (**1**) cast from imperfect cranidium, LACMIP 42370.14, LACMIP Type 14963; (**2**) small cranidium, LACMIP 42370.15, LACMIP Type 14964; (**3**) latex cast from partial thorax and pygidium, LACMIP 42370.16, LACMIP Type 14965; (**4**) pygidium, LACMIP 42370.17, LACMIP Type 14966. Scale bars = 3 mm.

feature of Asaphidae and unknown in Nileidae. Note that Whittington (2000) regarded *Nileus* as related to another effaced group, Illaenidae, rather than part of Asaphida, a view based on similarities of thoracic structure. This is a single character. Nileidae share the following with other Asaphida: a distinctive globular protaspis, a median suture that is present plesiomorphically in nileids (rather than a wide rostral plate as on illaenids), petaloid facets on the thoracic segments, transverse hypostome with wide, ear-like lateral borders, and hypostomal maculae that are smooth and frequently inclined forward. This larger number of important synapomorphies suggests that the similarity between *Illaenus* and *Nileus* is rather a matter of convergence. Nileidae should be retained in Asaphida.
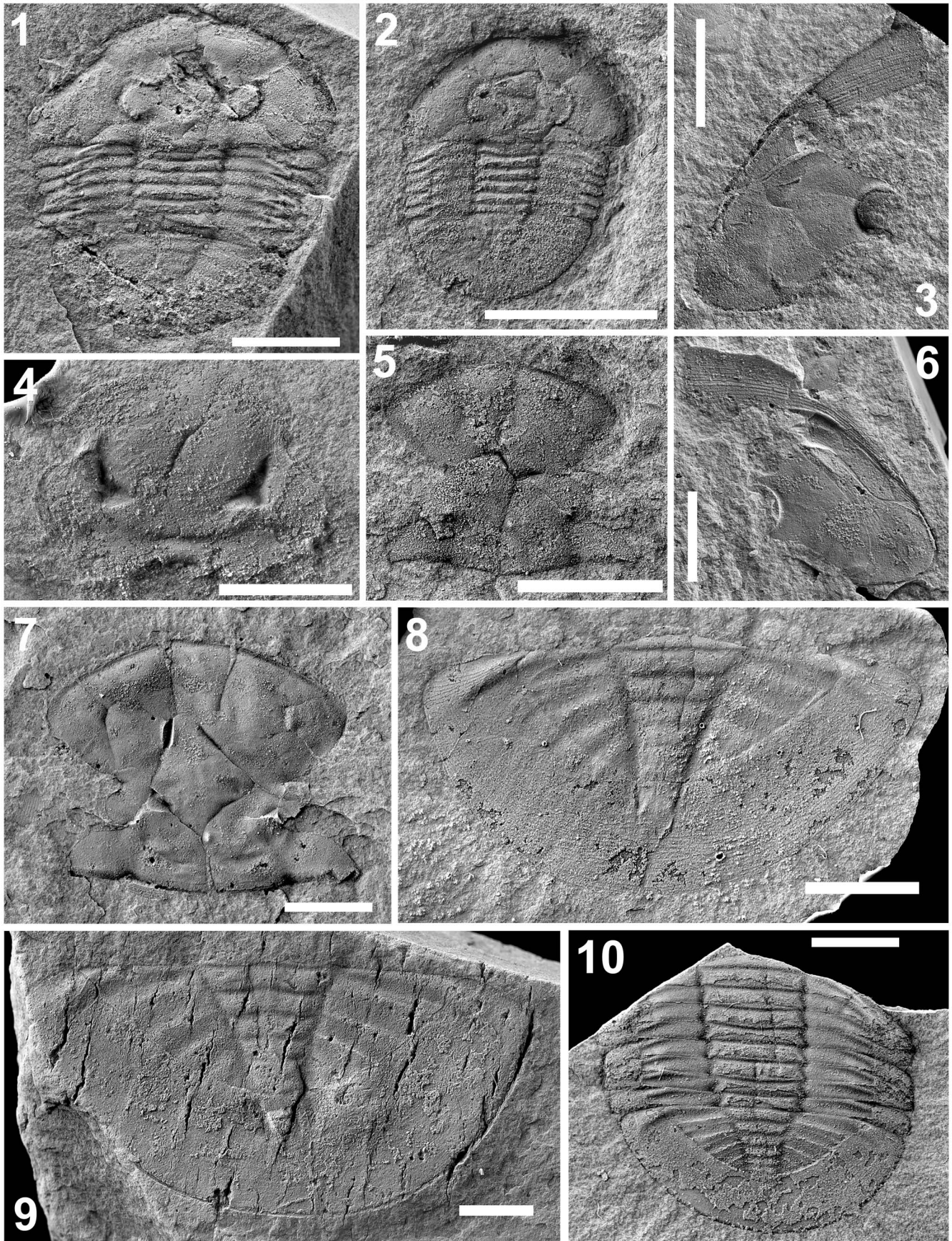
Protopresbynileus divergens new species
Figure 5

Holotype.—Cranidium, LACMIP 42370.24, LACMIP Type 14973 (Fig. 5.7).

Diagnosis.—*Protopresbynileus* species with highly divergent anterior branches of the facial sutures producing wide (tr.) anterior lobe on cranidium; small eye; eight thoracic segments; pygidium with defined axis and four pleural ribs.

Description.—If the exoskeletal parts are correctly associated, this is the commonest asaphoid in the Al Rose Formation. Specimens are all flattened so that the original convexity has to be inferred; the holotype shows distinct cracks in the exoskeleton, which indicates compression of a convex cranidium. However, the critical specific characters are not seriously affected by compression. Articulated material indicates exoskeletal width (tr.) about three-quarters length (sag.), with the thorax just longer than the pygidium. There is a size series of cranidia, the largest being the holotype. On all except the smallest, the maximum width is longer than its length, and on the holotype this width is equal across the anterior lobe and the posterior margin. On smaller specimens, the maximum width is slightly more across the posterior fixigenal limbs. The glabella is not defined except at its posterior end, where it is 0.5–0.6 cranidial width. A pair of basal muscle impressions on the holotype might mark the occipital furrow. A prominent median glabellar tubercle lies in front of these, just behind the transverse line connecting the posterior limits of the palpebral lobes. The palpebral lobes themselves are at one-third glabellar length (but this is on flattened material, and if the anterior glabellar lobe originally was downturned, the lobes would appear further forward) and close in, toward the glabellar region; highly curved. As is

invariably the case with asaphoids, the smooth palpebral lobes decrease in size during growth, from less than one-fifth cranidial length in the largest cranidium to one-third in the late meraspis. Very narrow anterior border, perhaps better described as a rim. Facial sutures unusually divergent in front of eyes, at least 60° to sagittal line on flattened profile; this angle is lower on small cranidia; decreases anteriorly to curve around anterior margin. Posterior branch initially recurves at a right angle to sagittal line and distally curves backward to cut the posterior margin at an acute angle.

Free cheeks are assigned confidently because of the unusually acute angle between the anterior and posterior branches of the facial sutures. Exsagittal length (not including doublure) approximately the same as transverse width; genal angles rounded from a small size. Doublure wide, and still wider toward genal angle, where it curves toward midline. Apparently unequivocal median suture. Eye lobe strongly curved and apparently no eye socle. Terrace ridges on doublure dense medially, this being the most prominent sculpture on the trilobite.

Thorax has eight segments (see remarks that follow) with axis quite well defined with zetoidal furrows and narrow (sag.) half rings. Segments are similar to each other except that the anterior segment has a much wider facet than the posterior six extending almost to the axis. A degree 6 meraspis is similar except for a relatively longer pygidium, presumably indicating two unreleased segments.

Pygidium twice as wide as long, with well-defined, funnel-shaped axis up to a third pygidial width at anterior margin, but rapidly tapering initially, and then less so posteriorly to tip (not sharply defined) at three-quarters pygidial length. Up to six axial rings are defined, the first three distinctly, of only slightly decreasing length (sag.). Pleural fields with four ribs and weaker interpleural ridges stopping at paradoublural line (anterior half rib passes on to border). Doublure has concave inner margin and even width along its length except where presumably excavated around the tip of the axis.

Hypostome much wider transversely than long, with wide, ear-shaped posterolateral borders separated by a wide shallow notch. Anterior wings prominent. Triangular forward-facing maculae prominent; some evidence of transverse terrace ridges on middle body.

Etymology.—Referring to the highly divergent anterior branches of the facial sutures.

Material.—Holotype, cranidium, LACMIP 42370.24, LACMIP Type 14973; paratypes: exoskeletons, LACMIP 42370.18, LACMIP Type 14967; LACMIP 42370.19, LACMIP Type 14968; LACMIP 42370.45, LACMIP Type 14994; LACMIP 42370.46, LACMIP Type 14995; cranidia, LACMIP 42370.22, LACMIP Type 14971; LACMIP 42370.47, LACMIP Type 14996; LACMIP 42370.48, LACMIP Type 14997; LACMIP 42370.49, LACMIP Type 14998; free

cheeks, LACMIP 42370.20, LACMIP Type 14969; LACMIP 42370.23, LACMIP Type 14972; LACMIP 42370.52, LACMIP Type 15001; LACMIP 42370.53, LACMIP Type 15002; thorax + pygidium, LACMIP 42370.27, LACMIP Type 14976; LACMIP 42370.54, LACMIP Type 15003; LACMIP 42370.55, LACMIP Type 15004; pygidia, LACMIP 42370.25, LACMIP Type 14974; LACMIP 42370.26, LACMIP Type 14975; LACMIP 42370.50, LACMIP Type 14999; hypostomes, LACMIP 42370.21, LACMIP Type 14970; LACMIP 42370.51, LACMIP Type 15000.

Remarks.—This species is easily distinguished from the type species, *P. willdeni,* by its strongly divergent anterior branches of the facial sutures and by the inner margin of the pygidial doublure, which is concave forward rather than convex forward. The eyes are smaller, and the better-developed pygidial furrows may also be a distinguishing feature (but the type material of *P. willdeni* is not well preserved, and flattening may exaggerate the furrows). Another species requiring consideration is *Presbynileus (P.) latifrons* Dean, 1989 from the Outram Formation, Alberta, which is the same age as *P. divergens*. Dean (1989) did not firmly assign a hypostome to this species, so whether it might be better assigned to *Protopresbynileus* is uncertain. However, this species does have strongly divergent anterior branches of the facial sutures like *P. divergens* and similarly short postocular fixed cheeks (tr.). Interestingly, the vincular furrow on the doublure of the free cheek (Dean, 1989, pl. 37, fig. 11) is much like that of the nileid *Poronileus* (Fortey, 1975b, pl. 41, fig. 6), and the comparatively well-defined glabella apparently expands forward in front of the eyes like that in other primitive cyclopygoids. It seems possible that *Presbynileus latifrons* might prove to be another *Protopresbynileus* species; its strongly ridged surface sculpture and wide pygidial and cephalic doublure clearly distinguish it from *P. divergens*. Dean (1989, pl. 37) illustrated a selection of unassigned asaphoid hypostomes, none of which is typically nileid.

As noted, the family assignment of *P. divergens* is particularly difficult. One additional feature requires mention—it has eight thoracic segments, like Asaphidae. Nileids typically have seven. However, the sister group of Nileidae and Cyclopyidae is Taihungshaniidae (following Fortey and Chatterton, 1988), with eight segments in the thorax, and hence this is likely to be the primitive number for the group as a whole. If this is the case, the presence of eight segments is a plesiomorphic character and hence not relevant to the classification of the genus. A degree 6 meraspis is very similar to a meraspis of the same degree of the nileid *Symphysurus arcticus* Fortey, 1975 (Fortey, 1975b, pl. 21, fig. 16). The peculiar combination of characters shown by *P. divergens* provides justification for naming the species formally, while recognizing that the material from the Al Rose Formation has certainly been flattened during compaction, and full-relief material would be desirable.

Family Asaphidae Salter, 1864
Genus *Lachnostoma* Ross, 1951

Type species.—*Lachnostoma latucelsum* Ross, 1951 from the late Ibexian of the Garden City Formation.

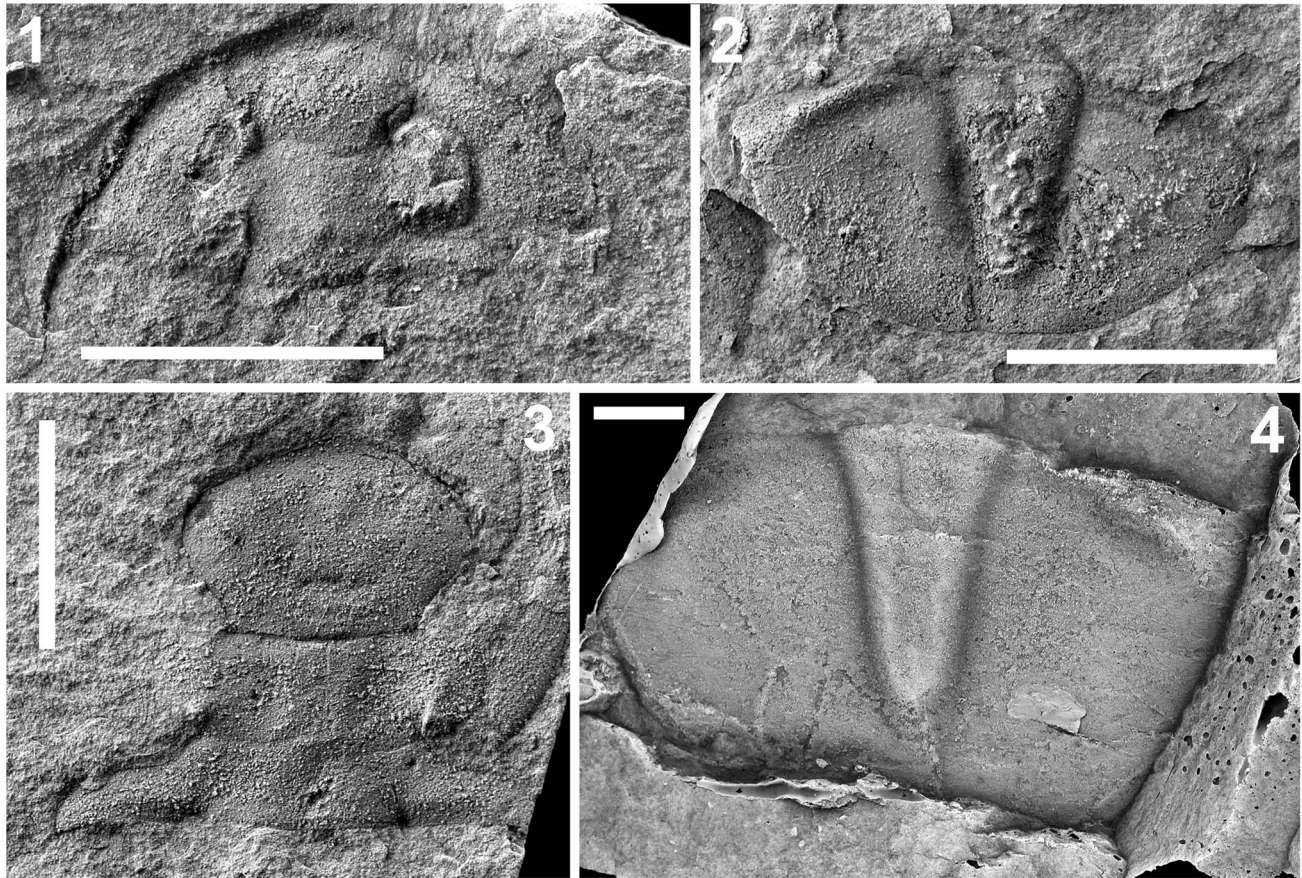*Lachnostoma* cf. *L. disputa* Fortey, 1975
Figure 6

Material.—Cephalic material, LACMIP 42370.28, LACMIP Type 14977; cranidia, LACMIP 42370.30, LACMIP Type 14979; LACMIP 42370.56, LACMIP Type 15005; LACMIP 42370.57, LACMIP Type 15006; pygidia, LACMIP 42370.29, LACMIP Type 14978; LACMIP 42370.31, LACMIP Type 14980.

Remarks.—Fragmentary remains of this species do not permit formal taxonomic recognition. They can be compared with the commonest trilobite fossils of the *Pseudocybele nasuta* (J) Biozone of Utah and Nevada, *Lachnostoma latucelsum* Ross, 1951 (also see Hintze, 1953; Fortey and Droser, 1999). The same species was described from western Canada by Dean (1989), so its morphology is well known. The same comments apply to the flattening of this species as were previously noted for *Protopresbynileus divergens*. A small and imperfect cephalic shield shows the presence of genal spines and proves that its transverse width was at least twice its length. The cranidium itself is comparatively long and narrow, with the greatest width at the posterior margin along the strap-like postocular cheeks, this somewhat exceeding the sagittal length. The glabella is not defined as material is preserved, except by axial pits at its posterior end. Palpebral lobes probably about 25% cephalic length; this is, longer than in mature *L. latucelsum*, where they are proportionately about half as long. However, the principal difference between *Lachnostoma* cf. *L. disputa* Fortey, 1975 (Fortey, 1975b) and *L. latucelsum* is in the much lower divergence of the anterior branches of the facial sutures of the Al Rose material, which means that the width across the anterior part of the cranidium is less; in addition, the cranidial border is not clearly defined in the latter. The likely associated larger pygidium has a long, narrow axis like the type species and unfurrowed pleural fields, but the material is too incomplete to say much about the border. A smaller pygidium is much like those attributed to *L. latucelsum* by Ross (1951).

Note that the Al Rose species is clearly distinct from *L. latucelsum,* a species we have found to be a ubiquitous trilobite across the Great Basin in shallower facies and whose geographic range extended the length of the western Laurentian platform (Dean, 1989). A somewhat similar fragmentary cranidium

Figure 6. *Lachnostoma* cf. *L. disputa* Fortey, 1975: (**1**) poorly preserved small cephalon, LACMIP 42370.28, LACMIP Type 14977; (**2**) pygidium, LACMIP 42370.29, LACMIP Type 14978; (**3**) cranidium, LACMIP 42370.30, LACMIP Type 14979; (**4**) latex cast from an incomplete large pygidium, LACMIP 42370.31, LACMIP Type 14980. Scale bars = 4 mm.

from the basal bed of the Whiterockian at Meiklejohn Peak, Nevada, was figured by Fortey and Droser (1999, figs. 7–16). At the eastern margin of the Laurentian paleocontinent, two species of *Lachnostoma* are known from the top of the Kirtonryggen Formation and base of the overlying Valhallfonna Formation in Spitsbergen (Floian) (Fortey and Bruton, 2013). The stratigraphically earlier *L. platypyga* Fortey and Bruton, 2013 has a broader cranidial border than the species from California and a relatively wide pygidium. *L. disputa* Fortey, 1975 was originally considered a ptychopygine (Asaphidae) by Fortey (1975b) but reassigned by Fortey and Bruton (2013); it offers the closest match to the Al Rose species, sharing with it a thin cranidial anterior border, narrow glabella, and weakly divergent anterior branches of the facial sutures. However, the large free cheeks of *L. disputa* figured by Fortey (1975b) lack genal spines—although they do frequently become reduced in later ontogeny in Asaphidae. The pygidium attributed to *L. disputa* is very like that of *L. platypyga* and probably wider (tr.) than that of either *L. latucelsum* or the Al Rose species, although the preservation on the latter is unfortunately incomplete. *L.*

disputa is slightly older than the Al Rose fauna (i.e., Bendigonian). In view of the several uncertainties, a comparative determination is given to our material.

<div align="center">

Family Olenidae Burmeister, 1843
Subfamily Balnibarbiinae Fortey, 1974
Genus *Cloacaspis* Fortey, 1974

</div>

Type species.—*Cloacaspis senilis* Fortey, 1974, Lower Ordovician, Valhallfonna Formation, Spitsbergen.

<div align="center">

Cloacaspis cf. *C. ceryx anataphra* Fortey, 1974
Figure 7

</div>

1967 aff. *Parabolinella* sp.; Ross, pl. 11.

Material.—Cranidia, LACMIP 42370.32, LACMIP Type 14981; LACMIP 42370.34, LACMIP Type 14983; LACMIP 42370.35, LACMIP Type 14984; LACMIP 42370.58,
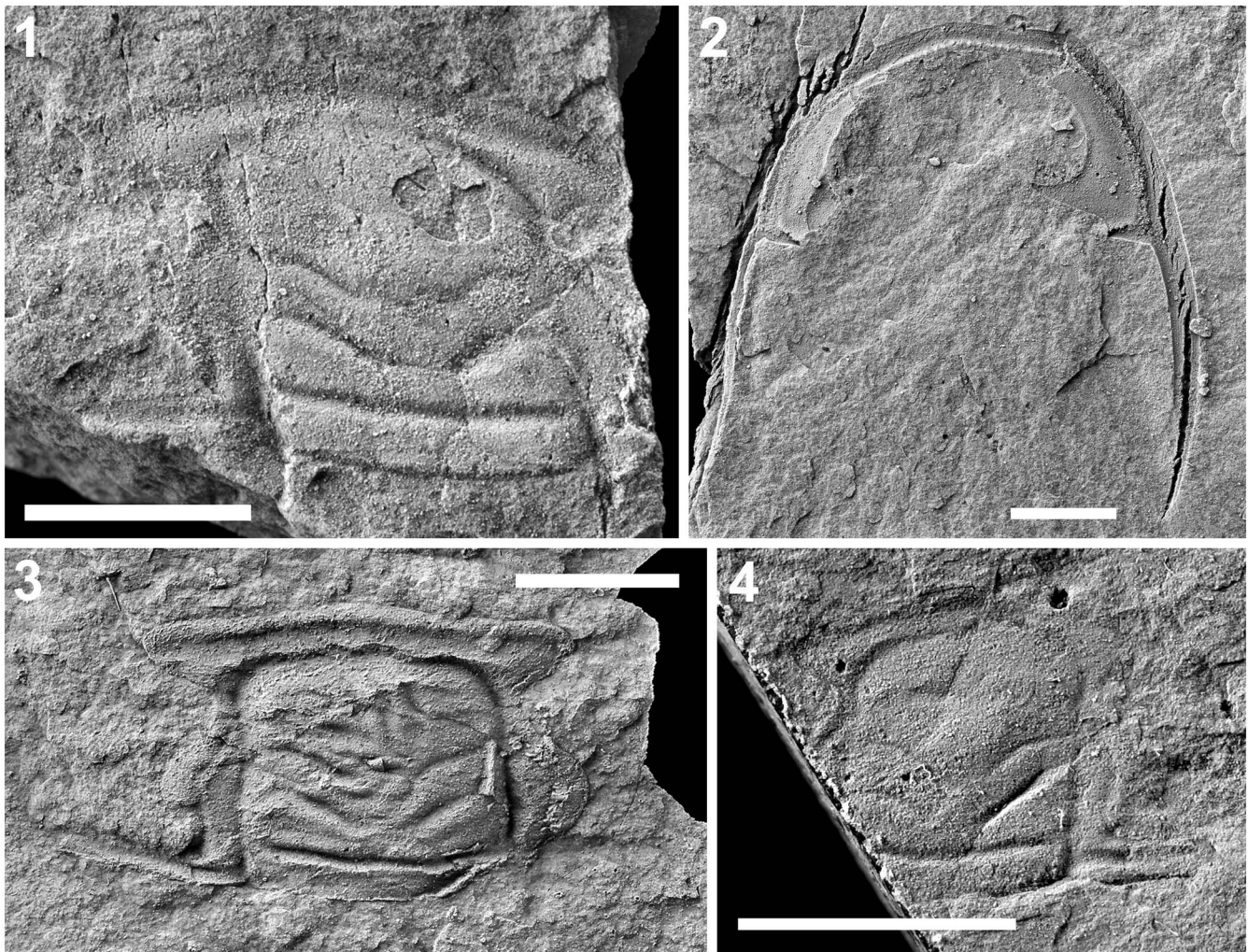
Figure 7. *Cloacaspis* cf. *C. ceryx anataphra* Fortey, 1974 (**1**) cranidium, LACMIP 42370.32, LACMIP Type 14981; (**2**) fused free cheeks showing narrow doublure, LACMIP 42370.33, LACMIP Type 14982; (**3**) cranidium, LACMIP 42370.34, LACMIP Type 14983; (**4**) latex cast from small cranidium, LACMIP 42370.35, LACMIP Type 14984. Scale bars = 4 mm.

LACMIP Type 15007; LACMIP 42370.59, LACMIP Type 15008; fused free cheeks, LACMIP 42370.33, LACMIP Type 14982; LACMIP 42370.60, LACMIP Type 15009.

Remarks.—This species is of interest as the only olenid trilobite in the Al Rose fauna. Indeed, apart from the "Olenid bed" at Little Rawhide Mountain, Nevada (Fortey and Droser, 1999), and specimens from Ike's Canyon, Nevada (Hopkins, 2019), it is the only olenid from the Floian–Whiterockian of the Great Basin. Balnibarbiines differ from olenines in their large size, square to forwardly expanding glabellas, highly divergent anterior branches of the facial sutures, and pleural nodes adjacent to the axis on the thorax (where known). Many species have wide preglabellar fields, and all have large eyes close to the glabella. The cuticle of these olenids is very thin and readily distorted, which applies to most of our Al Rose material, and this places limits on the formal taxonomy. However, the cranidium of the Californian species is very like that of *Cloacaspis ceryx anataphra* Fortey, 1974 from the lower part of the Olenidsletta Member of the Valhallfonna Formation in northern Spitsbergen. This species was originally included in *Balnibarbi* by Fortey (1974) on the basis of the anterior divergence of the facial sutures; however, a phylogenetic analysis of the Balnibarbiinae by Hopkins (2019) indicated that more characters supported attribution to *Cloacaspis*, which is followed here. The extremely long palpebral lobes are noted, which constrict narrow, strap-like postocular fixed cheeks; this species has the longest eye of any olenid. The anterior branches of the facial sutures, although short, are more divergent than they are in *Bienvillia* species with long eyes, but they are like *Cloacaspis ceryx anataphra* in this regard. That the species attained a large size with a square glabella typical of balnibarbiines is proved by a fragment of a very large cranidium, LACMIP 42370.59, LACMIP Type 15008. One significant difference is noted between the Spitsbergen species and that from the Al Rose Formation: a pair of fused free cheeks of the latter prove that the genal spines were not far advanced from the level of the posterior border whereas on the type material of *C. ceryx anataphra*, the origin of the genal spines was far enough forward to be opposite the eyes. This difference is probably of taxonomic significance, but the material available from California is not sufficient to recognize this formally.

Family Pliomeridae Raymond, 1913
Genus *Hintzeia* Harrington, 1957

Type species.—*Protopliomerops aemula* Hintze, 1953, *Pseudocybele nasuta* Biozone, Wahwah limestone Formation, Utah.

Hintzeia sp.
Figure 2.4

Material.—Pygidia, LACMIP 42370.6, LACMIP Type 14955; LACMIP 42370.63, LACMIP Type 15012; LACMIP 42370.64, LACMIP Type 15013; poorly preserved cranidia, LACMIP 42370.61, LACMIP Type 15010; LACMIP 42370.62, LACMIP Type 15011.

Remarks.—This is of interest as the only pliomerid in the Al Rose Formation, whereas pliomerids are ubiquitous in correlative faunas further to the east. It is evidently not the narrow kind of pygidium belonging to the zone fossil *Pseudocybele* in those sections. It may be compared with the pygidium of the species originally described by Hintze (1953) as *Pseudomera* aff. *P. insolita* (Poulsen, 1927) from the *nasuta* Zone and subsequently transferred to *Hintzeia* by Demeter (1973). A number of species of *Hintzeia* from the Great Basin have now been described from superbly silicified material by McAdams and Adrain (2011). However, it is clear that pliomerid pygidia are often conservative, and it is not possible to confidently assign the relatively poorly preserved Al Rose material to any one of these species; hence, we are obliged to use open nomenclature here.

Acknowledgments

Declaration of competing interests

The authors declare that there are no competing interests.

References

Adrain, J.M., McAdams, N.E.B., and Westrop, S.R., 2009, Trilobite biostratigraphy and revised bases of the Tulean and Blackhillsian stages of the Ibexian Series, Lower Ordovician, western United States: Memoirs of the Australasian Association of Palaeontologists, v. 37, p. 541–610.

Ahlberg, P., 1989, The type species of the Ordovician agnostid trilobite *Geragnostus* Howell, 1935: Paläontologische Zeitschrift, v. 63, p. 309–317.

Angelin, N.P., 1854, Palaeontologia Scandinavica. I: Crustacea Formations Transitionis: Leipzig, T.O. Weigel, 72 p.

Berry, W.B.N., 1960, Graptolite faunas of the Marathon Region, west Texas: University of Texas Publication no. 6005, 179 p.

Braithwaite, L.F., 1976, Graptolites from the Lower Ordovician Pogonip Group of western Utah: Geological Society of America Special Papers, v. 166, 106 p.

Brongniart, A.T., 1828, Prodrome d'une histoire des végétaux fossils: Paris, F.G. Levrault, 223 p.

Burmeister, H., 1843, Die Organisation der Trilobiten, aus ihren lebenden Verwandten entwickelt; nebst systematischen Uebersicht aller zeither beschrieben Arten: Berlin, G. Reimer, 148 p.

Cooper, R.A., and Fortey, R.A., 1982, The Ordovician graptolites of Spitsbergen: Bulletin of the British Museum (Natural History) Geology, v. 36, p. 157–302.

Dean, W.T., 1989, Trilobites from the Survey Peak, Outram and Skoki Formations (Upper Cambrian–Lower Ordovician) at Wilcox Pass, Jasper National Park, Alberta: Geological Survey of Canada Bulletin, v. 389, 141 p.

Demeter, E.J., 1973, Lower Ordovician pliomerid trilobites from western Utah: Geology Studies Brigham Young University, v. 20, p. 37–65.

Elles, G.L., 1933, The Lower Ordovician graptolite faunas with special reference to the Skiddaw Slates: Summary of Progress of the Geological Survey, London 1932, p. 94–111.

Elles, G.L., and Wood, E.M.R., 1902, A monograph of British Graptolites. Part II—Dichograptidae: Monograph of the Palaeontographical Society, v. 56, p. 55–102.

Fortey, R.A., 1974, The Ordovician trilobites of Spitsbergen 1. Olenidae: Norsk Polarinstitutt Skrifter, v. 160, 129 p.

Fortey, R.A., 1975a, Early Ordovician trilobite communities: Fossils and Strata, v. 4, p. 331–352.

Fortey, R.A., 1975b, The Ordovician trilobites of Spitsbergen II. Asaphidae, Nileidae, Telephinidae, Raphiophoridae of the Valhallfonna Formation: Norsk Polarinstitutt Skrifter, v. 162, 207 p.

Fortey, R.A., and Bruton, D.L., 2013, Lower Ordovician trilobites of the Kirtonryggen Formation, Spitsbergen: Fossils and Strata, v. 59, 118 p.

Fortey, R.A., and Chatterton, B.D.E., 1988, Classification of the trilobite suborder Asaphina: Palaeontology, v. 31, p. 165–222.

Fortey, R.A., and Droser, M.L., 1996, Trilobites at the base of the Middle Ordovician, western United States: Journal of Paleontology, v. 70, p. 73–99.

Fortey, R.A., and Droser, M.L., 1999, Trilobites from the base of the type Whiterockian (Middle Ordovician) in Nevada: Journal of Paleontology, v. 73, p. 182–201.

Fortey, R.A., and Owens, R.M., 1987, The Arenig Series in South Wales: Bulletin of the British Museum (Natural History) Geology, v. 41, p. 69–305.

Fortey, R.A., and Owens, R.M., 1999, Feeding habits in trilobites: Palaeontology, v. 42, p. 429–465.

Fortey, R.A., Wernette, S.J., and Hughes, N.C., 2022, Revision of F. R. C. Reed's Ordovician trilobite types from Myanmar (Burma) and western Yunnan Province, China: Zootaxa, v. 5162, p. 301–356.

Hall, J., 1858, Note upon the genus *Graptolithus*, and description of some remarkable new forms from the shales of the Hudson River Group: Canadian Naturalist and Quarterly Journal of Science, v. 4, p. 139–150.

Hall, J., 1865, Figures and Descriptions of Canadian Organic Remains. Decade II, Graptolites of the Quebec Group: Montreal, Dawson Brothers, 154 p.

Harrington, H.J., 1957, Notes on new genera of Pliomeridae (Trilobita): Journal of Paleontology, v. 31, p. 811–812.

Hintze, L.F., 1953, Lower Ordovician trilobites from western Utah and eastern Nevada: Utah Geological and Mineralogical Survey Bulletin, v. 48, 249 p.

Hintze, L.F., 1954, *Presbynileus* and *Protopresbynileus*, new generic names proposed for *Pseudonileus* and *Paranileus* Hintze, preoccupied: Journal of Paleontology, v. 28, p. 16–20.

Hintze, L.F., 1973, Lower and Middle Ordovician stratigraphic sections in the Ibex area, Millard County, Utah: Geology Studies Brigham Young University, v. 20, p. 3–36.

Hopkins, M.J., 2019, Phylogenetic analysis and revision of the trilobite subfamily Balnibarbiinae (Olenidae): American Museum Novitates, v. 3928, 20 p.

Howell, B.F., 1935, Cambrian and Ordovician trilobites from Herault, southern France: Journal of Paleontology, v. 9, p. 222–238.

Jaekel, O., 1909, Ueber die Agnostiden: Zeitschrift deutsch Geologische Gesellschaft, v. 61, p. 380–401.

Ketner, K.B., and Alpha, A.G., 1992, Mesozoic and Tertiary rocks near Elko, Nevada: evidence for Jurassic to Eocene folding and low-angle faulting: evolution of sedimentary basins–eastern Great Basin: U.S. Geological Survey Bulletin 1988-C, 13 p.

Kobayashi, T., 1940, Lower Ordovician fossils from Caroline Creek, near Latrobe, Mersey River District, Tasmania: Papers and Proceedings of the Royal Society of Tasmania, v. 1939, p. 67–76.

Linnarsson, J.G.O., 1869, Om Vestergötlands Cambriska och Siluriska Aflagringar: Kongliga Svenska Vetenskaps–Akademiens Handlingar, v. 8, 89 p.

Marek, L., 1952, Contribution to the stratigraphy and fauna of the uppermost part of the Kraluv Dvur Shales: Sbornik Ustredniho Ustavu Geologicky, v. 19, p. 429–455.

McAdams, N.E.B. and Adrain, J.M., 2011, Systematics of the Lower Ordovician pliomerid trilobite *Hintzeia*, with species from the Great Basin, western USA: Zootaxa, v. 2910, p. 1–45.

McCormick, T., and Fortey, R.A., 1999, The most widely distributed trilobite species: Ordovician *Carolinites genacinaca*: Journal of Paleontology, v. 73, p. 202–218.

Nielsen, A.T., 1997, A review of Ordovician agnostid genera (Trilobita): Transactions of the Royal Society of Edinburgh Earth Sciences, v. 87, p. 463–501.

Norford, B.S., and Ross, R.J., 1978, New species of brachiopods and trilobites from the Middle Ordovician (Whiterockian) of southeastern British Columbia: Geological Survey of Canada Bulletin, v. 267, p. 1–11.

Owens, R.M., Fortey, R.A., Cope, J.C.W., Rushton, A.W.A, and Bassett, M.G., 1982, Tremadoc faunas from the Carmarthen district, South Wales: Geological Magazine, v. 119, p. 1–38.

Poulsen, C., 1927, The Cambrian, Ozarkian, and Canadian faunas of Northwest Greenland: Meddelelser om Grønland, v. 70, p. 237–343.

Raymond, P.E., 1913, Note on some new and old trilobites in the Victoria Memorial Museum, and revision of the species which have been referred to *Bathyurus*: Bulletin of the Victoria Memorial Museum, v. 1, p. 33–39, 51–69.

Raymond, P.E., 1925, Some trilobites of the lower Middle Ordovician of Eastern North America: Bulletin of the Museum of Comparative Zoology, Harvard University, v. 67, 180 p.

Ross, R.J., 1951, Stratigraphy of the Garden City Formation in northeastern Utah and its trilobite faunas: Bulletin of the Peabody Museum of Natural History, Yale University, v. 6, 161 p.

Ross, R.J., 1967, Some Middle Ordovician brachiopods and trilobites from the Basin Ranges, western United States: United States Geological Survey Professional Paper 523-D, 43 p.

Ross, R.J., 1972, Fossils from the Ordovician bioherm at Meiklejohn Peak, Nevada: United States Geological Survey Professional Paper 685, 47 p.

Ross, R.J., Hintze, L.F., Ethington, R.L., Miller, J.F., Taylor M.E., and Repetski, J.E., 1997, The Ibexian, lowermost series in the North American Ordovician: United States Geological Survey Professional Paper 1579, 50 p.

Salter, J.W., 1864, A monograph of the British trilobites from the Cambrian, Silurian and Devonian formations. Part 1: Monograph of the Palaeontographical Society, v. 16, 80 p.

Schrank, E., 1972, Proetacea, Encrinuridae und Phacopina (Trilobita) aus silurischen Geschieben: Geologie Beiheft, v. 76, 117 p.

Stevens, C.H., 1986, Evolution of the Ordovician through Middle Pennsylvanian carbonate shelf in east-central California: Geological Society of America Bulletin, v. 97, p. 11–25.

Vandenberg, A.H.M., 2017, *Didymograptellus kremastus* n. sp. a new name for the Chewtonian (mid Floian, Lower Ordovician) graptolite *D. protobifidus* sensu Benson & Keble, 1935, non Elles, 1933: Alcheringa, v. 42, p. 258–267.

Whittington, H.B., 1963, Middle Ordovician trilobites from Lower Head, western Newfoundland: Bulletin of the Museum of Comparative Zoology Harvard University, v. 129, 118 p.

Whittington, H.B., 1965, Trilobites of the Ordovician Table Head Formation, western Newfoundland: Bulletin of the Museum of Comparative Zoology Harvard University, v. 132, p. 275–442.

Whittington, H.B., 2000, *Stygina, Eobronteus* (Ordovician Styginidae, Trilobita): morphology, classification and affinities of Illaenidae: Journal of Paleontology, v. 74, p. 879–889.

Williams, S.H., and Stevens, R.K., 1988, Early Ordovician (Arenig) graptolites of the Cow Head Group, western Newfoundland, Canada: Palaeontographica Canadiana, v. 5, 167 p.