


Variation in eye lenses of two new Late Devonian phacopid trilobites from western Junggar, NW China

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Abstract.—The suborder Phacopina, characterized by schizochroal eyes, is among the most common groups of trilobites in Devonian strata. The marine sediments of the Famennian in western Junggar, Xinjiang, contain abundant low-disparity phacopids, which have previously been designated to *Omegops accipitrinus mobilis*, *Phacops circumspectans tuberculatus*, and *Omegops cornelius* on the basis of small numbers of poorly preserved specimens. In this study, these phacopids were identified as two new species of *Omegops*, *O. honggulelengensis* n. sp. and *O. xiangi* n. sp., on the basis of nearly 200 well-preserved specimens. The intraspecific variations of eye lenses of these specimens were quantitatively analyzed. On the basis of differences in the total number, number of dorsoventral files, and arrangement of the eye lenses, the absence of lenses in the middle part of the visual surface, and asymmetry of the number and/or arrangement of lenses in the two eyes, it was concluded that the reasons for intraspecific variation in eye lenses of Late Devonian *Omegops* from western Junggar were different from previously described factors but were likely genetic or embryological malfunctions or abnormalities caused by pathological conditions. Diversity of lenses in the schizochroal eyes shows that the number and arrangement of eye lenses was not stable in Phacopina. Therefore, many specimens are needed for quantitative study to determine the true characteristics of the number or arrangement of eye lenses when these features are used in the systematic taxonomy of Phacopina.

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Introduction

The suborder Phacopina is a common and globally distributed group of trilobites found in the Devonian sediments (Chlupáč, 1975; Crônier and François, 2014). Unlike the compound (holochroal) eyes of most trilobites, the eyes of the Phacopina are schizochroal, with surfaces that consist of numerous small lenses segmented by interlensar cuticles (sclerae); each lens is covered by a separated cornea (Clarkson, 1975; Clarkson et al., 2006). These lenses, in addition to providing members of the Phacopina with a more efficient visual system (Clarkson and Levi-Setti, 1975; Clarkson et al., 2006; Schoenemann, 2021), are used in systematic taxonomy, according to their number and arrangement (e.g., Clarkson, 1966, 1969; Eldredge, 1972; Zhou and Campbell, 1990; McKellar and Chatterton, 2009; Ghobadi Pour et al., 2018). However, quantitative study of eye lenses in some members of the Phacopina has shown that the lens numbers of the same species were not stable; their numbers could change with individual ontogeny and evolution (Thomas, 1998; Crônier and Clarkson, 2001), and even members of the same species living in different environments could show changes in the number of eye lenses (Crônier et al., 2004). Therefore, the emphasis on eye lens numbers in the taxonomic study of the Phacopina should be reconsidered. Quantitative

study of eye lens numbers will provide a new understanding of the changes to the visual system during ontogeny and evolution, as well as the influence of environmental factors on the visual system of the Phacopina (Clarkson and Tripp, 1982; Crônier et al., 2015).

Omegops Struve, 1976, one of the last phacopid trilobites, is found only in the Famennian and persists to the Devonian–Carboniferous boundary in many sections (Xiang, 1989; Brauckmann et al., 1992; Feist et al., 2021). Although *Omegops* has been found in Europe (Richter and Richter, 1933; Struve, 1976; Weber, 2000), North Africa (Alberti, 1972; Belka et al., 1999), Kazakhstan (Struve, 1976), Iran (Feist et al., 2003; Ghobadi Pour et al., 2018), Afghanistan (Farsan, 1998), and China (Xiang, 1981, 1989; Yuan and Xiang, 1998), the number of specimens reported in the past was small, and the eyes of some specimens were not completely preserved. Therefore, it was difficult to carry out quantitative study on the eye lenses, and it was unclear whether the eye lenses of this genus were as diverse as those of other members of the Phacopina (Ghobadi Pour et al., 2018).

In the Devonian, western Junggar belonged to the Kazakhstan Block in the Northern Hemisphere. The marine deposits are rich in trilobite fossils in this area, but most of these trilobites have been listed only briefly in the Geological Survey Reports from the 1960s to the 1980s or simply described in the Paleontological Atlas of Northwest China (Xinjiang part) (Zhang, 1983). Only a few species have been systematically studied (Xiang,

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1981; Guo, 1989; Yuan and Xiang, 1998; Crônier and Waters, 2022), including *Omegops* from the Hongguleleng Formation in western Junggar, Xinjiang. *Omegops* in the Hongguleleng Formation has low disparity but high abundance. I collected nearly 200 specimens with preserved eyes from this formation to conduct quantitative analysis on the numbers and distribution of their eye lenses and evaluate the possible causes for the diversity of these eye lenses.

Geological setting and materials

The Upper Devonian marine deposits in western Junggar include mainly three sedimentary types: marine and continental transitional facies (Tielieketi and Taketai formations), shallow marine facies (Hongguleleng Formation), and flysch facies (Taerbahatai Formation) (Gong and Zong, 2015). Among these, the Hongguleleng Formation has abundant fossils and can be divided into three lithologic members (Hou et al., 1993). The lower member comprises thin-bedded bioclastic limestones, shelly limestones, argillaceous limestones, calcareous siltstones, and shales. The middle member is composed of grayish-green and grayish-purple pyroclastic rocks and a few sandy limestones. The upper member is mostly grayish yellow calcareous clastic rocks with a few bioclastic limestones. The formation is Famennian in age (Ma et al., 2017; Zong et al., 2020). Trilobites are located mainly within the upper part of the lower member and the middle member, and a few trilobites extend near the Devonian/Carboniferous boundary (Suttner et al., 2014; Zong and Gong, 2017; Zong et al., 2020).

Xiang (1981) systematically described phacopid trilobites from the Hongguleleng Formation for the first time, but he did not document the specific horizon of these fossils. Judging from the preservation of trilobites, they seem to have been collected from the upper part of the lower member to the middle member of the revised Hongguleleng Formation (Zong et al., 2020). Yuan and Xiang (1998) described the other two species of phacopids from the Hongguleleng Formation and registered their horizon as the upper part of the Hongguleleng Formation. It should be noted that in the early stratigraphic classification of the Hongguleleng Formation (e.g., Xu et al., 1990; Zhao and Wang, 1990), the lower part was a set of continental sandy conglomerates (now incorporated into the underlying Zhulumute Formation), and the upper part was the marine beds (roughly equivalent to the revised Hongguleleng Formation), and Yuan and Xiang (1998) probably used the old stratigraphic division scheme. This inference can be drawn from their field specimen numbers of trilobites (i.e., AEJ 484, AEJ 460, and AEJ 563); all three numbers appear in the description of the Hongguleleng Formation measured by Xu et al. (1990). These three fossil horizons are located in the limestones from the upper part of the lower member, rather than the upper member/part of the revised Hongguleleng Formation (Zong et al., 2020). Their age corresponds roughly with the upper *Palmatolepis rhomboidea* to *Palmatolepis marginifera* conodont biozones of the Famennian (Suttner et al., 2014). More recently, Crônier and Waters (2022) described the phacopids of the Hongguleleng Formation that were collected from the Bulongguoer Reservoir section (type section of the Hongguleleng Formation) and the Aomage

locality by Waters in 1995 and 2005, and they believed these phacopids occurred in the *Palmatolepis crepida* conodont biozone. However, the stratigraphic data they provided were not consistent with the conodont biozones. They suggested that Bulongguoer Reservoir section exposes the marly beds of the lower part of the Hongguleleng Formation and dark bryozoan-rich shales and coarse crinoidal grainstones from the upper part of the Hongguleleng Formation. Their studied trilobites were collected from bed 5 of this section. The “marly beds” of the Hongguleleng Formation were first reported in the stratigraphic study of the Hongguleleng Formation by Waters and his partners (see Hou et al., 1993), equivalent to bed 4 of their measured Bulongguoer Reservoir section. Bed 4 and the overlying bed 5 are located in the upper part of the lower member of the revised Hongguleleng Formation, corresponding to Unit 2 of the Hongguleleng Formation divided by Suttner et al. (2014). The age is roughly equivalent to the upper *P. rhomboidea* to *P. marginifera* conodont biozones rather than the *P. crepida* biozone (Suttner et al., 2014). Moreover, the fossil horizon labeled by Crônier and Waters (2022) in figure 2 of their paper is a set of silty shales with a few limestone interlayers, equivalent to bed 3 of Hou et al. (1993) or the upper part of Unit 1 of Suttner et al. (2014); this horizon is trilobite free.

The specimens described as two new species (*Omegops honggulelengensis* and *O. xiangi*) in this study were collected from the bioclastic limestones and argillaceous limestones of the upper part of the lower member of the Hongguleleng Formation in the Buninuer and Bulongguoer sections, northern Hoxtolgay (Fig. 1). The stratigraphic extents of the two species are not exactly the same. Specifically, *Omegops honggulelengensis* also occurred in the middle member to top of this formation (from middle to top of the Famennian), but *O. xiangi* existed only in the upper part of lower member (middle Famennian) (Fig. 1.3). In addition to trilobites, abundant brachiopods, crinoids, corals, and bryozoans, smaller numbers of gastropods, bivalves, and cephalopods also occurred in the upper part of the lower member, deposited in a distal storm lithofacies sedimentary environment (Fan and Gong, 2016). All trilobites were preserved three-dimensionally. Apart from some enrolled and articulated exoskeletons, which represent corpses, most trilobites were scattered sclerites. Some thoraces articulated with pygidia, but with cephalae nearby, are identified here as exuviae (Zong et al., 2016; Zong and Gong, 2017). In other cases, the cephalae, thoraces, and pygidia were separated from each other, including some isolated thoracic segments. This preservation indicates that the corpses and exuviae of trilobites might have been carried by seawater before they were ultimately buried.

A total of 170 isolated cephalae, 15 articulated cephalae and thoraces, two enrolled exoskeletons, and nine exuviae consisting of articulated thoracopyga and isolated cephalae were collected in this study. Among 196 cephalae, 73 specimens had two intact schizochroal eyes, 62 specimens had only an intact left eye, and the other 61 specimens had only an intact right eye. All specimens were measured using vernier calipers or ImageJ software (Schneider et al., 2012), and the fossils were coated for photography with magnesium oxide; all photographs were captured using a Nikon D5100 camera with a Micro-Nikkor 55 mm F3.5 lens. The morphological terminology follows Whittington and Kelly (1997).

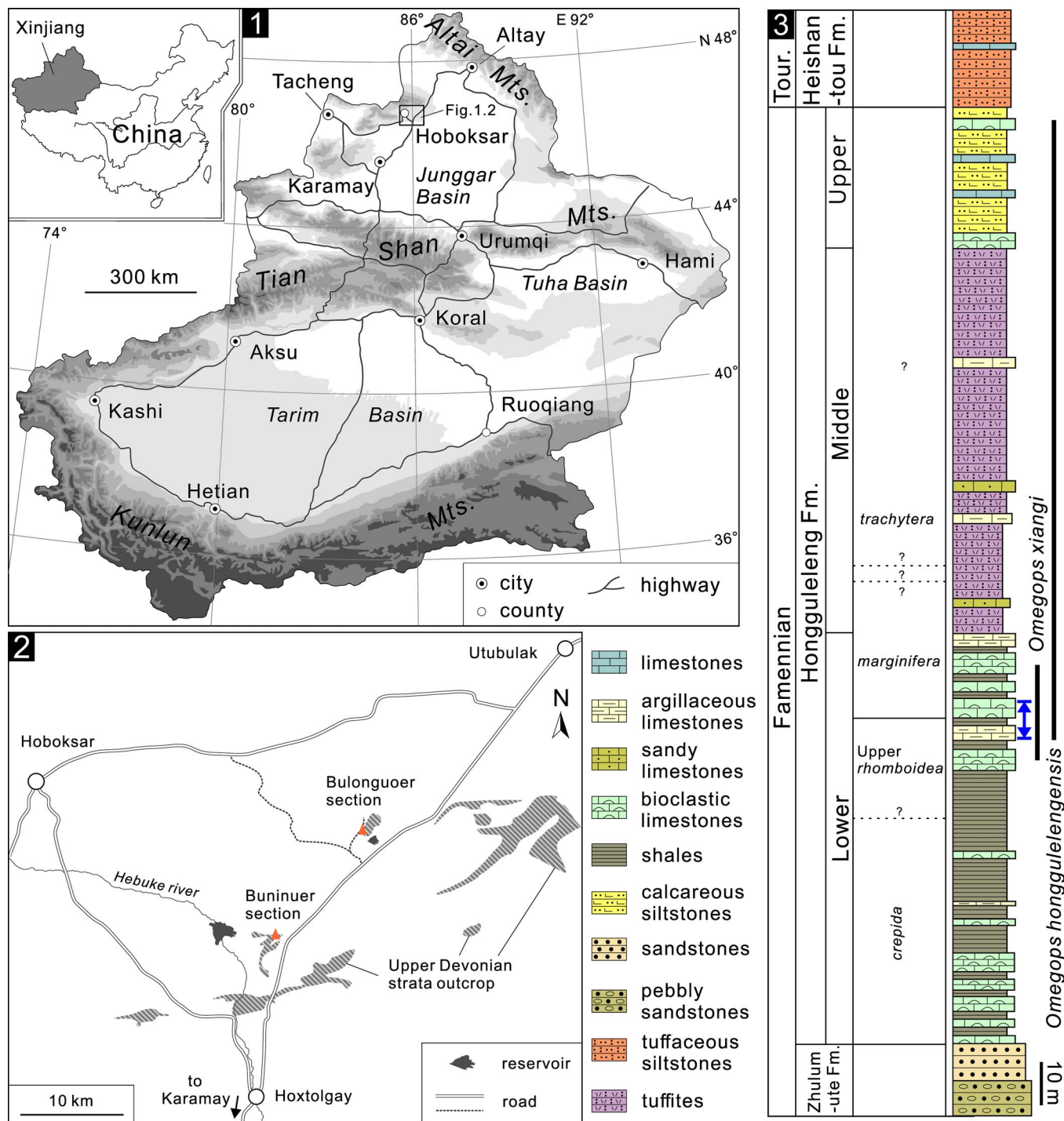


Figure 1. (1, 2) Fossil locality maps of the Late Devonian *Omegops* in western Junggar, Xinjiang. (3) Stratigraphic column of the Hongguleleng Formation, stratigraphic distribution of *Omegops*, and the horizon of samples collected in this study (blue arrow). Conodont biozones after Suttner et al. (2014) and Zhang et al. (2021).

Repository and institutional abbreviation.—BGEG = State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences (Wuhan).

Family Phacopidae Hawle and Corda, 1847
 Subfamily Phacopinae Hawle and Corda, 1847
 Genus *Omegops* Struve, 1976

Systematic paleontology

Order Phacopida Salter, 1864
 Superfamily Phacopoidea Hawle and Corda, 1847

Type species.—*Calymene accipitrina* Phillips, 1841

Omegops honggulelengensis new species
 Figures 2

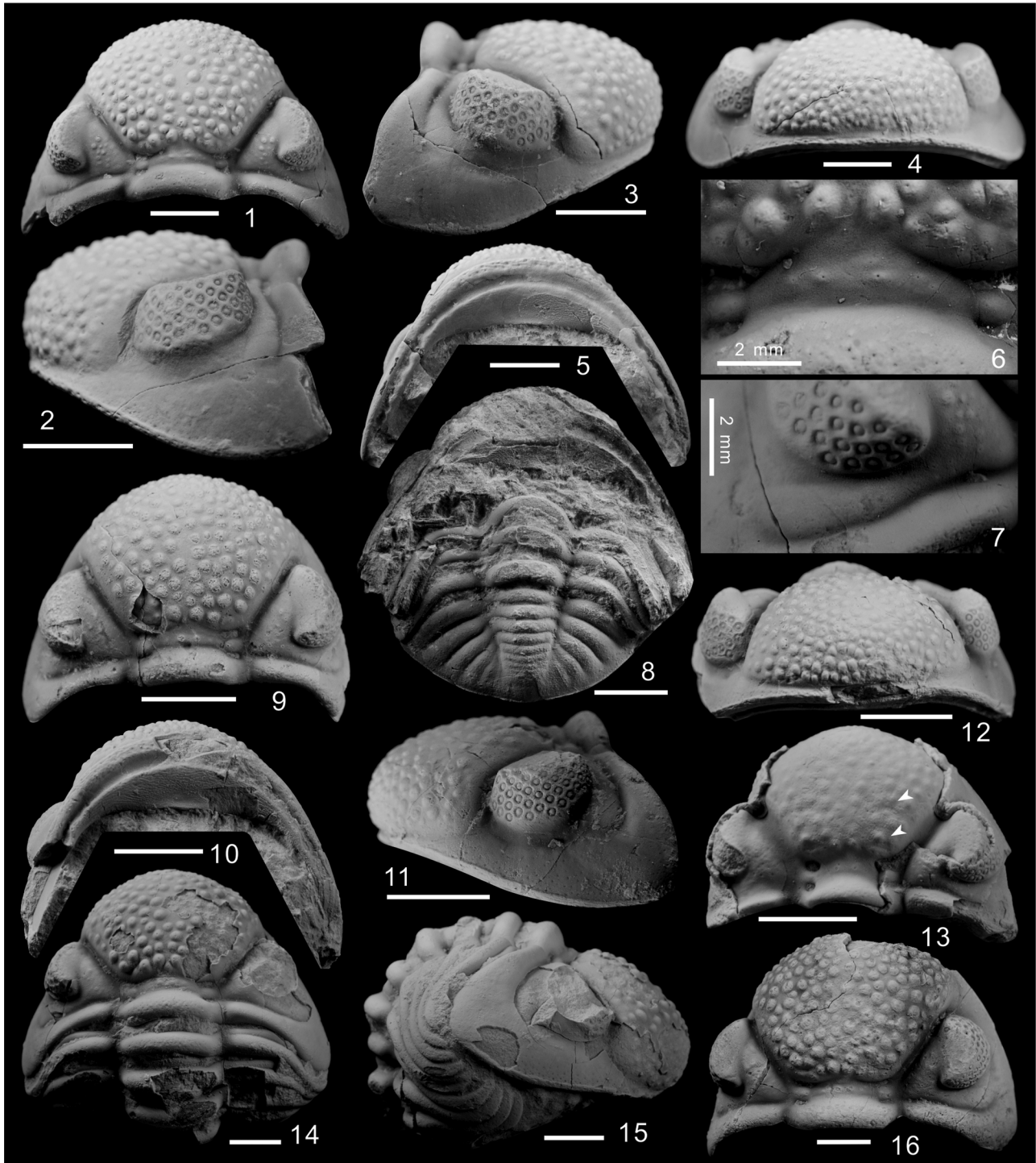


Figure 2. *Omegops honggulelengensis* n. sp. from the Upper Devonian Fammenian Hongguleleng Formation in western Junggar, NW China. (1–7) Cephalon (BGEG–HB–59): (1) dorsal view; (2) left side view; (3) right side view; (4) anterior view; (5) ventral view; (6, 7) close-ups of the intercalating ring (6) and postocular pad (7). (8) The exuvia consist of enrolled thoracopygon and isolated cephalon (BGEG–HB–55), ventral view of cephalon, and dorsal view of thoracopygon. (9–12) Cephalon (BGEG–HB–03): (9) dorsal view; (10) ventral view; (11) left side; (12) anterior view. (13) Incomplete cephalon (BGEG–HB–178), dorsal view; part of the shell was detached, revealing impressions of S2 and S3 (white arrows). (14, 15) Enrolled cephalon and thorax (BGEG–HB–05): (14) dorsal view; (15) right side view. (16) Cephalon (BGEG–HB–02), dorsal view. Specimen BGEG–HB–178 was collected from the Bulongguoer section; the other specimens were taken from the Bunier section. Scale bars = 5 mm unless otherwise specified.

1981 *Phacops (Omegops) accipitrinus mobilis* Xiang, p. 186, pl. 2, figs. 1–10.

1983 *Phacops accipitrinus mobilis*; Zhang, p. 547, pl. 182, figs. 15–16.

1998 *Phacops (Phacops) circumspectans tuberculatus* Yuan and Xiang, p. 29, pl. 1, fig. 3.

1998 *Phacops (Omegops) cornelius* (Richter and Richter); Yuan and Xiang, p. 33, pl. 1, fig. 2.

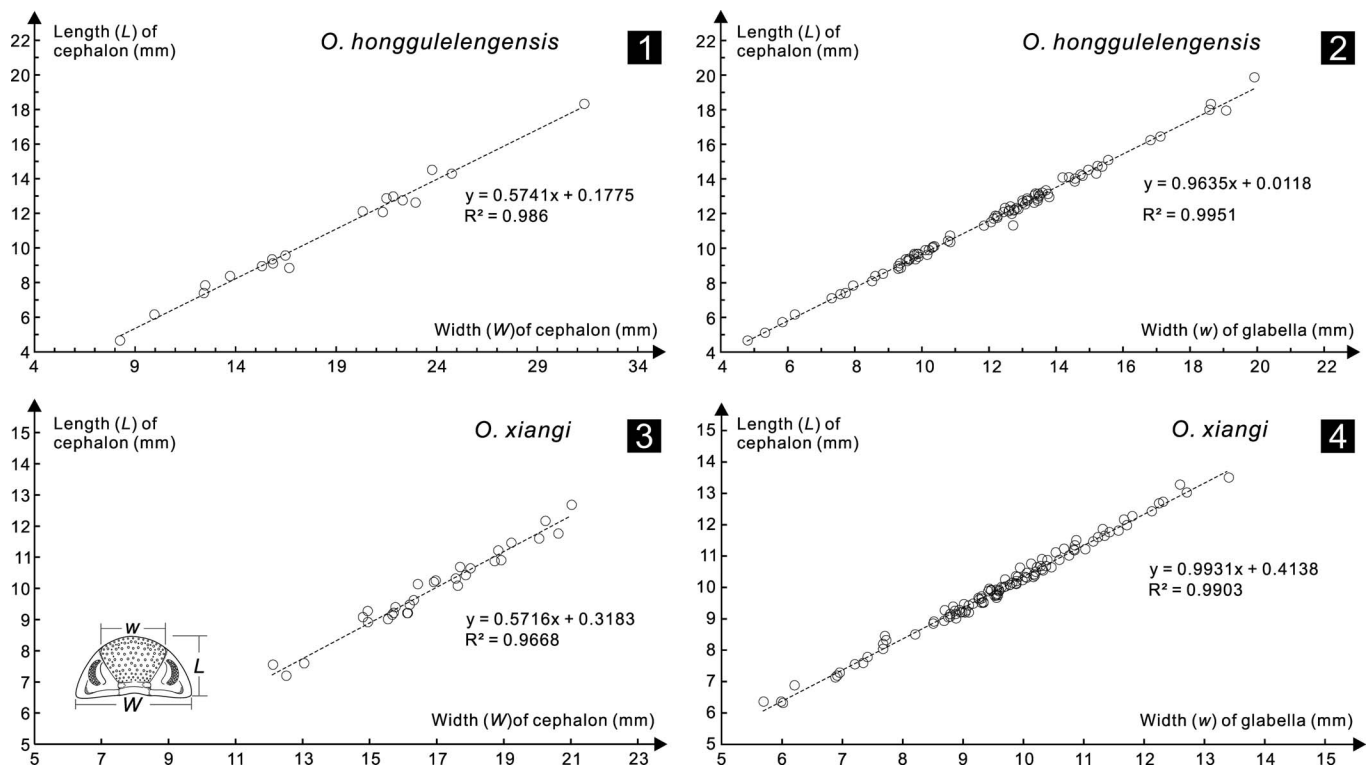


Figure 3. (1, 2) *Omegops honggulelengensis* n. sp.: (1) length versus width of cephalon; (2) length of cephalon versus maximum width of glabella. (3, 4) *Omegops xiangi* n. sp.: (3) length versus width of cephalon; (4) length of cephalon versus maximum width of glabella. From the Hongguleleng Formation in western Junggar, NW China.

2017 *Omegops cornelius* (Richter and Richter); Zong and Gong, p. 159, fig. 1A–C.

2020 *Omegops* sp.; Zong et al., p. 2470, fig. 7a–h.

2022 ?*Houseops* cf. *olonbulagensis* Crônier in Crônier and Waters, fig. 6a–c.

2022 Undetermined phacopid; Crônier and Waters, fig. 6d.

Holotype.—Nearly complete cephalon, BGEGB-HB-59 (Fig. 2.1–2.7), from the upper part of the lower member of the Hongguleleng Formation (middle Famennian), Buninuer section, northern Hoxtolgay, western Junggar, Xinjiang, China.

Diagnosis.—Species of *Omegops* with a broadly and evenly rounded anterior margin of the glabella. Glabellar axial furrows almost straight, posteriorly and medially divergent at 60–70°. The median part of the intercalating ring is barely visible, replaced by a pair of tubercles. Eyes moderately high with 45–49 lenses arranged in 15 dorsoventral files and with up to four lenses in one file. Occipital ring, postocular pad, and posterior border of cephalon are smooth. Thorax composed of 11 smooth thoracic segments. Pygidium with five pleural ribs, pygidial axis up to 85% of pygidial length, tapering posteriorly, with eight axial rings plus a short terminal piece. The surface of the pygidium is smooth.

Occurrence.—Upper part of lower member to top of the Hongguleleng Formation (middle to top of the Famennian), Buninuer and Bulongguoer sections, northern Hoxtolgay, western Junggar, Xinjiang, China.

Description.—Cephalon transverse, semicircular, ratio of length to width is 1:1.65–1.80 (Fig. 3.1; Supplemental file S1). Glabella subtrapezoid, slightly curved in front, and extending to the cephalic border (Fig. 2.1, 2.2, 2.4, 2.9, 2.11, 2.12); maximum glabellar width at the anterior termination of axial furrows. The width of cephalon is 1.60–1.75 times the maximum glabella width, while the latter is slightly larger than the length of the cephalon (Fig. 3.2; Supplemental file S1). The surface of the glabella is covered by irregularly arranged coarse tubercles that are larger and sparser in the glabella middle and rear and gradually become dense and smaller forward and to both sides (Fig. 2.1, 2.9, 2.16). S1 transverse, incised laterally, broadening and shallowing adaxially, and slightly upward sloping. S2 and S3 absent on the dorsal glabellar surface, but present faint impressions on the ventral side (Fig. 2.13); slightly arched, not connected in the middle part of glabella. Intercalating ring, transverse, weakly defined with a pair of smooth lateral tubercles (Fig. 2.6, 2.9, 2.16); the median part is barely visible, replaced by a pair of medium-sized tubercles and a few smaller tubercles (Fig. 2.6, 2.9). Occipital ring high, smooth, strongly vaulted transversely, slightly broadening adaxially (Fig. 2.9, 2.16). Posterior border curved posteriorly adaxially in dorsal view. Posterior border furrow gradually fading abaxially, curving along the rounded genal angles (Fig. 2.2, 2.11). Anterior border narrow, ridge-like, delineated by the narrow and shallow border furrow (Fig. 2.4, 2.11, 2.12). Axial furrows deep and broad, divergent at about 60–70°, almost straight posteriorly and medially. Palpebral furrows

moderately deep, subparallel, very gently curved outward (Fig. 2.1). Palpebral lobes long, crescent in outline, distinctly raised above the palpebral area, with the outer rim of faint densely spaced fine tubercles. Palpebral area of fixigena moderately broad, covered by a few fine to medium-size tubercles (Fig. 2.1). Eyes large, kidney-shaped. Visual surface steeply falling down laterally, mostly consisting of 45–49 lenses arranged in 15 dorsoventral files and up to four lenses in one file; the most common pattern is 3/4/4/4/4/4/4/3/4/3/3/2/2/1. Postocular area of the fixigena slightly inflated, narrow adaxially widening abaxially with a smooth postocular pad (Fig. 2.7). Vincular furrow evenly deep, evenly curved. Middle part of postvincular doublure (Feist et al., 2016) almost flat, slightly inward curved on both sides, about 2.5 times as wide as the vincular furrow, ornamented with faint terrace lines and fine tubercles (Fig. 2.5, 2.10).

Thorax composed of 11 smooth segments. Thoracic axial rings strongly arched, lacking lateral lobes (Fig. 2.14, 2.15), up to 36% as wide as whole segment in anterior segments and down to 32% in posterior segments. Anterior bands of thoracic pleurae narrow (exs. = exsagittal). Pleural furrow weakly defined abaxially, becoming prominent at the transition to a fulcrum, then gradually fading adaxially (Fig. 2.14). Posterior bands up to two times as wide as anterior bands.

Pygidium short, smooth, semielliptical; the ratio of length to width is 1:1.7–1.9. Pygidial axis conical, tapering posteriorly at 15–17°, almost 85% as long as pygidium and about 33% as wide as maximum pygidial width; eight axial rings plus a small terminal piece, separated by deep, almost transverse axial furrows. Axial furrows narrow and deep, moderately shallowing posteriorly. Pleural field gently vaulted, with five pleural ribs evenly bent posteriorly adaxially (Fig. 2.8). Three anterior pairs of the pleural furrows deep, posterior fourth pair significantly shallower. Pygidial border weakly defined without border furrow (Fig. 2.8).

Etymology.—After Hongguleleng Formation, which yielded the holotype of *O. honggulelengensis*.

Materials.—In addition to the holotype, assigned specimens including an exuvia consist of articulated thoracopygon and isolated cephalon (BGEG–HB–55), an articulated cephalon and thorax (BGEG–HB–05), and three cephalata (BGEG–HB–03, BGEG–HB–178, BGEG–HB–02).

Remarks.—This species was originally identified as a subspecies of *Omegops accipitrinus*, i.e., *Omegops accipitrinus mobilis* (= *Phacops (Omegops) accipitrinus mobilis*), by Xiang (1981). However, many of its characteristics are not consistent with the *Omegops accipitrinus* group, specifically, the postocular pad of *Omegops acc. accipitrinus* (Phillips, 1841) is ornamented with eight large tubercles, the glabellar axial furrows are posteriorly and medially divergent at 45–60°, the visual surface consists of 56–70 lenses, and the pleural field has six pleural ribs (Struve, 1976; Ghobadi Pour et al., 2018). In Xinjiang specimens, the postocular pad is smooth (Fig. 2.7), the glabellar axial furrows are posteriorly and medially divergent at 60–70°, the visual surface consists of 45–49 lenses, and the

pleural field has five pleural ribs (Fig. 2.8). In addition, the latter has a longer pygidial axis (85% versus 75% as long as pygidium). These characteristics distinguish it from other subspecies of *Omegops accipitrinus* (i.e., *Omegops acc. maretolensis* (Richter and Richter, 1933), *Omegops acc. bergicus* (Drevermann, 1902), and *Omegops acc. insolatus* Struve, 1976). *Omegops honggulelengensis* shows certain similarity to the Afghan *Omegops paiensis* Farsan, 1998 in cephalic and pygidial morphology, but the latter has 86 lenses on the visual surface with up to seven lenses in one file, which is obviously different from Xinjiang specimens. Although there is intraspecific variability in the number of eye lenses in some phacopid taxa (Crônier and Clarkson, 2001; Crônier et al., 2004, 2015), among 86 specimens of *Omegops honggulelengensis* preserved with visual surface, the largest number of lenses is only 53, which is far fewer than the number of lenses in *Omegops paiensis*.

Omegops honggulelengensis can also be distinguished from *Omegops cornelius* (Richter and Richter, 1933) by its smooth postocular pad, fewer eye lenses (45–49 versus 62), and five (not six) pleural ribs. Ghobadi Pour et al. (2018) named *Omegops tilabadensis* on the basis of the late Famennian specimens from northern Iran; *O. honggulelengensis* is very similar to it in terms of cephalic shape, number of eye lenses, and number of pleural ribs. The differences include the axial glabellar furrows diverge at an angle of about 60–70° (versus 40–45°), weak S2 and S3 impressions on the ventral side of the glabella, and a slightly shorter pygidial axis in *O. honggulelengensis*. In addition, the postocular pad is ornamented with eight tubercles, and the lateral lobes of the intercalating ring are ornamented with one pair of tubercles in Iranian specimens. However, the postocular pad and lateral lobes of *O. honggulelengensis* are smooth, and a pair of medium-sized tubercles and some smaller tubercles are arranged in the median part of the intercalating ring (Fig. 2.6). There are also differences between these two species in other ornamentations on the exoskeleton, i.e., the occipital ring, thoracic segments, pygidial axis, and pleural ribs of the Iranian specimens are covered with varisized tubercles, while these parts of the Xinjiang specimens are smooth (Fig. 2.1, 2.8, 2.14, 2.15). Xinjiang specimens have some similarity with *Omegops acc. accipitrinus* and *Omegops acc. maretolensis* from Afghanistan reported by Farsan (1998) in terms of the cephalic morphology, the number of eye lenses, and the number of pleural ribs. However, the latter two clearly do not belong to the *Omegops accipitrinus* group according to their number of eye lenses and pleural ribs, and Ghobadi Pour et al. (2018) questionably assigned them to *Omegops tilabadensis*.

Yuan and Xiang (1998) established a new subspecies of *Phacops circumspectans*, i.e., *Phacops circumspectans tuberculatus*, on the basis of an incomplete cephalon from the same horizon in the same region. This specimen is very similar to *O. honggulelengensis* in terms of cephalic and glabellar outlines, eye shape, and the decoration of the cephalon; the eye lens number is also within the variation range of *O. honggulelengensis*. The main difference lies in the fact that Yuan and Xiang (1998) believed that the former has a significant intercalating ring (especially the strongly convex median part). I reexamined the holotype of *Phacops circumspectans tuberculatus*

and found that there was an extruded rupture from the posterior part of the glabella to the occipital ring. I concluded that the so-called convex median part was an artifact formed by the extruded part of the posterior part of the glabella. Hence, I classify this specimen as *O. honggulelengensis* here. In addition, Yuan and Xiang (1998) described an enrolled cephalon and thorax and an isolated weathered pygidium from the same horizon and ascribed them to *Omegops cornelius*. This pygidium has five pleural ribs that should not be ascribed to *O. cornelius* (Ghobadi Pour et al., 2018); the first eight of the nine pygidial axes are clearer, but the ninth pygidial axis is poorly preserved, so it is difficult to exclude the artifact caused by weathering. The shape of this pygidium is very similar to the shape of my specimens, and I also assign it to *O. honggulelengensis*.

Crônier and Waters (2022) described one fragmented cephalon and one mostly exfoliated thoracopygon from the same horizon (upper *P. rhomboidea* to *P. marginifera* conodont biozones, rather than the *P. crepida* biozone) at Aomage locality (very close to Buninuer section) and identified them as ?*Houseops* cf. *H. olonbulagensis* and undetermined phacopid, respectively. The ratio of length to width of the cephalon and morphology of the intercalating ring of the former and the number of pleural ribs and the smooth thoracopygon of the latter are very similar to *O. honggulelengensis*, and I hereby classify them as such.

Omegops xiangi new species

Figure 4

- 1998 *Phacops (Omegops) cornelius* (Richter and Richter); Yuan and Xiang, p. 33, pl. 1, fig. 1.
 2000 *Omegops* sp.; Weber, p. 543, unfigured.
 2016 *Omegops cornelius* (Richter and Richter); Zong et al., p. 4, fig. 2 A–L.
 2022 *Clarksonops junggariensis* Crônier; Crônier and Waters, fig. 3a–s.

Holotype.—An exuvia consisting of articulated thoracopygon and isolated cephalon, BGEG–HB–04 (Fig. 4.1–4.4), from the upper part of the lower member of the Hongguleleng Formation (middle Famennian), Bulongguoer section, northern Hoxtolgay, western Junggar, Xinjiang, China.

Diagnosis.—Species of *Omegops* with a broadly and evenly rounded anterior margin of the glabella. Glabellar axial furrows almost straight, posteriorly and medially divergent at 45–55°. Intercalating ring is composed of the low median part and a pair of lateral lobes, and a pair of medium to large tubercles located on the median part. One medium-sized tubercle in the middle of S1. Occipital ring, postocular pad, and posterior border of cephalon are covered by fine tubercles. Eyes moderately high with 54–61 large lenses arranged in up to 15 dorsoventral files and with up to five lenses in one file. Thorax is composed of 11 segments ornamented with fine tubercles. Pygidium with six pleural ribs, pygidial axis up to 85% of pygidial length, tapering posteriorly, with eight axial rings plus a short terminal piece. The surface of pygidial axis and pleural ribs ornamented with fine tubercles.

Occurrence.—Upper part of the lower member of the Hongguleleng Formation (middle Famennian), Buninuer and Bulongguoer sections, northern Hoxtolgay, western Junggar, Xinjiang, China.

Description.—Cephalon transverse, semicircular, ratio of length to width is 1:1.65–1.75 (Fig. 3.3; Supplemental file S2). Glabella subtrapezoid, moderately vaulted, slightly curved in front, and extending to the cephalic border, maximum glabellar width at the anterior termination of axial furrows (Fig. 4.1, 4.5, 4.6, 4.10). The width of the cephalon is 1.71–1.81 times the maximum width of the glabella; the latter is slightly smaller than the length of the cephalon (Fig. 3.4; Supplemental file S2). The surface of the glabella is covered by irregularly arranged tubercles, which are composed of larger tubercles, and a few medium tubercles fill in the space among the larger ones (Fig. 4.1, 4.10, 4.12). S1 transverse, incised laterally, broadening and shallowing adaxially. S2 and S3 absent on the dorsal glabellar surface, but present clear impressions on the ventral side, straight but not connected in the middle part of glabella (Fig. 4.15). Intercalating ring, narrow, weakly defined with a pair of smooth lateral lobes and the low and flat median part (Fig. 4.1, 4.10); the median part ornamented with a pair of medium to large tubercles and a few smaller tubercles. A medium-sized tubercle near the intercalating ring in the middle of S1 (Fig. 4.7, 4.12). Occipital ring high, ornamented with dense fine tubercles (Fig. 4.1, 4.12). Posterior border transverse in the middle and curved posteriorly adaxially in dorsal view. Posterior border furrow narrow and deep, curving along the rounded genal angles (Fig. 4.6, 4.9). Anterior border narrow, ridge-like, delineated by the narrow and shallow border furrow (Fig. 4.13, 4.14). Axial furrows deep and broad, divergent at about 45–55°, straight posteriorly and medially. Palpebral furrows broad and shallow, very gently curved outward. Palpebral lobes crescentic in outline, distinctly raised above the palpebral area, with the outer rim of faint densely spaced fine tubercles. Palpebral area of fixigena moderately broad, slightly obliquely extends to posterior border furrow, covered by a few fine to medium tubercles (Fig. 4.1, 4.10, 4.12). Eyes large, kidney-shaped. Visual surface steeply inclined laterally, mostly consisting of 54–61 lenses arranged in 15 dorsoventral files, and up to five lenses in one file; the most common pattern is 4/5/4/5/4/5/4/4/4/4/3/3/3/3/2. Postocular area of the fixigena slightly inflated, narrow adaxially, widening abaxially with a distinct postocular pad covered with several small tubercles (Fig. 4.4, 4.9). Posterior border ornamented with dense fine tubercles (Fig. 4.6). Vincular furrow deep and broad, evenly curved. The middle part of postvincular doublure almost flat, slightly inward curved on both sides, about 2.5 times as wide as the vincular furrow, ornamented with faint terrace lines and fine tubercles (Fig. 4.11).

Thorax of 11 segments. Thoracic axial rings strongly arched, lacking lateral lobes (Fig. 4.1, 4.3, 4.12), up to 37% as wide as whole segment in anterior segments and down to 31% in posterior segments; ornamented by dense small tubercles (Fig. 4.1, 4.12). Anterior bands of thoracic pleurae narrow (exs.), smooth. Pleural furrow straight, slightly bend backward

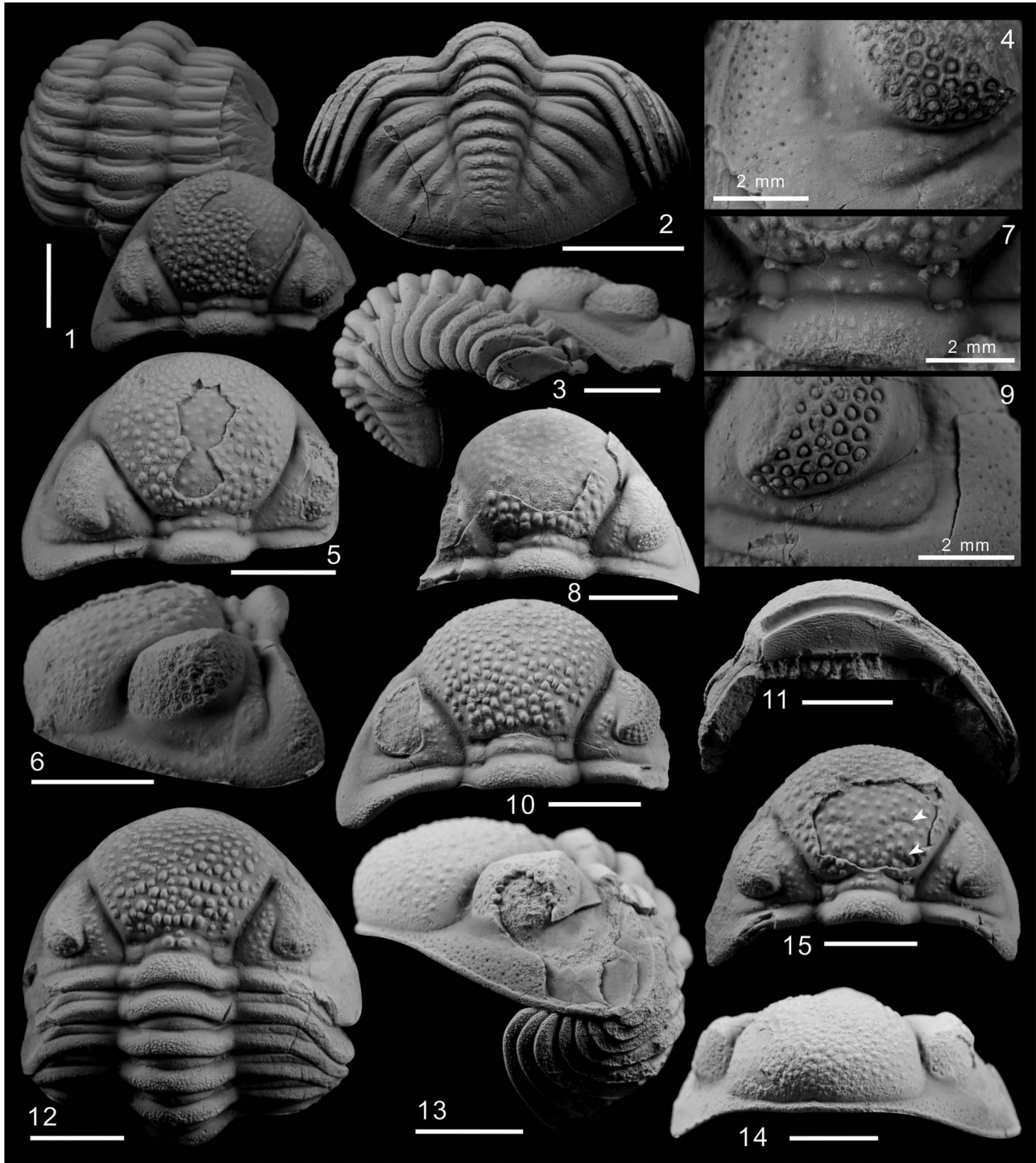


Figure 4. *Omegops xiangi* n. sp. from the Upper Devonian Famennian Hongguleleng Formation in western Junggar, NW China. (1–4) The exuvia consist of enrolled thoracopygon and isolated cephalon (BGEG–HB–04): (1, 3) dorsal and side views of exuvia; (2) dorsal view of pygidium and some thoracic segments; (4) close-up of left postocular pad. (5–7) Cephalon (BGEG–HB–49): (5) dorsal view; (6) side view; (7) close-up of intercalating ring. (8, 9) Incomplete cephalon (BGEG–HB–111): (8) dorsal view; (9) close-up of right postocular pad. (10, 11) Cephalon (BGEG–HB–32): (10) dorsal view; (11) ventral view. (12) Enrolled cephalon and thorax (BGEG–HB–68), dorsal view. (13, 14) Enrolled cephalon and thorax (BGEG–HB–16): (13) side view; (14) anterior view of cephalon. (15) Cephalon (BGEG–HB–86), dorsal view, part of the shell was detached, revealing impressions of S2 and S3 (white arrows). Specimen BGEG–HB–32 was collected from the Buninuer section; the other specimens were taken from the Bulongguoer section. Scale bars = 5 mm unless otherwise specified.

abaxially, becoming prominent at the transition to a fulcrum (Fig. 4.12). Posterior bands up to 2.5 times as wide as anterior bands, ornamented with fine tubercles, reducing adaxially and increasing abaxially (Fig. 4.12, 4.13).

Pygidium transverse, semioval; the ratio of length to width is 1:1.6–1.8. Pygidial axis conical, tapering posteriorly at 13–15°, almost 85% as long as pygidium and about 30% as wide as maximum pygidial width; eight axial rings plus a

small terminal piece, separated by slightly arched axial furrows. Axial rings covered with small tubercles. Axial furrows wide and deep, moderately shallowing posteriorly (Fig. 4.2). Pleural field gently vaulted, with six pleural ribs evenly bent posteriorly adaxially. Middle part of the pleural ribs covered with small to medium tubercles gradually fading outward and inward (Fig. 4.2). Three anterior pairs of the pleural furrows deep, posterior two pairs significantly shallower. Pygidial border smooth, weakly defined without border furrow.

Etymology.—For Chinese paleontologist Liwen Xiang, who first studied the trilobites from the Hongguleleng Formation.

Materials.—In addition to the holotype, assigned specimens including two articulated cephalons and thoraxes (BGEG-HB-16, BGEG-HB-68) and four cephalons (BGEG-HB-32, BGEG-HB-49, BGEG-HB-86, BGEG-HB-111).

Remarks.—This species was originally classified as *Omegops cornelius* by Yuan and Xiang (1998) on the basis of an enrolled cephalon and thorax. More well-preserved specimens were obtained in this study, and Weber (2000) provided some key information on the cephalon based on a topotype of *Omegops cornelius* (the holotype and paratype specimens were lost in World War II), allowing the Xinjiang specimens to be compared in greater detail with *Omegops cornelius*. Although there are some similarities between them (Yuan and Xiang, 1998), the differences are also obvious, reflected mainly in that the glabella of Xinjiang specimens is more convex, and the highest point is located in the middle of the glabella while the highest point of *Omegops cornelius* is located in the front of the intercalating ring (Weber, 2000). The cephalon of Xinjiang specimens are wider (length-to-width ratio is 1:1.65–1.75 versus 1:1.55–1.6), while the cephalon of *Omegops cornelius* is longer and narrower. The glabella of Xinjiang specimens are narrower (tr. = transverse) taking the width of the cephalon as reference (1:1.71–1.81 versus 1:1.5), and the maximum width of the glabella is slightly smaller than the cephalic length in Xinjiang specimens, while the maximum width of the glabella in *Omegops cornelius* is larger than the cephalic length (Weber, 2000). Another difference is that the axial glabellar furrows diverge at an angle of about 45–55° in Xinjiang specimens versus 45° in *Omegops cornelius*. In addition, the postocular pad of *Omegops cornelius* is club-like and expands outward, with dense tubercles on its surface that contact each other abaxially (Weber, 2000), while the Xinjiang specimens have a narrower, cudgel-shaped postocular pad with sparse tubercles on its surface that do not contact each other (Fig. 4.4, 4.9). The ornamentation of the intercalating ring is also different; in addition to two tubercles in the median part like *Omegops cornelius*, Xinjiang specimens have a medium tubercle near the intercalating ring in the middle of S1 (Fig. 4.7). Weber (2000) provided the arranged pattern of eye lens of the topotype of *Omegops cornelius*; it has 62 lenses on the visual surface arranged in 15 dorsoventral files and with up to five lenses in one file, i.e., 4/5/5/5/4/5/4/5/4/5/4/4/3/3/2. Although the eye lens numbers of Xinjiang specimens are similar, this arrangement is not seen in my collection of 110 specimens

with well-preserved visual surface (Supplemental files S2, S4). On the basis of these differences, I believe that the Xinjiang specimens should not be attributed to *Omegops cornelius*.

Omegops xiangi and *Omegops accipitrinus* are very similar in terms of axial glabellar furrows divergent angle, the eye lens number and arrangement, and the number of pleural ribs. According to the revised and measured data by Richter and Richter (1933), the latter has wider cephalon and glabella, and the maximum width of the glabella is larger than the cephalic length, while the glabella of *Omegops xiangi* is more convex forward, and the maximum width is slightly less than the cephalic length (Fig. 3.4). In addition, the intercalating ring of *Omegops acc. accipitrinus* is weakly defined with only a pair of lateral lobes. However, in the Xinjiang specimens, the median part of the intercalating ring is low and flat, and in addition to a pair of tubercles on the median part, there is a tubercle in the middle of S1 on the anterior side of the intercalating ring, which is arranged in a triangle with the two tubercles on the median part (Fig. 4.7, 4.12). In terms of pygidial morphology, the pygidium of *Omegops acc. accipitrinus* is wider (tr.) (width-to-length ratio is 1.9–2.16:1 versus 1.6–1.8:1). There is also a difference in the decorations of the postocular pad, which is smooth adaxially in *Omegops acc. accipitrinus* and ornamented with several large tubercles abaxially, but for Xinjiang specimens, the surface of the postocular pad is covered by several sparse and evenly distributed small tubercles. The ornamentation of the postocular pad of Xinjiang specimens is similar to *Omegops accipitrinus insolatus*, but there are distinct differences in the glabellar width, the convex degree of the frontal glabellar lobe, and the shape of the intercalating ring and its decorations, which can also distinguish the Xinjiang specimens from other subspecies of *Omegops accipitrinus*.

Omegops xiangi can be easily distinguished from Afghan *Omegops paiensis* according to the number and arrangement of eye lenses and the number of pleural ribs (Farsan, 1998). It is obviously different from *Omegops tilabadensis* from Iran in terms of the shape of the intercalating ring and its decorations, the ornamentation of the postocular pad, and the axial glabellar furrows divergent angle (Ghobadi Pour et al., 2018). Compared with *Omegops honggulelengensis* of the same area, the main differences are as follows: the glabella of the latter is slightly wider and the frontal glabellar lobe is less convex (the maximum width of the glabella is greater than the length of the cephalon), the median part of the intercalating ring is almost invisible, the number of eye lenses is between 45 and 49 (up to four lenses in one file), and the number of pleural ribs is five. By contrast, the maximum width of the glabella of *Omegops xiangi* is less than the cephalic length, and the intercalating ring can be divided into a pair of lateral lobes and a low and flat median part, the number of eye lenses is between 54 and 61 (up to five lenses in one file), and the number of pleural ribs is six. In addition, they are different in the ornamentation of the exoskeleton. The S1, postocular pad, occipital ring, posterior margin of cephalon, thoracic segment, pygidial axis, and pleural ribs are smooth in *Omegops honggulelengensis*, while those of *O. xiangi* are usually covered by varisized tubercles (Fig. 4.2, 4.4, 4.6, 4.7, 4.9, 4.12, 4.13).

Recently, Crônier and Waters (2022) described phacopids from the same horizon (upper *P. rhomboidea* to *P. marginifera* conodont biozones, rather than the *P. crepida* Biozone, see the

Geological setting and materials section) in the same area and established a new genus, *Clarksonops* (type species, *Clarksonops junggariensis*) on the basis of several fragmented and eroded specimens. They suggested that this new genus differs from genus *Omegops* or the *Omegops* specimens from the Hongguleng Formation mainly in that *Omegops* has a reduced intercalating ring and a distinct postocular pad. However, the character of the intercalating ring being divided into a median part and a pair of lateral lobes in *Clarksonops* is also present in some species of *Omegops* (e.g., *O. cornelius* Struve, 1976), and the postocular pad is clearly visible in some specimens of Crônier and Waters (2022, fig. 3e, i, o, p), so I do not think this new genus is sufficiently distinct from *Omegops*. Conversely, *Clarksonops junggariensis* is very similar to *Omegops xiangi* in terms of the length-to-width ratio of the cephalon, the shape and ornamentation of the intercalating ring, the arrangement of eye lenses, and the number of pygidial axial rings and pleural ribs (the number of pleural ribs is six instead of five, see Crônier and Waters, 2022, fig. 3r), so I think *Clarksonops* specimens from the Hongguleng Formation may belong to *Omegops xiangi*. Weber (2000) described an incomplete cephalon from the top of the Famennian in the Kornelimünster near Aachen, Germany. The shape of this cephalon is similar to *O. xiangi* (e.g., the maximum width of the glabella is less than cephalic length); the number of eye lenses and their arrangement are also within the variation range of the latter, but since there is no attached figure, it is difficult to achieve a more detailed comparison, so I provisionally classify it as *Omegops xiangi*.

Diversity of eye lenses in *Omegops*

Of the 86 *Omegops honggulelengensis* specimens, 31 had both eyes, 29 had only an intact left eye, and 26 had only an intact

right eye. The number of dorsoventral files on the visual surface of most specimens was 15, and a few specimens had only 14 or 13 files (Fig. 5.1, 5.2). The number of lenses in most files was up to four, but in a few specimens, that number reached five in the fourth and sixth files (Fig. 5.1, 5.2). For the total number of eye lenses, there were at least 40 and a maximum of 53; most specimens had lens numbers within the range of 45–49 (Fig. 6.1). Specimens with the same number of eye lenses often had diverse arrangement types (Supplemental file S3), but 49 eye lenses had only one pattern (i.e., 3/4/4/4/4/4/4/3/4/3/2/2/1), potentially representing the optimal arrangement of eye lenses in *O. honggulelengensis*. Another common arrangement type for eye lenses was 3/4/3/4/3/4/3/4/3/3/3/2/2/1 (45 lenses) (Supplemental file S3).

Among the 110 specimens of *Omegops xiangi*, 43 had both eyes well preserved, 32 had only an intact left eye, and 35 had only an intact right eye. Similar to *O. honggulelengensis*, the number of dorsoventral files on the visual surface of most *O. xiangi* specimens was 15, and a few specimens had 14 or 16 files (Fig. 5.3, 5.4). Most specimens had no more than five lenses in one file; however, a few specimens had up to six lenses in the second, fourth to sixth, and eighth files. The number of eye lenses varied greatly, ranging from 49 to 72, but most were concentrated between 54 and 61, and the numbers showed a normal distribution pattern (Fig. 6.2; Supplemental file S4). The most common eye-lens arrangement was 4/5/5/5/4/5/4/5/4/5/4/4/3/3/2 (57 lenses). Two additional arrangement patterns, 4/5/4/5/4/5/4/4/4/4/3/3/2/3/2 (56 lenses) and 4/5/4/5/4/5/4/4/4/3/4/3/3/2 (58 lenses), were also common (Supplemental file S4).

The diversity of eye lenses in *Omegops* is first reflected in the differences in the number of dorsoventral files. Although

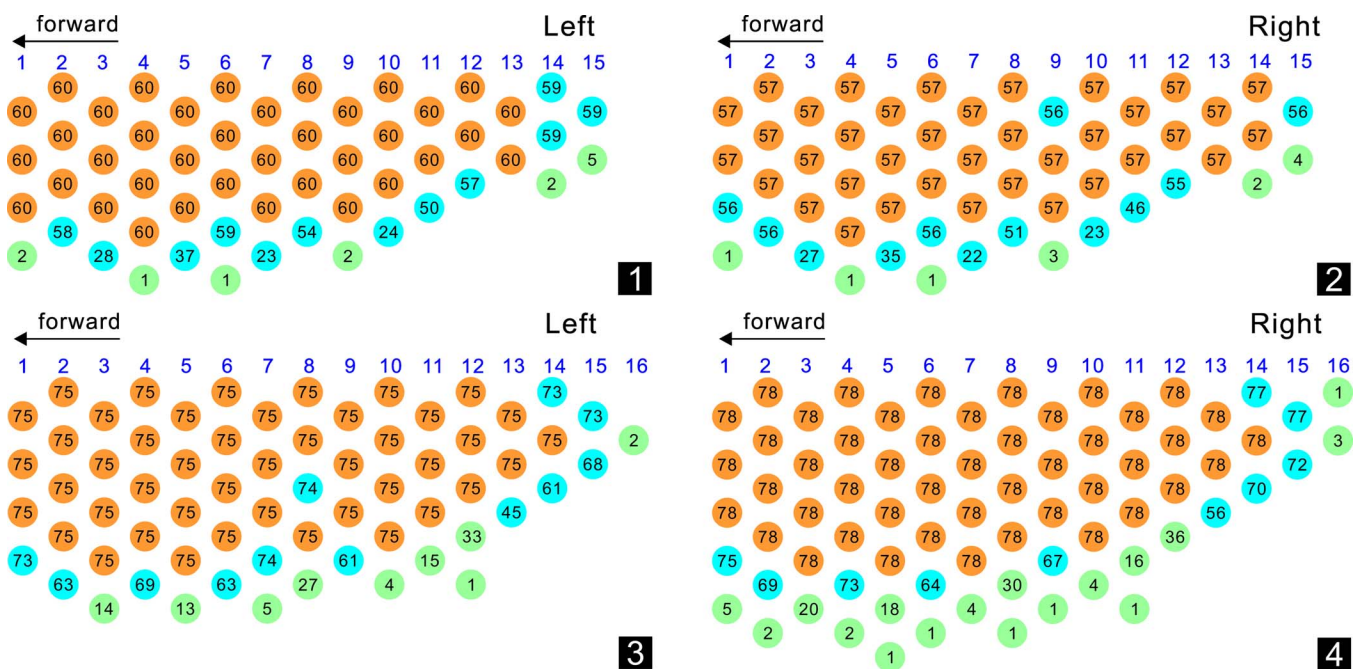


Figure 5. Schematic representations of eye lenses: (1, 2) *Omegops honggulelengensis* n. sp.; (3, 4) *Omegops xiangi* n. sp. From the Upper Devonian Hongguleng Formation in western Junggar, NW China. The number in each circle represents the number of individuals carrying a lens in that position; brown indicates that all individuals had a lens in this position, light blue indicates that some individuals lacked a lens in this position, and light green indicates that some individuals had a new lens in this position.

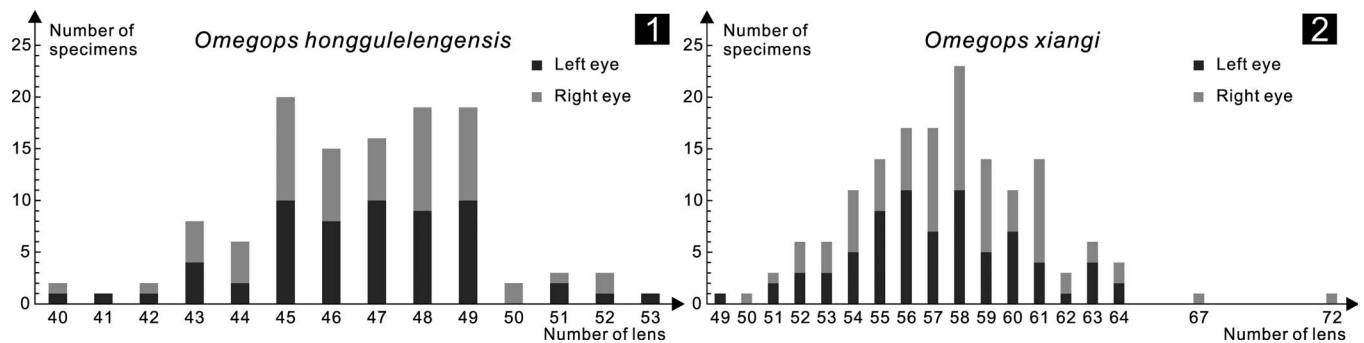


Figure 6. The frequency distribution of eye lens numbers: (1) *Omegops honggulelengensis* n. sp.; (2) *Omegops xiangi* n. sp. From the Upper Devonian Hongguleleng Formation in western Junggar, NW China.

most of the *Omegops* specimens had 15 files, a few specimens (6/196) had one file more or one file fewer, and a very small number of specimens (1/196) had two files fewer (Fig. 7.8; Supplemental files S1, S2). Some specimens showed an increase or decrease in the number of eye lenses in each file (Figs. 5, 7.3, 7.7). The numbers of lenses on the ventral and posterior sides of the visual surface were most likely to change, but a few changes occurred on the dorsal side or in the middle part (Figs. 5, 7.2, 7.6). A small number of specimens also had irregular arrangements of lenses because of the increased number of lenses (Fig. 7.9). In some specimens with both eyes preserved, the numbers or arrangements of eye lenses in the left and right eyes were different (Fig. 7.1, 7.2, 7.4, 7.5; Supplemental files S1, S2).

Discussion

The diversity of eye lenses in the suborder Phacopina has been identified in several genera, and individual growth and development have been interpreted as an important reason for this diversity (Thomas, 1998; Crônier and Clarkson, 2001). For these specimens from western Junggar, most with only cephalon preserved, it is difficult to distinguish between the meraspid and holaspid stages, but the cephalic size reflects the specimen's growth process. The eye-lens numbers of two new *Omegops* did not exhibit a distinctly linear change with the increase of cephalic length (Fig. 8). Therefore, the diversity of eye lenses of *Omegops* was likely not caused by individual growth. My material also reflects that the number of lenses in *Omegops* was likely fixed during certain ontogenetic stages and did not increase with the increase of body size.

Selwood and Burton (1969) cited differences in the number of eye lenses as a distinguishing feature of sexual dimorphism in the Devonian trilobite *Phacops schlotheimi schlotheimi* (Bronn, 1825) but also listed other differences in the exoskeleton. However, the sexual dimorphism of trilobites is often considered as difference in a single feature (Whittington, 1997), and those differences enumerated by Selwood and Burton (1969) are more likely to represent different species or subspecies (Ramsköld and Werdelin, 1991). Aside from the differences in the number of eye lenses, other characteristics of *Omegops* from Xinjiang are consistent. If the number of eye lenses were a secondary sexual characteristic, the eye lens

number would show two similar arrangements or a bimodal pattern (considering the numbers of females and males in the same population are likely to be similar), with no or almost no intermediate transitional form. However, the numbers of eye lenses of *Omegops* are generally close to a normal distribution. In addition, the lens number and/or arrangement differed between eyes in the same individual in some specimens; therefore, sexual dimorphism cannot explain the eye-lens diversity.

I propose that the lens diversity of *Omegops* in western Junggar is likely comparable to other Phacopina, reflecting intraspecific variation (Crônier et al., 2004, 2015), especially with an approximate normal distribution of the eye-lens number (Fig. 6). The causes of intraspecific variation are generally considered to be related to age or the living environment; that is, the number of lenses of specimens of the same species would change with evolution in different horizons or with different living environment (Crônier et al., 2004): the lens numbers of phacopids that lived in deep-water environments were found to be lower than those of phacopids that lived in shallow-water environments (Feist et al., 2009). In the Hongguleleng Formation, the water gradually deepened from the lower to the middle member. However, trilobites in the middle member are all flattened molds without well-preserved eyes. It is therefore not clear whether evolution and water depth affected the lens numbers of *Omegops*. The material presented here was collected from the same horizon in two proximal sites with a consistent sedimentary environment, and the intraspecific diversity of eye lenses cannot be explained by evolution or differences in the water environment.

Considering the different numbers and arrangements of eye lenses in the left and right eyes, the increase or decrease in the number of dorsoventral files, abnormal arrangements of lenses, and the missing lenses in the middle part of the visual surface in some specimens from Xinjiang (Figs. 5, 7), I propose that eye-lens diversity likely represents malformed specimens. Malformations are not rare in trilobites but consist primarily of body segments: shortened, missing, abnormally fused, or bifurcated. Such malformation may have been caused by predatory attacks, unsuccessful molting, genetic or embryological malfunctions, or pathological conditions (Owen, 1985; Babcock, 1993). More recently, abnormal ornamentations on exoskeletons have been identified as minor malformations that are believed to have been caused by developmental disorders (Bicknell and Smith,

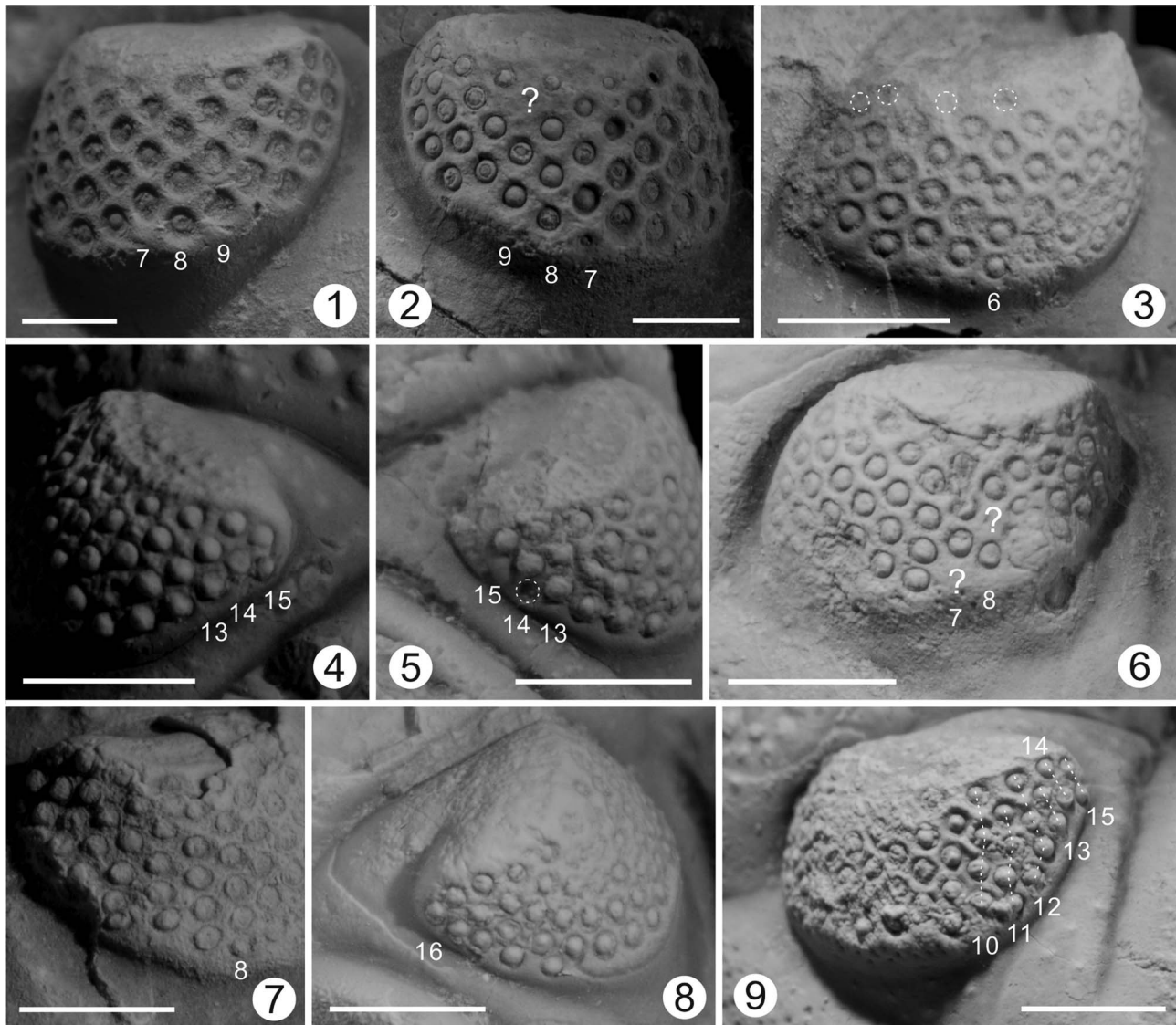


Figure 7. Abnormal arrangement of eye lenses in the Late Devonian *Omegops* from western Junggar, Xinjiang. (1, 2) *Omegops honggulelengensis* (BGEG–HB–02): (1) left eye; (2) right eye. Lens number is asymmetrical in the seventh and ninth files. (3) Left eye of *Omegops honggulelengensis* (BGEG–HB–123). Lens number is up to five in the sixth file. (4, 5) *Omegops xiangi* (BGEG–HB–157): (4) left eye; (5) right eye. There are two lenses in the fourteenth and fifteenth files in the left eye, whereas there are three lenses and one lens in the same positions of the right eye. (6) Left eye of *Omegops xiangi* (BGEG–HB–34), missing one lens each in the seventh and eighth files. (7) Right eye of *Omegops xiangi* (BGEG–HB–34). The maximum number of lenses reached six in the eighth file. (8) Right eye of *Omegops xiangi* (BGEG–HB–140) with 16 vertical files. (9) Left eye of *Omegops xiangi* (BGEG–HB–04). The lenses of the tenth to twelfth files are irregularly arranged. The numbers in the figure represent the numbers of dorsoventral files. Scale bars = 2 mm.

2021). There are few reported cases of ocular malformation (Fatka et al., 2021 and their references), and the numbers and arrangements of eye lenses are affected in some malformed specimens (Schoenemann et al., 2017; Fatka et al., 2021). However, in contrast to the Xinjiang specimens reported here, in addition to disturbance of the numbers or arrangements of lenses, the previously reported specimens had healed wounds on or near the visual surface, or the eyes became significantly smaller, which were interpreted as injuries caused by molting or predatory attacks (Schoenemann et al., 2017; Fatka et al., 2021). In these *Omegops* specimens, no injuries were identified on the visual surfaces except for minor abnormalities such as missing or newly added eye lenses. Therefore, injuries can be excluded as an explanation, but the abnormalities may have been related to

genetic or embryological malfunctions and/or pathological conditions (Owen, 1985; Babcock, 1993). An interesting phenomenon is that there were no visible deformities on the exoskeletons of these trilobites; this may have been related to the higher sensitivity of eyes to environmental factors compared with other organs as the eyes are an important visual system of arthropods.

Eye-lens diversity also occurred in a variety of other members of the Phacopina besides *Omegops* from western Junggar (e.g., Lorenz, 1991; Thomas, 1998; Crônier and Clarkson, 2001; Crônier et al., 2004, 2015; Rustán and Balseiro, 2016). Even in the systematic classification of Phacopina, it was possible to identify the diversity of eye lenses in a few specimens (Zhou and Campbell, 1990; McKellar and Chatterton, 2009).

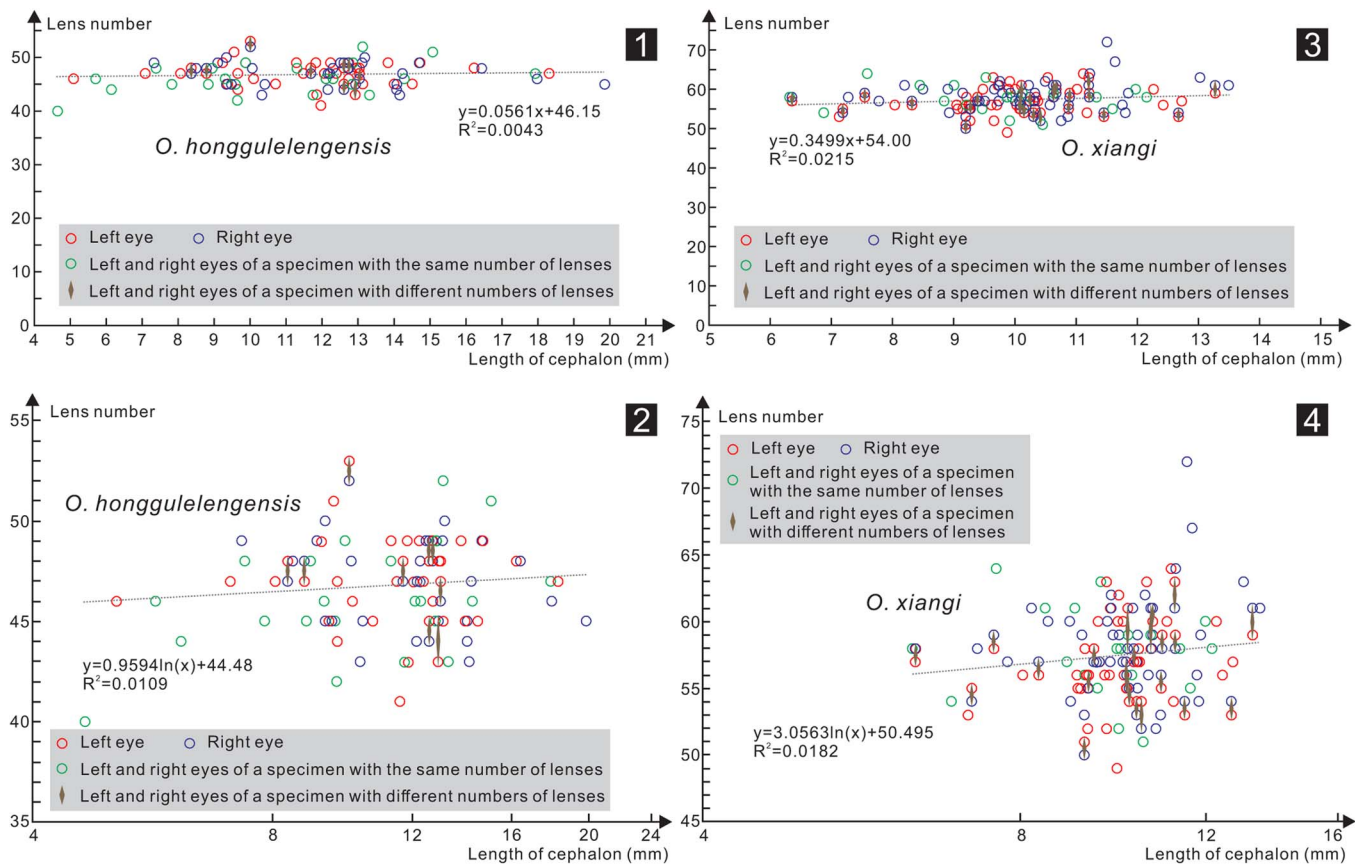


Figure 8. Plot of eye lens number versus cephalic length. (1, 2) *Omegops honggulelengensis* n. sp. (3, 4) *Omegops xiangi* n. sp. From the Upper Devonian Hongguleleng Formation in western Junggar, NW China.

Thus, in taxonomic study, a large number of specimens is needed to obtain quantitative study on the numbers and arrangements of eye lenses in the Phacopina. Using only a single specimen or a small number of specimens may lead to great errors.

Conclusions

On the basis of 196 well-preserved new specimens, Famennian (Late Devonian) *Omegops accipitrinus mobilis*, *Phacops circumspectans tuberculatus*, and *Omegops cornelius* from western Junggar, Xinjiang, were reclassified as two new species of *Omegops*: *O. honggulelengensis* and *O. xiangi*. The former is distinguished from other species of *Omegops* by its wider axial glabellar furrows divergent angle, smooth postocular pads, 45–49 eye lenses, and five pleural ribs. The main distinguishing features of the latter are the maximum width of the glabella less than the cephalic length, 54–61 eye lenses, distinctive ornamentation of the intercalating ring and postocular pads, and six pleural ribs. Their eye lenses had considerable diversity; the total numbers presented approximate normal distribution patterns, with variations characterized mainly by increases or decreases in the number of files, asymmetrical distribution of the lenses in the left and right eyes, abnormal arrangements, or missing lenses in the middle part of the visual surface. These variations could have been caused by genetic or embryological malfunctions and/or pathological conditions rather than

ontogeny, sexual dimorphism, evolution, or the water environment. My data also indicate that the eye-lens number did not increase with the increase of body size during certain growth stages of *Omegops*.

Acknowledgments

I appreciate much the constructive and critical comments from two anonymous reviewers, which aided in the further improvement of the manuscript. I thank Y.M. Gong, Z.H. Wang, R.Y. Fan, J.J. Song, Z. Shen, and X.S. Zhang for their help in the fieldwork. Thanks to D.J. Yuan and J.J. Song (NIGPAS) for their assistance when I observed the phacopids from the Hongguleleng Formation, which are housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. This work was supported by the National Natural Science Foundation of China (no. 42072041, 41702006).

Declaration of competing interests

The author declares none.

Data availability statement

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.sxksn037q>.

References

- Alberti, H., 1972, Ontogenie des Trilobiten *Phacops accipitrinus*: Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, v. 141, p. 1–36.
- Babcock, L.E., 1993, Trilobite malformations and the fossil record of behavioral asymmetry: Journal of Paleontology, v. 67, p. 217–229.
- Belka, Z., Klug, C., Kaufmann, B., Korn, D., Döring, S., Feist, R., and Wendt, J., 1999, Devonian conodont and ammonoid succession of the eastern Tafilalet (Ouidane Chebbi section), Anti-Atlas, Morocco: Acta Geologica Polonica, v. 49, p. 1–23.
- Bicknell, R.D.C., and Smith P.M., 2021, Teratological trilobites from the Silurian (Wenlock and Ludlow) of Australia: The Science of Nature, v. 108, n. 58, <https://doi.org/10.1007/s00114-021-01766-6>.
- Brauckmann, C., Chlupáč, I., and Feist, R., 1992, Trilobites at the Devonian–Carboniferous boundary: Annales de la Société Géologique de Belgique, v. 115, p. 507–518.
- Bronn, H.G., 1825, Über zwei neue Trilobiten-Arten zum *Calymene*-Geschlecht gehörig: Zeitschrift für Mineralogie, Taschenbuch, v. 1, p. 317–321.
- Chlupáč, I., 1975, The distribution of phacopid trilobites in space and time: Fossils Strata, v. 4, p. 399–408.
- Clarkson, E.N.K., 1966, Schizochroal eyes and vision in some phacopid trilobites: Palaeontology, v. 9, p. 464–487.
- Clarkson, E.N.K., 1969, On the schizochroal eyes of three species of Reedops (Trilobita: Phacopidae) from the Lower Devonian of Bohemia: Transactions of the Royal Society of Edinburgh, v. 68, p. 183–205.
- Clarkson, E.N.K., 1975, The evolution of the eye in trilobites: Fossils and Strata, v. 4, p. 7–31.
- Clarkson, E.N.K., and Levi-Setti, R., 1975, Trilobite eyes and the optics of Des Cartes and Huygens: Nature, v. 254, p. 663–667.
- Clarkson, E.N.K., and Tripp, R.P., 1982, The Ordovician trilobite *Calyptraulax bronngiartii* (Portlock): Transactions of the Royal Society of Edinburgh: Earth Sciences, v. 72, p. 287–294.
- Clarkson, E.N.K., Levi-Setti, R., and Horvath, G., 2006, The eyes of trilobites: the oldest preserved visual system: Arthropod Structure Development, v. 35, p. 247–259.
- Crônier, C., and Clarkson, E.N.K., 2001, Variation of eye-lens distribution in a new Late Devonian phacopid trilobite: Transactions of the Royal Society of Edinburgh, v. 92, p. 103–113.
- Crônier, C., and François A., 2014, Distribution patterns of Upper Devonian phacopid trilobites: paleobiogeographical and paleoenvironmental significance: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 404, p. 12–23.
- Crônier, C., and Waters, J.A., 2022, Late Devonian (Famennian) phacopid trilobites from western Xinjiang, Northwest China: Palaeobiodiversity and Palaeoenvironments, <https://doi.org/10.1007/s12549-022-00547-x>.
- Crônier, C., Feist, R., and Auffray, J.-C., 2004, Variation in the eye of Acuticryphops (Phacopina, Trilobita) and its evolutionary significance: a biometric and morphometric approach: Paleobiology, v. 30, p. 470–480.
- Crônier, C., Budil, P., Fatka, O., and Laibl, L., 2015, Intraspecific bimodal variability in eye lenses of two Devonian trilobites: Paleobiology, v. 72, p. 554–569.
- Drevermann, F., 1902, Ueber eine Vertretung der Etroengt-Stufe auf der rechten Rheinseite: Zeitschrift der Deutschen Geologischen Gesellschaft, v. 54, p. 480–524.
- Eldredge, N., 1972, Systematics and evolution of *Phacops rana* (Green, 1832) and *Phacops iowensis* Delo, 1935 (Trilobita) from the Middle Devonian of North America: Bulletin of the American Museum of Natural History, v. 147, p. 45–114.
- Fan, R.Y., and Gong, Y.M., 2016, Ichnological and sedimentological features of the Hongguleleng Formation (Devonian–Carboniferous transition) from the western Junggar, NW China: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 448, p. 207–223.
- Farsan, N.M., 1998, Das Etroengtium (Ober-Devon VI, Strunium) und die letzten Phacopinæ (Trilobita) im westlichen Zentral- und West-Afghanistan: Mainzer Naturwissenschaftliches Archiv Beiheft, v. 21, p. 17–37.
- Fatka, O., Budil, P., and Zicha, O., 2021, Exoskeletal and eye repair in *Dalmanitina socialis* (Trilobita): an example of blastemal regeneration in the Ordovician?: International Journal of Paleopathology, v. 34, p. 113–121.
- Feist, R., Yazdi, M., and Becker, T., 2003, Famennian trilobites from the Shotori Range, E-Iran: Annales de la Société Géologique du Nord, v. 10, p. 285–295.
- Feist, R., McNamara, K.J., Crônier, C., and Lerosey-Aubril, R., 2009, Patterns of extinction and recovery of phacopid trilobites during the Frasnian–Famennian (Late Devonian) mass extinction event, Canning Basin, Western Australia: Geological Magazine, v. 146, p. 12–33.
- Feist, R., Mahboubi, A., and Girard, C., 2016, New Late Devonian phacopid trilobites from Marhouma, SW Algerian Sahara: Bulletin of Geosciences, v. 91, p. 243–259.
- Feist, R., Cornée, J.-J., Corradini, C., Hartenfels, S., Aretz, M., and Girard, C., 2021, The Devonian–Carboniferous boundary in the stratotype area (SE Montagne Noire, France): Palaeobiodiversity and Palaeoenvironments, v. 101, p. 295–311.
- Ghobadi Pour, M., Popov, L.E., Omrani, M., and Omrani, H., 2018, The latest Devonian (Famennian) phacopid trilobite *Omegops* from eastern Alborz, Iran: Estonian Journal of Earth Sciences, v. 67, p. 192–204.
- Gong, Y.M., and Zong, R.W., 2015, Paleozoic stratigraphic regionalization and palaeogeographical evolution in Western Junggar, northwestern China: Earth Science—Journal of China University of Geosciences, v. 40, p. 461–484.
- Guo, L.Y., 1989, The discovery of *Plagiolaria* in the western Junggar region, Xinjiang: Xinjiang Geology, v. 7, p. 74–76.
- Hawle, I., and Corda, A.J.C., 1847, Prodom einer Monographie der böhmischen Trilobiten: Abhandlungen der Königlich-böhmischen Gesellschaft der Wissenschaften, v. 5, 176 p.
- Hou, H.F., Lane, N.G., Waters, J.A., and Maples, C.G., 1993, Discovery of a new Famennian echituberclerl fauna from the Hongguleleng Formation of Xinjiang, with redefinition of the formation, in Yang, Z.Y., ed., Stratigraphy and Paleontology of China, v. 2: Beijing, Geological Publishing House, p. 1–18.
- Lorenz, P., 1991, Die Variabilität und Ontogenie des Komplexauges von *Phacops granulatus* (Münster 1840) (Trilobita; Ober-Devon): Geologica et Palaeontologica, v. 25, p. 47–55.
- Ma, X.P., Zhang, M.Q., Zong, P., Zhang, Y.B., and Lü, D., 2017, Temporal and spatial distribution of the Late Devonian (Famennian) strata in the northwestern border of the Junggar Basin, Xinjiang, Northwestern China: Acta Geologica Sinica (English edition), v. 91, p. 1413–1437.
- McKellar, R.C., and Chatterton, B.D.E., 2009, Early and Middle Devonian Phacopidae (Trilobita) of southern Morocco: Palaeontographica Canadiana, v. 28, 110 p.
- Owen, A.W., 1985, Trilobite abnormalities: Transactions of the Royal Society of Edinburgh: Earth Sciences, v. 76, p. 252–272.
- Phillips, J., 1841, Figures and Descriptions of the Palaeozoic Fossils of Cornwall, Devon, and West Somerset: London, Longman, 231 p.
- Ramsköld, L., and Werdelin, L., 1991, The phylogeny and evolution of some phacopid trilobites: Cladistics, v. 7, p. 29–74.
- Richter, R., and Richter, E., 1933, Die letzten Phacopinæ: Bulletin du Musée Royal d'Histoire Naturelle de Belgique, v. 9, p. 1–19.
- Rustán, J.J., and Balseiro, D., 2016, The phacopid trilobite *Echidnops taphomimus* n. sp. from the Lower Devonian of Argentina: insights into infaunal molting, eye architecture and geographic distribution: Journal of Paleontology, v. 90, p. 1100–1111.
- Salter, I.W., 1864, A monograph of the British trilobites: Palaeontographical Society London, v. 16, 80 p.
- Schneider, C.A., Rasband, W.S., and Eliceiri, K.W., 2012, NIH Image to ImageJ: 25 years of image analysis: Nature Methods, v. 9, p. 671–675.
- Schoenemann, B., 2021, An overview on trilobite eyes and their functioning: Arthropod Structure & Development, v. 61, <https://doi.org/10.1016/j.asd.2021.101032>.
- Schoenemann, B., Clarkson, E.N.K., and Høyberget, M., 2017, Traces of an ancient immune system—how an injured arthropod survived 465 million years ago: Scientific Reports, v. 7, <https://doi.org/10.1038/srep40330>.
- Selwood, E.B., and Burton, C.J., 1969, Possible dimorphism in certain Devonian phacopids (Trilobita), in Westermann, G.E.G., ed., Sexual dimorphism in fossil metazoa and taxonomic implications: International Union of Geological Sciences, ser. A, p. 195–200.
- Struve, W., 1976, Beiträge zur Kenntnis der Phacopina (Trilobita), 9: *Phacops (Omegops)* n. sg. (Trilobita; Ober-Devon): Senckenbergiana Lethaea, v. 56, p. 429–451.
- Suttner, T.J., Kido, E., Chen, X., Mawson, R., and Waters, J.A. et al., 2014, Stratigraphy and facies development of the marine Late Devonian near the Boulongour reservoir, northwest Xinjiang, China: Journal of Asian Earth Sciences, v. 80, p. 101–118.
- Thomas, A.T., 1998, Variation in the eyes of the Silurian trilobites *Eophacops* and *Acaste* and its significance: Palaeontology, v. 41, p. 897–911.
- Weber, H.M., 2000, Neufund von *Omegops cornelius* Richter & Richter 1933 (Arthropoda, Trilobita) aus dem höchsten Oberdevon (“Strunium”) von Kornelimünster bei Aachen, Deutschland: Senckenbergiana Lethaea, v. 79, p. 541–546.
- Whittington, H.B., 1997, Mode of life, habits, and occurrence, in Kaesler, R.L., ed., Treatise on Invertebrate Paleontology, Part O, Arthropoda 1, Trilobita, Revised, Volume 1: Boulder, Colorado, Geological Society of America (and University of Kansas Press), p. 137–169.
- Whittington, H.B., and Kelly, S.R.A., 1997, Morphological terms applied to trilobites, in Kaesler, R.L., ed., Treatise on Invertebrate Paleontology, Part O,

- Arthropoda 1, Trilobita, Revised, Volume 1: Boulder, Colorado, Geological Society of America (and University of Kansas Press), p. 313–329.
- Xiang, L.W., 1981, Some Late Devonian trilobites of China: Geological Society of America, Special Paper, v. 187, p. 183–191.
- Xiang, L.W., 1989, Trilobites, in Ji, Q., Wei, J.Y., Wang, Z.J., Wang, S.T., Sheng, H.B., Wang, H.D., Hou, J.P., Xiang, L.W., Feng, R.L., and Fu, G.M., eds., The Dapoushang Section—An Excellent Section for the Devonian–Carboniferous Boundary Stratotype in China: Beijing, Science Press, p. 120–123.
- Xu, H.K., Cai, C.Y., Liao, W.H., and Lu, L.C., 1990, The Hongguleleng Formation and the Devonian–Carboniferous boundary in western Junggar: Journal of Stratigraphy, v. 14, p. 292–301.
- Yuan, J.L., and Xiang, L.W., 1998, Trilobite fauna at the Devonian–Carboniferous boundary in South China (S. Guizhou and N. Guangxi): Bulletin National Museum of Natural Science (Special Publication), v. 8, 281 p.
- Zhang, T.R., 1983, Trilobita, in Regional Geological Survey Team of Xinjiang Geological Bureau, Institute of Geological Sciences of Xinjiang Geological Bureau, and Geological Survey Team of Xinjiang Petroleum Bureau, eds., Palaeontological Atlas of Northwest China. Xinjiang, v. 2: Beijing, Geological Publishing House, p. 534–555.
- Zhang, X.S., Over, D.J., and Gong, Y.M., 2021, Famennian conodonts from the Hongguleleng Formation at the Bulongguoer stratotype section, western Junggar, Northwest China: Palaeoworld, v. 30, p. 677–688.
- Zhao, Z.X., and Wang, C.Y., 1990, On the age of the Hongguleleng Formation in Junggar Basin, Xinjiang: Journal of Stratigraphy, v. 14, p. 144–146.
- Zhou, Z.Q., and Campbell, K.S.W., 1990, Devonian Phacopacean trilobites from the Zhusilenghaierhan Region, Ejin Qi, western Inner Mongolia, China: Palaeontographica Abteilung A, v. 214, p. 57–77.
- Zong, R.W., and Gong, Y.M., 2017, Behavioural asymmetry in Devonian trilobites: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 476, p. 158–162.
- Zong, R.W., Fan, R.Y., and Gong, Y.M., 2016, Seven 365-million-year-old trilobites moulting within a nautiloid conch: Scientific Reports, v. 6, n. 34914, <https://doi.org/10.1038/srep34914>.
- Zong, R.W., Wang, Z.H., Fan, R.Y., Song, J.J., Zhang, X.S., Shen, Z., and Gong, Y.M., 2020, New knowledge on the Hongguleleng Formation and Devonian–Carboniferous boundary in western Junggar, Xinjiang: Acta Geologica Sinica, v. 94, p. 2460–2475.

Accepted: 10 April 2023