Development of the early Cambrian oryctocephalid trilobite *Oryctocarella duyunsensis* from western Hunan, China

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**Abstract.**—Abundant articulated specimens of the oryctocarine trilobite *Oryctocarella duyunsensis* from the lower Cambrian (Stage 4, Series 2) Balang Formation at the Bulin section in western Hunan Province, South China, permit the description of all meraspid degrees. The maximum number of thoracic segments observed in this collection is 11. Meraspid growth was accompanied by progressive and gradual change in overall form, and this animal showed an homonymously segmented trunk with variation in the number of pygidial segments during ontogeny. Such variation permits a variety of plausible explanations, but a model of successive instars defined by the number of thoracic segments, and in suborder by the number of pygidial segments, is highly unlikely to explain the growth pattern because it would result in the loss of trunk segments between some instars. Degree-based ontogenetic staging is compatible with the variation observed.

**Introduction**

Corynexochids are a major trilobite clade with representation both in the Cambrian and Ordovician evolutionary radiations of Trilobita, being found from lower Cambrian to Middle Devonian deposits. They are characterized by a fused hypostome and rostral plate (Rasetti, 1952; Fortey, 1990; Whittington, 1995, but also see Bergström et al., 2014). Ontogenies have been described for a number of corynexochide taxa (e.g., Walcott, 1916; Poulsen, 1958; Suvorova, 1964; Rasetti, 1967; Robison, 1967; Chatterton, 1971; Robison and Campbell, 1974; Opik, 1982; Lu and Qian, 1983; McNamara and Rudkin, 1984; Fortey and Chatterton, 1988; Lee and Chatterton, 2003; Park and Choi, 2009). Occasionally, their ontogenies are represented by abundant articulated exoskeletons. This combination of putative monophyly, long stratigraphic range, and good ontogenetic representation justifies a series of detailed case studies of the development of individual corynexochid species because of the clade’s potential for insights into how trilobite life cycles evolved at a relatively fine taxonomic scale. In particular, the abundance of articulated ontogenies for a number of early Cambrian corynexochids from South China permits exploration of how developmental schedules varied among contemporary and rather closely related species (e.g., McNamara et al., 2003, 2006; Dai et al., 2014, 2017; Hou et al., 2015; Lei, 2016; Du et al., 2020), and perhaps, as we suggest below, even within individual species. As opposed to the more traditional, typological approach necessitated where examples are few, these animals offer glimpses into the natural variability of development. This paper is the first of a series on the ontogeny of *Oryctocarella duyunsensis* from the Bulin section in western Hunan that will explore its growth dynamics. Herein we discuss the systematic and geological context of the occurrence and provide a descriptive account of its ontogeny as a foundation for the more quantitative approach of subsequent papers. Fundamental and unique features of its development are documented.

McNamara et al. (2003, 2006) conducted pioneering ontogenetic investigations into the development of seven oryctocephalid species from the Balang Formation at Balang, Guizhou Province, China: *Oryctocarella duyunsensis* Qian, 1961 (which those authors considered to be *Arthricocephalus chauveauei* Bergeron, 1899); *Oryctocarella balangensis* Lu and Qian in Yin and Li, 1978 (considered by them to be *Arthricocephalus xinzhaiheensis* Qian and Lin in Lu et al., 1974a); *Arthricocephalus xinzhaiheensis* (considered to be *Arthricocephalus balangensis* Lu and Qian in Yin and Li, 1978; *Arthricocephalus chauveauei* (considered to be *Arthricocephalus pulchellus* Zhang and Qian in Zhang et al., 1980); *Balangia balangensis* Qian, 1961; *Changapis elongata* Lee in Qian, 1961; and *Duyunaspis duyunsensis* Zhang and Qian in Zhou et al., 1977). Of these seven ontogenies, that of *Oryctocarella duyunsensis* was one of the two most complete. McNamara et al.’s (2003) analysis of the ontogeny of *Oryctocarella duyunsensis* illustrated specimens from each meraspid degree up to degree 9, thus laying the foundation for a more detailed exploration presented in this and forthcoming papers.

**Geological setting**

Oryctocephalids inhabited relatively deep-water, outer shelf and upper slope facies and were widely distributed in such settings across the Cambrian world (Whittington, 1995). *Oryctocarella*
is not only widely distributed in South China (including southeastern Guizhou, western Hunan, northern Jiangxi, northwestern Zhejiang, and eastern Jiangsu), but also occurs in northern Greenland and Siberia (Tomashpolskaya and Karpinski, 1961; Blaker and Peel, 1997; Yuan et al., 2006). On account of its worldwide occurrence, *O. duyunensis* plays an important role in correlating across different continents within the traditional late early Cambrian and thus carries potential utility for defining the traditional lower/middle Cambrian boundary (=Cambrian Stage 4, Series 2). Accordingly, the combination of abundant articulated specimens available from a relatively narrow stratigraphic interval and intraspecific variation in its segmentation schedule offers potential for examining geographic variation in developmental patterns not only within southern China, but also among collections made from different continents.

On the South China block, oryctoceratids occur in abundance in a band of dark mudstone facies, referred to as the Jiangnan Belt (Peng and Babcock, 2001), that represents the shelf-slope transition during Cambrian Stage 4 and the subsequent Wuluuan. The Balang Formation, which hosts the great majority of *O. duyunensis*, crops out sporadically within an area of ~15,000 km² in eastern Guizhou and western Hunan (Fig. 1). In some places it is ~300 m thick and constitutes a series of mudstones and siltstones differentiated most evidently by color and amounts of carbonaceous and carbonate material (Lei, 2016; Zhao et al., 2019; Du et al., 2020). The total range of *Oryctocarella duyunensis* within the Balang Formation is as much as 290 m (Zhao et al., 2019, fig 2; Du et al., 2020, fig. 1), and it also extends into the overlying Qingxudong Formation, but it is most common within an interval of ~150 m in the middle to lower part of the Balang Formation. The great majority of our collections were recovered from interbedded argillaceous, arenaceous, and calcareous mudstones in an interval only 4 m thick (Fig. 1) in the lower part of the Balang Formation at the Bulin section, 6.3 km northwest of Jiwei village, Huayuan County, Hunan Province, South China (GPS coordinates 28.355°N, 109.384°E). Biostratigraphically, these fossils occur in Cambrian Series 2, Stage 4, depending on how the boundary between those stages is ultimately defined (Zhao et al., 2019, fig. 2), and possibly also in Stage 3.

Due both to the fine scale of bedding in these deposits, which makes tracing an individual bedding surface along strike difficult, and the fact that many beds contain fossils, to date many collections made for ontogenetic analysis of Balang Formation trilobites have paid limited attention to recording exactly where in the section specimens studied originated. This limits our ability to infer possible controls on patterns of variation witnessed within the sample (see Hughes et al., 2020). For example, several studies have recognized different meraspid “morphs” of the same degree based on different numbers of pygidial axial rings (e.g., Dai et al., 2017; Du et al., 2020), but we cannot determine if these occurred at all or only some of the stratigraphic levels sampled. Nevertheless, the studies of trilobites and other fossils from the Balang Formation reveal some level of consistency in preservational features among the beds. Specimens occur along bedding planes, and are usually partially or completely articulated. While they are quite common along certain bedding surfaces, the distribution of individuals along bedding planes appears overall to be sporadic, without the distinctive clustering seen in some later trilobite assemblages (e.g., Hughes and Cooper, 1999; Karim and Westrop, 2002). The density of specimen occurrence varies among bedding planes, but *O. duyunensis* and other trilobites are common at many levels in the formation.

**Materials and methods**

Herein we adopt suggestions for a methodological standard in the description of articulated trilobite ontogeny as recommended by Hughes et al. (2020). The fossils were photographed with a Canon 5Ds Digital SLR camera equipped with a Canon EF-S 60 mm 1:2.8 macro lens, in lower-angle lighting from the northwest direction and higher-angle lighting from the northeast direction, or, for the specimens smaller than 5 mm in length, with a Leica M205C stereomicroscope with a Planapo 1.0X lens, and the associated Leica Application Suite v. 4.10 software.

**Materials.**—More than 1700 specimens of *O. duyunensis*, including 1276 complete specimens, were recovered during fieldwork in 2012–2014. Of these complete specimens, various subsets were identified for particular analyses (see below). A detailed taphonomic analysis of trilobite distribution in the Balang Formation has yet to be conducted, but articulated specimens are found both in dorsal-up and dorsal-down positions along individual bedding surfaces. While isolated sclerites do occur, the majority of specimens are articulated, although not all are complete (Figs. 2.6, 6.1). Rarely, specimens are preserved in which the free cheeks and attached hypostome has swung beneath the cranidium, resulting in an inverted position facing posteriorly, and situated beneath the anterior part of trunk (Figs. 3.9, 4.1). Whittington (1990) made convincing arguments that this posture likely represents the result of molting behavior. Quite a number of specimens are also “axial shields” (sensu Henningsmoen, 1975) with free cheeks, and apparently also hypostomes, absent (e.g., Figs. 2.6, 3.9, 6.1, 6.3, 6.5, 6.8, 6.9). These may represent exuviae, but could result from post mortem sclerite displacement. On the other hand, many specimens of complete dorsal shields appear to have all sclerites in place (and include cracks in the glabella indicating that the hypostome was in position during compaction (e.g., Figs. 3.2, 3.6, 4.5–4.8, 5.1, 5.3, 5.5, 5.8, 5.9, 6.2, 6.7). Some of these likely represent carcasses, although an exuvium could possibly assume the appearance of a completely articulated exoskeleton on burial (Whittington, 1990). There is no indication of mechanical sorting of any of sclerite associations.

**Measurements.**—All dimensions were measured in mm as straight-line distances, and the measurements of the sagittal length are made from the anterior cranidial margin to the posterior pygidial margin.

**Repository and institutional abbreviation.**—All described and illustrated specimens are deposited in the paleontological collections of the Geology Department of Northwest
University, Xi’an, China as part of the NWU-DYXJT 0001–1710 series.

**Systematic paleontology**

*Terminology.*—The morphological terms and abbreviations used in this paper follow Whittington and Kelly (1997). Abbreviations used in the descriptions include: exs. = exsagittal; LA = frontal glabellar lobe; sag. = sagittal; tr. = transverse; T = thoracic segment; T1–T11 = the first to the eleventh thoracic segment from anterior to posterior, respectively; D0–D11 = degrees 0 to 11, respectively.

Order Corynexochida Kobayashi, 1935
Suborder Corynexochina Kobayashi, 1935
Family Oryctocephalidae Beecher, 1897

*Remarks.*—This group is characterized by a distinctive, pit-like structure of the glabellar furrows (Raymond, 1913), although not all taxa commonly assigned to the group possess this feature.
Phylogenetic relationships within the group have been considered recently (Whittington, 1995; Sundberg and McCollum, 1997; Sundberg, 2006, 2014; Peng et al., 2018), with the group traditionally divided phenetically into those animals with prominent marginal spines (Oryctocephalinae) and those without (Oryctocarinae and cheiuroids). Oryctocarinae generally share the

Figure 2. Complete meraspids of *Oryctocarella duxunensis* (Qian, 1961) from the Cambrian Stage 4 Balang Formation, Huayuan County, western Hunan Province, South China. (1–3) Degree 0; (1) m0,2 morph with two pygidial segments (NWU-DYXJT 0878), (2, 3) m0,5 morph with five pygidial segments (NWU-DYXJT 0460, NWU-DYXJT 2091). (4–6) Degree 1; (4) m1,5 morph with five pygidial segments (NWU-DYXJT 0046), (5, 6) m1,6 morph with six pygidial segments (NWU-DYXJT 2021, NWU-DYXJT 1596). (7, 8) Degree 2; (7) m2,5 morph with five pygidial segments (NWU-DYXJT 0009), (8) m2,6 morph with six pygidial segments (NWU-DYXJT 0407). (9) Degree 3; m3,5 morph with five pygidial segments (NWU-DYXJT 0693). Scale bars = 0.2 mm. Arrows indicate the boundary between cephalon or thorax and pygidium.
Figure 3. Complete meraspids of *Oryctocarella duyunensis* (Qian, 1961) from the Cambrian Stage 4 Balang Formation, Huayuan County, western Hunan Province, South China. (1) Degree 2; m2,7 morph with seven pygidial segments (NWU-DYXJT 1382). (2, 3) Degree 3; (2) m3,6 morph with six pygidial segments (NWU-DYXJT 0688), (3) m3,7 morph with seven pygidial segments (NWU-DYXJT 1206). (4–6) Degree 4; (4) m4,5 morph with five pygidial segments (NWU-DYXJT 1114), (5) m4,6 morph with six pygidial segments (NWU-DYXJT 1405), (6) m4,7 morph with seven pygidial segments (NWU-DYXJT 0383). (7–9) Degree 5; (7) m5,5 morph five pygidial segments (NWU-DYXJT 1130), (8) m5,6 morph with six pygidial segments (NWU-DYXJT 1216), (9) m5,7 morph with seven pygidial segments (NWU-DYXJT 0475). Scale bars = 0.5 mm. Arrows indicate the boundary between thorax and pygidium.
pit-like glabellar furrows with the spiny Oryctocarinae, whereas
cheiruroids do not. Sundberg (2006) considered whether
Oryctocarinae and cheiruroids might root within the spiny
Oryctocarinae, and found a solution (Sundberg, 2006, fig. 2)
in which cheiruroids were sister taxa to a larger group that
included Oryctocarinae and Oryctocarinae. This placement
for Oryctocarinae was consistent with McNamara et al.’s
(2006) view that this group rooted within Oryctocarinae.
However, based on their long branch lengths, Sundberg (2006,
p. 65–66) rejected the placements of both Oryctocarinae and
cheiruroids that his analysis suggested, but did not evaluate
alternatives (such as whether Oryctocarinae and/or cheiruroids
are sister taxa to all Oryctocarinae), partly due to the
difficulty of identifying a suitable outgroup assessing basal
corynexochid relationships.

We find the phylogeny shown by Sundberg (2006, fig. 2)
interesting in that it placed oryctocarine trilobites in a more
crownward position than cheiruroids, and allied with members
of the genus Tonkinella. In addition to its absent or greatly
reduced marginal spines, Tonkinella is known for its reduced
number of holaspisid thoracic segments relative to spiny orycto-
carines, and has long been considered to be a paedomorphic
form (Hupé, 1953; McNamara, 1986b, p. 139). More specifically,
it has been considered progenetic (McNamara, 1986a) due to its reduced holaspisid segment count and small
size, both at onset of trunk maturity and at its maximum
size observed. These features suggest an abbreviated or con-
densed ontogeny compared to that of its putative oryctoche-
line ancestors. Such features also characterize oryctocarines
and cheiruroid trilobites when compared to sister taxa
among oryctocarines (Sundberg, 2014), and so a dominantly
progenetic origin might have applied to all. This would
explain both converge in form among them, and their
marked phenetic differences from spiny forms (and thus
long branch lengths). Hence, while we agree with Sundberg
(2006, 2014) that relationships among these taxa are far
from being confidently resolved, and have some reservations
about heterochronous accounts of trilobite phylogeny (Webster
et al., 2001; Hunda et al., 2006), the conclusion that processes
broadly defined as progenetic played a role in many oryctocar-
ines characters appears reasonable. Whatever oryctocarine sis-
ter taxon is ultimately resolved, it was apparently larger and
possessed more trunk segments at maturity than any
oryctocarine.

Subfamily Oryctocarinae Hupé, 1953
Genus Oryctocarella Tomashpolskaya and Karpinski, 1961

Type species.—Oryctocare siberica Tomashpolskaya in
Khalfin, 1960.

Oryctocarella duyunensis (Qian, 1961)

Figures 2–6

1961 Arthricocephalus duyunensis Qian (part), p. 97, pl. 1, fig.
19, pl. 2, figs. 5, 7, 8, 10, ?fig. 9; non pl. 1, fig. 20, pl. 2, fig. 6.
For synonymy up to 2017 see Peng et al. (2017, p. 951).

2019 Oryctocarella duyunensis (Qian, 1961); Zhao et al., fig.
3b, e.
2020 Arthricocephalus chauveaui Bergeron, 1899; Du et al.,
figs. 3–5.

Holotype.—Incomplete exoskeleton NIGP 11484 (Qian, 1961,
pl. 2, fig. 8) from the Balang Formation, Duyun, eastern
Guizhou, South China.

Remarks.—There has been recent debate about the correct name
for the species considered herein. Some authors have applied the
name A. chauveaui (e.g., Zhou et al., 1977; Zhang et al., 1980;
Blaker and Peel, 1997; McNamara et al., 2003; Yuan et al.,
2006, Du et al., 2020) to fossils from the Balang Formation
that we consider belong to Oryctocarella duyunensis.
Bergeron (Bergeron, 1899) first described A. chauveaui based
on the material collected by M. Chauveau from the lower
Cambrian Balang Formation in Tongren County, Guizhou
Province, China. It differs notably from Oryctocarella by
possessing an anteriorly expanded rather than cylindrical
(or parallel-sided) glabella, glabellar furrows that are
connected with dorsal furrows, fewer mature thoracic
segments (8), and a larger pygidium that is almost equal in
length and area to the craniid (see Peng et al., 2015, 2017
for a detailed consideration of these issues). On the basis of an
error in the published specimen number of the lectotype
published in the 1980s, Du et al. (2020) continued to apply
the name A. chauveaui to what is here considered to be
O. duyunensis, but without providing reasoning as to why the
acknowledged error should be further perpetuated. Here we
use Oryctocarella duyunensis following the arguments of
Peng et al. (2017).

Ontogeny

Of the 1276 complete specimens of O. duyunensis, 968 permit-
ted measurement of their sagittal dorsal length. These vary from
0.65 to 10.20 mm in length and constitute what we refer to as
“dataset 1.” In 643 of these specimens, the segment number in
both the thorax and pygidium can be counted with confi-
dence: this is “dataset 2” (Figs. 2–6) (see Supplementary
Material for summary statistics on this dataset). Here we recognize a series of
degrees based on the number of thoracic segments, that
include morphs (m) determined by the number of segments in
the pygidium. While these degrees are defined by the number
of thoracic segments, they are not all necessarily meraspis
degrees. The notation m2,5 indicates a specimen with two thor-
acic segments, because degree 9 is numerically the most abundant form.

Degree 0.—Exoskeleton 0.65–1.02 mm in length, represented
by nine articulated specimens (Fig. 2.1–2.3). Based upon the
available material, this degree can be subdivided into two
morphs according to the number of segments in the pygidia.

Morph m0,2. Exoskeleton sub-circular in outline (Fig. 2.1),
cephalon sub-elliptical in outline. Anterior margin curved
forward; anterior border indistinct. Glabella narrow and of low convexity, parallel-sided and slightly expanded forward, with frontal glabellar lobe (LA) reaching anterior border furrow; four pairs of conjoined glabellar furrows weakly impressed. Fixigena wide (tr.) and protuberant, twice width (tr.) of glabella. Occipital ring (LO) shorter (sag.) and wider (tr.) than L1, with posterior margin slightly curved backward. Facial suture indistinct. Eye ridge and palpebral lobe weakly defined. Posterior border furrow weakly defined. Genal angle obtuse. Trunk small, semi-elliptical in outline, with posterior margin concave medially. Axis narrow (tr.) and poorly segmented, probably small, semi-elliptical in outline, with posterior margin concave at least four or five articulated specimens (Figs. 2.7, 2.8, 3.1). Cephalon of moderate convexity. Posterior border furrow shallow. Pygidium proportionally larger than previous stage with the addition of new segments, semi-circular in outline; at least four or five axial segments can be defined.

Degree 1.—Exoskeleton 0.73–1.19 mm in length, represented by nine articulated specimens (Fig. 2.4–2.6). Cranidium semi-circular in outline. Anterior margin curved anteriorly; anterior border narrow and of uniform width (sag., exs.), curved laterally to palpebral lobe. Glabella narrow (tr.) from L1 to L3, and then slightly expanded anteriorly from L4 to LA, with anterior margin reaching anterior border furrow; glabellar furrows weakly impressed, S1–S3 transverse, conjoined, S4 shallow and extending anteromedially. Facial suture proparian, anterior branch short, strongly convergent forward, posterior branch extending posterolaterally. Eye ridge weakly defined, located anteriorly, close to anterior border; palpebral lobe narrow (tr.) and short (sag.). Fixigenal field obturant. Posterior margin straight laterally and then curved anterolaterally to intersect lateral margin. Posterior border extremely narrow (exs.); posterior border furrow shallow, extending anterolaterally.

Thorax with one segment. Axial ring weakly defined by shallow axial furrows, notably narrower than pleurae. Pleurae moderately flat, of equal length (exs.) laterally, with pleural spine short and obtuse; pleural furrow shallow.

Pygidium semi-circular in outline, with posterior margin concave medially, W-shaped in outline. Axis narrow (tr.), segments weakly incised, tapering evenly backward, with posterior tip close to posterior border. Pleural furrow weakly impressed. Two morphs are recognized in this degree, with five (m1,5; Fig. 2.4) and six (m1,6; Fig. 2.5, 2.6) segments in the pygidia.

Degree 2.—Exoskeleton 1.02–1.92 mm in length, represented by 55 articulated specimens (Figs. 2.7, 2.8, 3.1). Cranidium semi-circular in outline. As for Degree 1, except eye ridge moderately well defined, extending from LA or S4 and then curved posterolaterally; palpebral lobe small and curved outward, with posterior tip opposite S1. Thorax with two segments. Axis of moderate convexity, defined by shallow axial furrows. Pleurae moderately flat, gently shorter (exs.) and narrower (tr.) from T1 to T2. Pygidium with anterior margin extending posterolaterally and posterior margin concave medially, W-shaped in outline. Pygidal border narrow, weakly defined by shallow border furrow. Three morphs can be recognized, with five (m2,5; Fig. 2.7), six (m2,6; Fig. 2.8), and seven (m2,7; Fig. 3.1) segments in the pygidial axis.

Degrees 3–11.—Exoskeletons range from 1.38 to 10.20 mm in length (Figs. 2.9, 3.2–3.9, 4–5). In addition to the extra thoracic segments, morphological changes among the subsequent phases were subtle, consisting most obviously of a progressive decrease in the relative width of the fixigenae, increased curvature of the palpebral lobes, more firmly incised glabellar furrows, contraction of the pronounced posteromedial notch in the pygidium, along with relative lengthening of the postaxial margin compared to the axial length. Various morphs can be recognized in these degrees according to the number of pygidial segments.

Degree 3.—Exoskeleton 1.43–2.13 mm in length, represented by 84 articulated specimens (Figs. 2.9, 3.2, 3.3). Thorax with three segments. Three morphs are recognized, with five (m3,5; Fig. 2.9), six (m3,6; Fig. 3.2), and seven (m3,7; Fig. 3.3) segments in the pygidium.

Degree 4.—Exoskeleton 1.38–3.19 mm in length, represented by 109 articulated specimens (Fig. 3.4–3.6). Thorax with four segments. Three morphs are recognized, with five (m4,5; Fig. 3.4), six (m4,6; Fig. 3.5), and seven (m4,7; Fig. 3.6) segments in the pygidium.

Degree 5.—Exoskeleton 1.71–3.82 mm in length, represented by 117 articulated specimens (Fig. 3.7–3.9). Thorax with five segments. Three morphs are recognized, with five (m5,5; Fig. 3.7), six (m5,6; Fig. 3.8), and seven (m5,7; Fig. 3.9) segments in the pygidium.

Degree 6.—Exoskeleton 2.13–4.42 mm in length, represented by 136 articulated specimens (Fig. 4.1–4.5). Thorax with six segments. Three morphs are recognized, with five (m6,5; Fig. 4.1, 4.2), six (m6,6; Fig. 4.3, 4.4), and seven (m6,7; Fig. 4.5) segments in the pygidial axis.

Degree 7.—Exoskeleton 2.89–5.05 mm in length, represented by 165 articulated specimens (Fig. 4.6–4.9). Thorax with seven segments. Two morphs are recognized, with five (m7,5; Fig. 4.6, 4.7) and six (m7,6; Fig. 4.8, 4.9) segments in the pygidium.

Degree 8.—Exoskeleton 3.31–7.81 mm in length, represented by 268 articulated specimens (Fig. 5.1–5.3). Thorax with eight segments. Two morphs are recognized, with four (m8,4; Fig. 5.1) and five (m8,5; Fig. 5.2, 5.3) segments in the pygidial axis.

Degree 9.—Exoskeleton 4.55–10.05 mm in length, represented by 288 articulated specimens (Fig. 5.4–5.9). Thorax with nine segments. Exoskeleton oval in outline. Cranidium semi-elliptical in outline, with granules preserved in some specimens. Cranidium sub-trapezoidal in outline. Anterior margin curved forward; anterior border extremely narrow (sag.) and upturned, of uniform width (sag., exs.) laterally to lateral border; anterior border furrow shallow. Glabella narrow, sub-cylindrical in outline, defined by deeply incised axial furrow; parallel-sided from L1 to L3, and then slightly expanded forward from L4 to LA; LA slightly expanded anteriorly and rounded in front, with anterior margin across anterior border furrow and reaching anterior border; S1–S3 pit-like, not extending to axial furrow, shallowing inward across middle of glabella; S4 short and shallow, extending slightly convergent and forward. Occipital ring...
Figure 4. Complete meraspids of *Oryctocarella duyunensis* (Qian, 1961) from the Cambrian Stage 4 Balang Formation, Huayuan County, western Hunan Province, South China. (1–5) degree 6; (1, 2) m6,5 morph with five pygidial segments (NWU-DYXJT 0184, NWU-DYXJT 0540), (3, 4) m6,6 morph with six pygidial segments (NWU-DYXJT 0047, NWU-DYXJT 0418), (5) m6,7 morph with seven pygidial segments (NWU-DYXJT 0097). (6–9) Degree 7; (6, 7) m7,5 morph with five pygidial segments (NWU-DYXJT 1641, NWU-DYXJT 0304), (8, 9) m7,6 morph with six pygidial segments (NWU-DYXJT 0087, NWU-DYXJT 0533). Scale bars = 1 mm. Arrows indicate the boundary between thorax and pygidium.
Figure 5. Larger articulated specimens of *Oryctocarella duyunensis* (Qian, 1961) from the Cambrian Stage 4 Balang Formation, Huayuan County, western Hunan Province, South China. (1–3) Degree 8; (1) m8.4 morph with four pygidial segments (NWU-DYXJT 1252), (2, 3) m8.5 morph with five pygidial segments (NWU-DYXJT 0572, NWU-DYXJT 1319). (4–9) Degree 9; (4, 5) m9.3 morph with three pygidial segments (NWU-DYXJT 1079, NWU-DYXJT 1294), (6, 7) m9.4 morph with four pygidial segments (NWU-DYXJT 1325, NWU-DYXJT 0876), (8, 9) m9.5 morph with five pygidial segments (NWU-DYXJT 1636, NWU-DYXJT 1607); (9) shows a leading pygidial segment that appears disarticulated in the axial region, but remains fused in the pleural region. Scale bars = 1 mm. Arrows indicate the boundary between thorax and pygidium.
Figure 6. Large articulated specimens of *Oryctocarella duyunensis* (Qian, 1961) from the Cambrian Stage 4 Balang Formation, Huayuan County, western Hunan Province, South China. (1–6) Degree 10; (1–4) m10.3 morph with three pygidial segments (NWU-DYXJT 1670, NWU-DYXJT 1434, NWU-DYXJT 0010, NWU-DYXJT 1980), (5, 6) m10.4 morph with four pygidial segments (NWU-DYXJT 1813, NWU-DYXJT 0003). (7–9) Degree 11 specimens, m11.3, with three pygidial segments (NWU-DYXJT 1823, NWU-DYXJT 1329, NWU-DYXJT 1282). Scale bars = 1 mm. Arrows indicate the boundary between thorax and pygidium.
(LO) gently convex, shorter (sag.) and slightly wider (tr.) than transverse L1, with posterior margin curved backward, lacking an occipital spine or node; occipital furrow deeper abaxially and shallower adaxially, slightly curved backward. Eye ridge narrow and weakly defined, extending laterally from LA or S4, and then gently curved posterolaterally to palpebral lobe; palpebral lobe narrow, crescentic in outline, with anterior tip situated opposite L4 and posterior tip situated opposite L2. Facial suture proparian, anterior branches short, slightly convergent forward, cutting anterior border in a rounded curve.

Posterior margin extending laterally from axis curving slightly posterolaterally to genal angle. Posterior border wide (exs.) and convex, expanding abaxially; posterior border furrow shallow, extending anterolaterally. Fixigenal field broad, with maximum width across posterior border, twice width (tr.) of glabella. Librigena narrow in anterior portion and wider in posterior portion, lateral margin curved laterally.

Thorax with nine segments. Axis strongly narrower (tr.) than pleurae. Axial rings convex, defined by deeply incised axial furrows. Pleural lobe slightly convex (tr.), straight and parallel-sided.
represent cephalic, thoracic, and pygidial regions, respectively.

... by McNamara et al. (2003), in which they reported all degrees other than degree 3 had only one morph. In that study, the two morphs of meraspid degree 3 shared similar numbers of trunk segments, and differed only in size. Although McNamara et al. (2003) did not give details of their sample size, our analysis likely includes many more specimens. The presence of multiple morphs within meraspid degrees is supported by analysis of 216 specimens of the same species by Du et al. (2020) from the Lazizhai section, ~9 km WSW of Balang. In their study, the multiple morphs within degrees included degree 0 (four morphs), degree 1 (three morphs), degree 3 (two morphs), degree 4 (two morphs), degree 6 (two morphs), and degree 8 (two morphs).

Figure 8. Trunk segmentation schedule for an individual of Oryctocarella duxunensis (Qian, 1961) from Bulin that is compatible with the observed changing mean number of segments allocated to the pygidium during meraspid ontogeny (see Fig. 9). The last instar in this individual is shown to have 10 thoracic segments. Dotted lines represent forms hypothesized but not observed; gray, dark gray, and white represent cephalic, thoracic, and pygidial regions, respectively.

Our study of *O. duxunensis* has an unusually large sample, and provides information on the relative abundances of the various morphs within meraspid degrees (Fig. 9). In terms of pygidal segment numbers, the median morph of degrees 2–6 and of degree 9, in each of which we recognize three morphs, consistently has the largest sample size. Among earlier meraspid degrees, in no case does any morph exceed 66% of the sample size. The data also show that within meraspid degrees, segment-rich morphs are generally larger than their segment-poor equivalents.

These observations alone are insufficient to discriminate with confidence among plausible developmental scenarios. However, the facts that three morphs are found within many of the degrees, and that some specimens of earlier degrees had more trunk segments than specimens of the subsequent degree, exclude applying the two successive instars per degree model of Du et al. (2020) to *O. duxunensis* from Bulin. This is not simply because there are commonly three, rather than two, morphs within a degree, but also because a strictly progressive interpretation of successive instars within a meraspid degree, based on...
the number of pygidial segments (as proposed by Du et al., 2020) would require the number of trunk segments between successive degrees to have decreased, something unknown in living arthropods. Thus, it is highly unlikely that there were three successive instars within any meraspid degree of this animal beyond degree 0.

Phenotypic variance within the sample provides an alternative explanation for observed variation in number of pygidial segments expressed, with various types of phenotypic variation that might apply. For example, from degree 2 onwards, a possible interpretation of the data is the presence of three different morphotypes, each with a different number of pygidial segments at any given stage (Fig. 10). Alternatively, successive instars of the same individual trilobite might have shown different numbers of pygidial segments, even during the period of development in which pygidial segment accretion and release were in balance (the “stasis phase” of Simpson et al., 2005) (also see Hou et al., 2015, 2017 for a similar discussion). The mean segment number of all specimens per degree summarizes the average degree-based ontogenetic pathway (Fig. 11), and the segmentation schedule presented for an individual of this species from this outcrop (Fig. 8) was constructed to conform closely to this average. With the observed early onset of variation in the number of pygidial segments, a variety of standard degree-based staging models is compatible with the data observed.

Discussion

The various ontogenetic schemes proposed above make different predictions about the patterns of size frequency distribution of individuals observed in the dataset, and these will be explored in forthcoming analyses. Pending these, our results can be
compared with those of Du et al. (2020) for the same species. Differences include the following: (1) the sizes of comparable degrees in the Du et al. (2020) study are earlier ontogenetic stages are consistently larger than those described herein (for example, degree 2 in this study varies from 1.02–1.92 mm in length, whereas in their study, degree 2 varies from 2.06–2.76); (2) the number of morphs present and distinguished in meraspid degree 0 is four in their study and only two in ours; (3) the constancy in number of segments in the meraspid pygidium after degree 0 in their study as opposed to the changing mean shown in ours; and (4) the onset of the holaspis phase at nine thoracic segments in their sample, as opposed to the 9–11 segments in our sample, representing a possible example of polymorphism. The latter observation in particular might provide grounds for distinguishing their sample and ours as different species, but we have not chosen this interpretation because other large specimens assigned to the same species from additional localities (including the type locality) are reported to bear many as 12 segments, suggesting a range of subtle ontogenetically related variation in mature segment numbers among collections (Peng et al., 2017, p. 951), rather than the appearance of novel morphologies per se.

We interpret this pattern to represent local intraspecific modification of ontogenetic mode, but acknowledge that such variation was likely the substrate for microevolutionary shifts in character states of a kind commonly associated with species-level distinction. Intraspecific variation in thoracic segment numbers is not uncommon, especially among Cambrian
and later trilobites with homonymous trunks (e.g., Hughes et al., 1999, 2017). What is more significant, perhaps, is the ability to observe such subtle differences in ontogenetic patterning among close relatives—something that is achieved quite rarely in studies of fossils (e.g., Webber and Hunda, 2007; Hopkins and Webster, 2009; Webster, 2015), and which offers a glimpse into the developmental basis for ancient microevolutionary change.

All O. duyunensis at Bulin apparently had a higher mean number of pygidal segments early in ontogeny than their conspecific relatives from the Lazizhai section in Guizhou, but converged on a similar number later in their ontogeny. If not an artefact of preservation, this may be a further example of the documentation of subtle patterns of developmental variance in ancient fossils.

A surprising aspect of the development of O. duyunensis at Bulin is the fact that the forms with the largest number of thoracic segments (degrees 10 and 11) span a relatively short range of sizes. Further work will explore the growth dynamics of the size and shape of this species in detail.

Acknowledgments

We thank G. Fusco for extensive discussions that form the basis of ongoing work on this taxon. An anonymous reviewer, J. Holmes, T.-Y. Park, and B. Pratt are thanked for many helpful suggestions during evaluation. This work was funded by the National Key Research and Development Program (Grant No. 2017YFC0603101), Natural Science Foundation of China (Grants: 42072021, 41890844, 41890840, 41621003, 41330101, 41521061, 41290260), the 111 Project (Grant No. D17013), the Ministry of Science and Technology of China (Grant No. 2015FY310100), the National Commission on Stratigraphy of China (Grant No. DD20160120-04), the key project of the State Key Laboratory of Continental Dynamics (Grant No. 20121028), IGCP 668 project “The Stratigraphic and Magmatic History of Early Paleozoic Equatorial Gondwana and its Associated Evolutionary Dynamics,” the Strategic Priority Research Program of Chinese Academy of Sciences (Grant No. XDB26000000), Shaanxi Provincial Education Department (Program No. 17JK0762), Shaanxi Natural Science Basic Research Project (Grant 2018JMJ4038), and Key Scientific and Technological Innovation Team Project in Shaanxi Province. N.C.H.’s contribution was supported by the US National Science Foundation grant EAR-1849963 and by the Fulbright Academic and Professional Excellence Award 2019 APE-R/107, held at the Indian Statistical Institute, Kolkata.

Accessibility of supplemental data

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.qftzd0fn.

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