

ONTOGENY, SYSTEMATICS, AND EVOLUTION OF THE EFFACED EARLY CAMBRIAN TRILOBITES *PEACHELLA* WALCOTT, 1910 AND *EOPEACHELLA* NEW GENUS (OLENELLOIDEA)

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ABSTRACT—Although used in biostratigraphy and in studies of early Cambrian trilobite evolution, the olenelloid genus *Peachella* has received little research attention. The ontogenetic and evolutionary origins of its derived features—an effaced cephalon and grossly inflated genal spines—have remained mysterious. Based on examination of new and existing collections, *P. iddingsi* and *P. brevispina* are here described in detail, including aspects of their respective ontogenies and the first description of the thorax of *P. iddingsi*. A new monotypic genus, *Eopeachella*, is also described from recently collected material from the Delamar Member of the Pioche Formation, Nevada. *Eopeachella angustispina* n. gen. n. sp., is less derived and stratigraphically older than both *Peachella* species and bridges the morphological gap between *Peachella* and typical olenelloids. The study reveals that cephalic effacement was progressively attained during both ontogeny and phylogeny in the *Eopeachella* + *Peachella* clade. Comparative ontogeny with other olenelloids reveals that progressive effacement was a trend superimposed upon and independent of a conserved pattern of ontogenetic shape change in the glabella and did not represent a peramorphic “extension” of glabellar ontogeny. Genal spine inflation was also achieved progressively (in a proximal-to-distal direction) through both ontogeny and phylogeny in the *Eopeachella* + *Peachella* clade. Genal spine inflation that convergently arose in later trilobite groups may have been similarly ontogenetically dynamic. Discovery of *E. angustispina* and *P. brevispina* in the Delamar Member raises olenelloid diversity in this member to at least 20 species; a higher diversity than in any coeval unit.

INTRODUCTION

WITH ITS bizarrely inflated, balloon-like genal spines and generally effaced cephalic features, *Peachella* Walcott, 1910 represents one of the most distinctive genera of olenelloid trilobites. Although only known from the Laurentian Cordilleran margin in the southwestern United States (Fig. 1), the genus has considerable significance. It has biostratigraphic utility within the Laurentian upper “*Olenellus* Zone” (upper Dyeran, traditional “Lower Cambrian”): Palmer and Halley (1979) listed it as a characteristic element of their *Bristolia* Zonule, and the developing species-level biostratigraphic zonation scheme for the upper Dyeran (Webster, 2003) recognizes a zonule named for and defined by the first appearance of the type species, *Peachella iddingsi* (Walcott, 1884). *Peachella* was also included in a cladistic analysis of olenelloid trilobites (Lieberman, 1998, 1999), which has subsequently formed the basis for studies of Cambrian biogeography (Lieberman, 2002, 2003) and evolution (Smith and Lieberman, 1999). The genus represents one of the first to exhibit cephalic effacement and genal spine inflation, features which would later convergently evolve in numerous trilobite clades (see below) but which are poorly understood in terms of developmental origin and functional significance. Despite its importance, *Peachella* has received very little research attention, particularly in terms of the ontogenetic and evolutionary origins of its characteristic and derived morphology.

Recent field collections made by the present author, complemented with examination of previously collected specimens in museums, provide much additional information regarding the morphology and ontogeny of *P. iddingsi* and *P. brevispina* Palmer in Palmer and Halley, 1979, the only other species in the genus. They also reveal the existence of a new taxon here described as *Eopeachella angustispina* n. gen. n. sp., which is stratigraphically older than both *Peachella* species and which possesses rather more “normal,” tapered, genal spines and shallow but clear glabellar furrows. This new species therefore bridges the morphological gap between the derived *Peachella* species and their closest non-effaced olenelloid relatives such as *Bristolia* Harrington, 1956, *Nephrolenellus* Palmer and Repina, 1993, and *Paranephrolenellus* Webster, 2007c. This paper presents a comprehensive

(re)description of all *Peachella* and *Eopeachella* species, including the first detailed documentation of their respective ontogenies, and discusses the origin and evolutionary history of *Peachella*. Understanding of the ontogeny, morphology, and morphological variation of these species is important given their employment as biostratigraphic zone fossils, and offers insight into the development and evolution of cephalic effacement and genal spine inflation in trilobites.

SYSTEMATIC PALEONTOLOGY

Terminology.—Morphological terminology follows that of Whittington and Kelly (1997), with modifications to cephalic and thoracic terminology proposed by Webster (2007b) and Palmer (1998), respectively. Following Webster (2007c), genal spine advancement is measured by finding the point at which the axial furrow of the glabella is intersected by a transverse line drawn between the genal spine bases (i.e., the adaxial margins of the genal spine bases where they contact the posterolateral cephalic margin). The qualitative location of this point of intersection relative to the contact of glabellar lobes and furrows with the axial furrow is expressed in the species descriptions. The “slot position” of glabellar furrow S2 refers to a location along S2 approximately midway (tr.) between the sagittal axis and the axial furrow. Ontogenetic terminology is discussed below.

Phases of cephalic development.—Articulated specimens of *Peachella* are rare, and *Eopeachella* is known solely from disarticulated material. Small, isolated cephalons cannot be unambiguously assigned to a traditional post-protaspid subdivision of the trilobite life cycle (the meraspide and holaspide periods; Beecher, 1895; Raw, 1925; reviewed by Chatterton and Speyer, 1997). In this paper, ontogeny of the *Peachella* and *Eopeachella* cephalon is subdivided into the sequential phases of cephalic development previously identified in other olenelloids (Webster et al., 2001; Webster and Zelditch, 2005; Webster, 2007b, c). These phases (summarized below) offer an alternative scheme for subdividing olenelloid cephalic ontogeny without reference to trunk articulation.

Cephalons in phases 1 and 2 of development lack genal spines; the transition from phase 1 into phase 2 is characterized by a shift in the dynamic pattern of distance between the intergenal spine

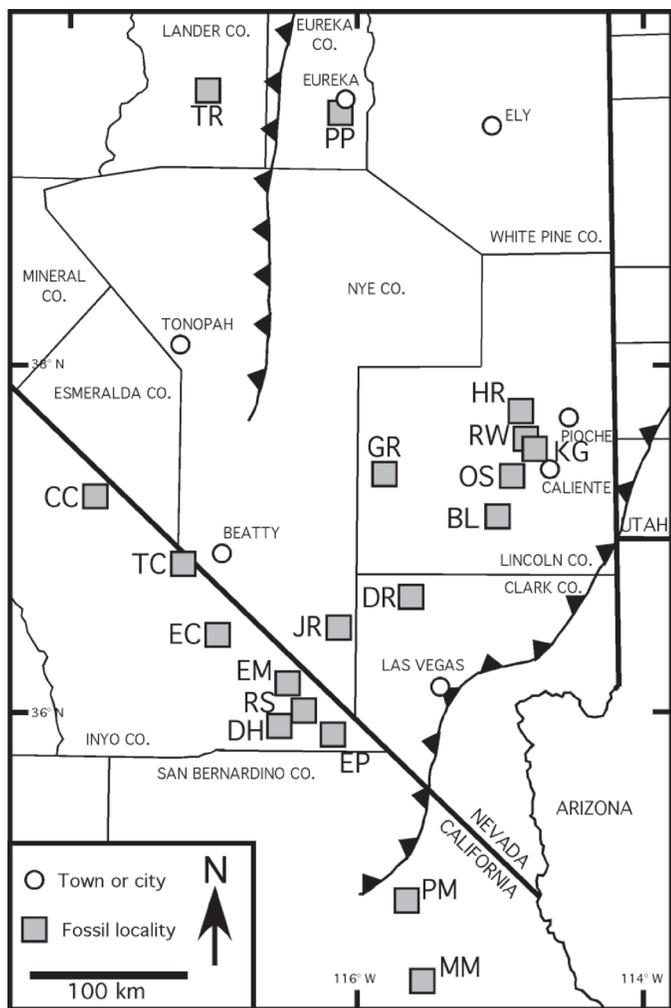


FIGURE 1.—Map of localities in the southwestern United States from which *Peachella* and *Eopeachella* specimens have been recovered. Black lines with triangles mark the eastern limit of thrusting (Antler Orogenic Belt in the north, Sevier Orogenic Belt in the southeast; overthrust block to the west in each case). Abbreviations: BL, Big Lime Mountain, Delamar Mountains; CC, Cucumungo Canyon, Last Chance Range; DH, Dublin Hills; DR, Desert Range; EC, Echo Canyon, Funeral Mountains; EM, Eagle Mountain; EP, Emigrant Pass, Nopah Range; GR, Groom Range; HR, Highland Range (Happy Face and Log Cabin Mine sections); JR, Jaybird Ridge, Spring Mountains; KG, Klondike Gap, Chief Range; MM, Marble Mountains; OS, Oak Spring Summit, Delamar Mountains; PM, Providence Mountains; PP, Prospect Peak; RS, Resting Springs Range; RW, Ruin Wash, Chief Range; TC, Titanother Canyon, Grapevine Mountains; TR, Toiyabe Range.

bases relative to sagittal cephalic length (Webster, 2007b). Entry into phase 3 of cephalic development is defined by the initial differentiation of genal spines, which appear as tiny nubbins located adjacent to the abaxial margin of the intergenal spine bases (Webster, 2007b). Entry into phase 4 is defined by the onset of marked lateral expansion of the third glabellar segment (L3) relative to the second (L2); this expansion is associated with effective isolation of the third glabellar furrow (S3) from the axial furrow in some taxa (e.g., *Nephrolenellus*; Webster, 2007b) but not in others (e.g., *Paranephrolenellus*; Webster, 2007c). During subsequent ontogeny in many olenelloids (e.g., *Peachella* and *Eopeachella* spp. [here], *Olenellus* Hall, 1862 and most species of *Bristolia* [unpublished data]), L2 also underwent marked relative lateral expansion, leading to the merger of the anterolateral portions of L2 with the posterolateral portions of L3 and consequent isolation of the S2 furrow from the axial furrow; this merger defines entry into phase 5 of cephalic development (sensu Webster

et al., 2001, pp. 118–119). The pronounced lateral expansion of L2 and isolation of S3 did not occur in some olenelloids (e.g., *Nephrolenellus* spp.; Webster, 2007b), which terminated their cephalic development in phase 4.

Materials.—Specimens listed below are housed the Field Museum, Chicago (FMNH), the Institute for Cambrian Studies, University of Chicago (ICS), the Natural History Museum of Los Angeles County (LACMIP), the Museum of Comparative Zoology, Harvard (MCZ), the San Diego Natural History Museum (SDNHM), the University of California, Riverside (UCR), the Smithsonian Institution, Washington, D.C. (USNM), and the private collection of N. Brown (NSB). Stratigraphic information (such as distance from marker beds) following ICS and UCR numbers refers to collateral field descriptions deposited at those institutions.

Order REDLICHIDA Richter, 1932
 Suborder OLENELLINA Walcott, 1890
 Superfamily OLENELLOIDEA Walcott, 1890
 Family BICERATOPSIDAE Pack and Gayle, 1971
 Genus PEACHELLA Walcott, 1910

Peachella WALCOTT, 1910, p. 342; POULSEN, 1932, p. 35; SHIMER AND SHROCK, 1944, p. 615; POULSEN, 1959, p. O192; PALMER AND HALLEY, 1979, pp. 74–75; PALMER AND REPINA, 1993, p. 23; PALMER AND REPINA, 1997, p. 409; JELL AND ADRAIN, 2003, pp. 423, 475.

Type species.—*Olenellus iddingsi* Walcott, 1884.

Other species.—*Peachella brevispina* Palmer in Palmer and Halley, 1979.

Diagnosis.—Biceratopsids of relatively small size (sagittal length of cephalon rarely exceeds 15 mm). Glabella hourglass-shaped, constricted at S1, transverse width of L1 less than width of LO; glabellar furrows very shallow or effaced; preglabellar field absent. Ocular lobes short, posterior tips located close to glabella opposite anterior half of L1, S1, or posterior half of L2. Posterior margin of cephalon straight or with distal portion flexing anteriorly by up to 34° relative to proximal portion at rounded adgenal angle. Intergenial spines absent or represented by small dorsal swelling on posterior cephalic border. Genal spines less than half cephalic length (sag.), wide, bulbous and inflated in relief; base opposite or posterior to LO. Lateral cephalic border distinctly broadened laterally and inflated dorsally posterior to point opposite lateral margin of posterior third of LA, L3, L2, or L1, merging into swollen genal spine. Thorax sharply divided into prothorax of 14 segments and opisthothorax of at least nine segments; T3 hyperpleural, dolichospinous.

Occurrence.—Upper Dyeran, *Bristolia* Zonule of Palmer and Halley (1979); U.S.A. (California, Nevada).

Discussion.—The diagnosis above refines and expands upon that provided by previous workers (Poulsen, 1959; Palmer in Palmer and Halley, 1979; Palmer and Repina, 1993, 1997), taking into account the inter- and intraspecific morphological variation documented in the present study. Palmer and Repina (1993, 1997) included a long axial spine on T15 and an opisthothorax of at least 10 segments in their generic diagnosis. However, *Peachella iddingsi* apparently lacks an axial spine on T15, and although eleven opisthothoracic segments are known in *P. iddingsi* the present author has yet to see a specimen of *P. brevispina* bearing more than nine. The emended generic diagnosis above therefore excludes a T15 axial spine and is based on this more conservative count of opisthothoracic segment number.

The bulbous genal spines and generally effaced glabella are easily recognized characteristics of *Peachella*. The genal spine bases and lateral cephalic border are also inflated in *Paranephrolenellus inflatus* Webster, 2007c, but this taxon differs markedly from both *Peachella* species in having pointed (rather than bluntly

rounded) genal spines, clearly visible glabellar furrows, and strongly divergent ocular lobes.

The oculo-glabellar morphology of *Peachella*, including the generally effaced glabellar furrows, is also found in *Biceratops nevadensis* Pack and Gayle, 1971 and in a new species (below) from the middle Delamar Member of the Pioche Formation. The new species possesses moderately stout, blunt-tipped, genal spines which taper along their length, representing something of an intermediate in form between “typical” olenelloids (such as *Olenellus*, *Nephrolenellus*, and *Bolbolenellus* Palmer and Repina, 1993) and the derived bulbous morphology developed in *P. iddingsi* and *P. brevispina*. The new species is described below as *Eopeachella angustispina* n. gen. n. sp.

Lieberman's (1998) cladistic analysis found support for a *Peachella* + *Biceratops* Pack and Gayle, 1971 clade within the Biceratopsidae (see also Palmer and Repina, 1993, 1997). *Biceratops* differs most obviously from *Peachella* (and *Eopeachella*) in lacking genal spines. A full revision of *Biceratops*, including description of its ontogeny, will be presented elsewhere.

PEACHELLA IDDINGSI (Walcott, 1884)

Figures 2, 3, 4, 5, 6

Olenellus iddingsi WALCOTT, 1884, pp. 28, 36, 37, 38, 268, pl. 9, fig. 12; HAGUE, 1883, p. 256; MARCOU, 1885, p. 231; WALCOTT, 1886, pp. 32, 34, 35, 36, 47, 170, pl. 19, fig. 1; BRÖGGER, 1886, p. 183, 186; HOLM, 1887, p. 515; MARCOU, 1890, p. 100; WALCOTT, 1890, p. 636, pl. 84, fig. 2; VOGDES, 1893, p. 327.

Peachella iddingsi WALCOTT, 1910, pp. 343–345, pl. 40, figs. 17–19; WALCOTT, 1912, pp. 140, 158, 189, 201, 246; WESTGATE AND KNOPE, 1932, p. 10; GRABAU, 1936, pp. 67, 134; CALLAGHAN, 1937, p. 18; MASON, 1938, p. 290; WHEELER, 1943, p. 1804; SHIMER AND SHROCK, 1944, p. 615, pl. 254, fig. 17; WHEELER, 1948, p. 50; NOLAN, MERRIAM, AND WILLIAMS, 1956, p. 8; POULSEN, 1959, p. O192, fig. 135.6a, b; STEWART, 1970, p. 76; MOUNT, 1976, pp. 175, 176, 180, fig. 17; NELSON, 1976, pl. 8 [lower left corner, as *Peachella*]; MCNAMARA, 1978, p. 642 [as *Peachella*]; PALMER AND HALLEY, 1979, pp. 13, 75, pl. 5, figs. 4–9; MOUNT, 1980a, p. 22, fig. 17; MOUNT, 1980b, pp. 79, 80; STITT AND CLARK, 1984, p. 146; HAHN, HAHN, AND BRAUCKMANN, 1992, p. 93; PALMER AND REPINA, 1993, p. 23, fig. 4.2; PALMER AND REPINA, 1997, p. 409, fig. 257.2; LIEBERMAN, 1998, pp. 62, 67; FOWLER, 1999, pp. 48, 49; LIEBERMAN, 1999, pp. 141, 143; SMITH AND LIEBERMAN, 1999, p. 462; SUNDBERG, 2000, p. 266; LIEBERMAN, 2002, p. 699; LIEBERMAN, 2003, p. 63; JELL AND ADRAIN, 2003, p. 423; WEBSTER, SADLER, KOOSER, AND FOWLER, 2003, figs. 3, 9, 10, pp. 103, 104, 124, 125; WEBSTER, 2007c, pp. 35, 41, 43, fig. 2.

Description (mature morphology).—Cephalon semicircular in outline; proximal portion of posterior cephalic margin angled slightly posteriorly away from axial furrow by 2° to 15° relative to transverse line, straight (Fig. 3.1, 3.4) or with distal portion flexing anteriorly by up to 34° relative to proximal portion (Fig. 4.4) at rounded adgenal angle located 55% to 90% of distance along posterior cephalic margin from axial furrow to base of genal spine (Fig. 8.2). Greatest observed cephalic length approximately 15.7 mm (sag.). Genal spines wide, bluntly rounded, bulbous and inflated in relief; posterolaterally oriented; base opposite or posterior to LO; length less than half cephalic length (sag.). Intergenal spine absent (Fig. 2.6) or represented by small dorsal swelling on posterior cephalic border at or distal to adgenal angle (Figs. 4.5, 5.5). Cephalic border poorly defined by an extremely weak cephalic border furrow which is virtually absent posterolaterally on some specimens (Fig. 3.1, 3.4, 3.5); evenly or acutely rounded dorsally anteriorly, steeply sloping to cephalic margin, gently

sloping into cephalic border furrow; width of anterior border opposite junction of ocular lobes with LA approximately 30% to 80% length (exsag.) of LO; posterior border defined by very weak border furrow, narrows adaxially and poorly defined or absent at base of genal spine. Lateral cephalic border distinctly broadened laterally and inflated dorsally posterior to point opposite lateral margin of posterior third of LA, L3 or L2 (Fig. 7.4), merging into swollen genal spine. Glabella extends to anterior border furrow, 88% to 96% of cephalic length (sag.), hourglass-shaped, constricted at S1. Maximum width of LA up to 35% wider (tr.) than basal glabellar width. Posterior margin of glabella strongly convex posteriorly. Axial furrow and all glabellar furrows very shallow, rarely entirely effaced (Fig. 2.8). SO deepest abaxially, abaxial end slightly anterior to adaxial end. S1 deepest abaxially, oriented strongly anterolaterally abaxially. LO and L1 subtrapezoidal, narrowing anteriorly. S2 deepest in slot position, isolated from axial furrow, abaxial end slightly anterior to adaxial end. L2 and L3 merged distally, widening (tr.) anteriorly until contact with ocular lobes. S3 oriented anterolaterally away from axis until contact with ocular lobes. LA slightly wider (tr.) than long (sag.), 30% to 45% of glabellar length (sag.), slightly inflated dorsally above extraocular area (Fig. 2.2), summit slightly higher than posterior glabellar lobes (Figs. 2.2, 2.4, 4.6); widest point slightly anterior to contact with anterior margin of ocular lobes. Relatively large axial node on LO; L1 rarely with low, broad swelling axially (Figs. 2.7, 4.1, 4.2). Ocular lobes divergent from exsagittal axis by 25° to 40° (measured as angle between exsagittal axis and line from posterior tip of ocular lobe to contact of adaxial margin of ocular lobe with abaxial margin of L3; Fig. 7.1) or 30° to 45° (measured as angle between exsagittal axis and line from most abaxial point along ocular lobe to contact of abaxial margin of ocular lobe with abaxial margin of LA; Fig. 7.2), crescentic, posterior tip close to axial furrow and opposite anterior third of L1 (Fig. 3.5), S1 (Fig. 2.7), or rarely posterior half of L2 (Fig. 4.8), convex dorsally; ocular furrow typically not developed; one specimen shows a very shallow ocular furrow slightly abaxial to midline of ocular lobe (Fig. 2.9). Interocular area sloping down from ocular lobes to axial furrow (Fig. 3.2), slightly narrower than width (tr.) of ocular lobes and approximately one-sixth to one-fifth width (tr.) of extraocular area opposite L2. Extraocular area moderately strongly vaulted (Fig. 3.2). Posterior ocular line (Figs. 2.1, 2.6, 2.7, 2.10, 3.1, 4.1, 4.2, 5.5), anterior ocular line (Fig. 2.10), intergenal ridge (Fig. 3.5), and genal ridge (Fig. 4.7) present on some individuals. Genal caeca occasionally developed on extraocular area (Figs. 2.6, 2.7, 2.10, 3.1, 4.7), typically stronger on internal relative to external surface. Terrace lines on cephalic doublure (Figs. 3.7, 4.3) and rarely dorsally on anterior cephalic border (Fig. 3.6), lateral cephalic border and base of genal spines (Fig. 3.1). Bertillon markings rarely developed on base of genal spines (dorsally; Fig. 3.6). Hypostome unknown.

Prothorax of 14 segments (Fig. 4.1, 4.2); width (tr.) of axis approximately equal to width (tr.) of inner pleural region on T1, gently tapering posteriorly. Axial nodes developed on T1 to at least T9 (Fig. 4.3, presence or absence unclear posterior to T9). Inner pleural regions of T1 and T2 transverse, tapering distally, with straight margins; tips blunt or possibly with miniscule sentate pleural spine. T3 hyperpleural; pleural spine robust, dolichospinous, sharp-tipped. Inner pleural region of T4 and to progressively lesser extent T5 and T6 tapering, divergent relative to transverse line proximally, curving to more transverse orientation distally. Inner pleural regions of T6 to T10 transverse, parallel-sided, with straight margins. Inner pleural regions of T11 to T14 increasingly divergent, parallel-sided, margins increasingly curved on more posterior segments. Pleurae of T4 to T14 blunt-tipped. Pleural furrows barely extend onto base of pleural spines of T3. Dorsal and ventral surfaces of T3 pleural spines bear terrace lines, grading into bertillon markings on dorsal surface in places (Fig. 4.3). Bertillon markings developed on posterior margin of inner pleural

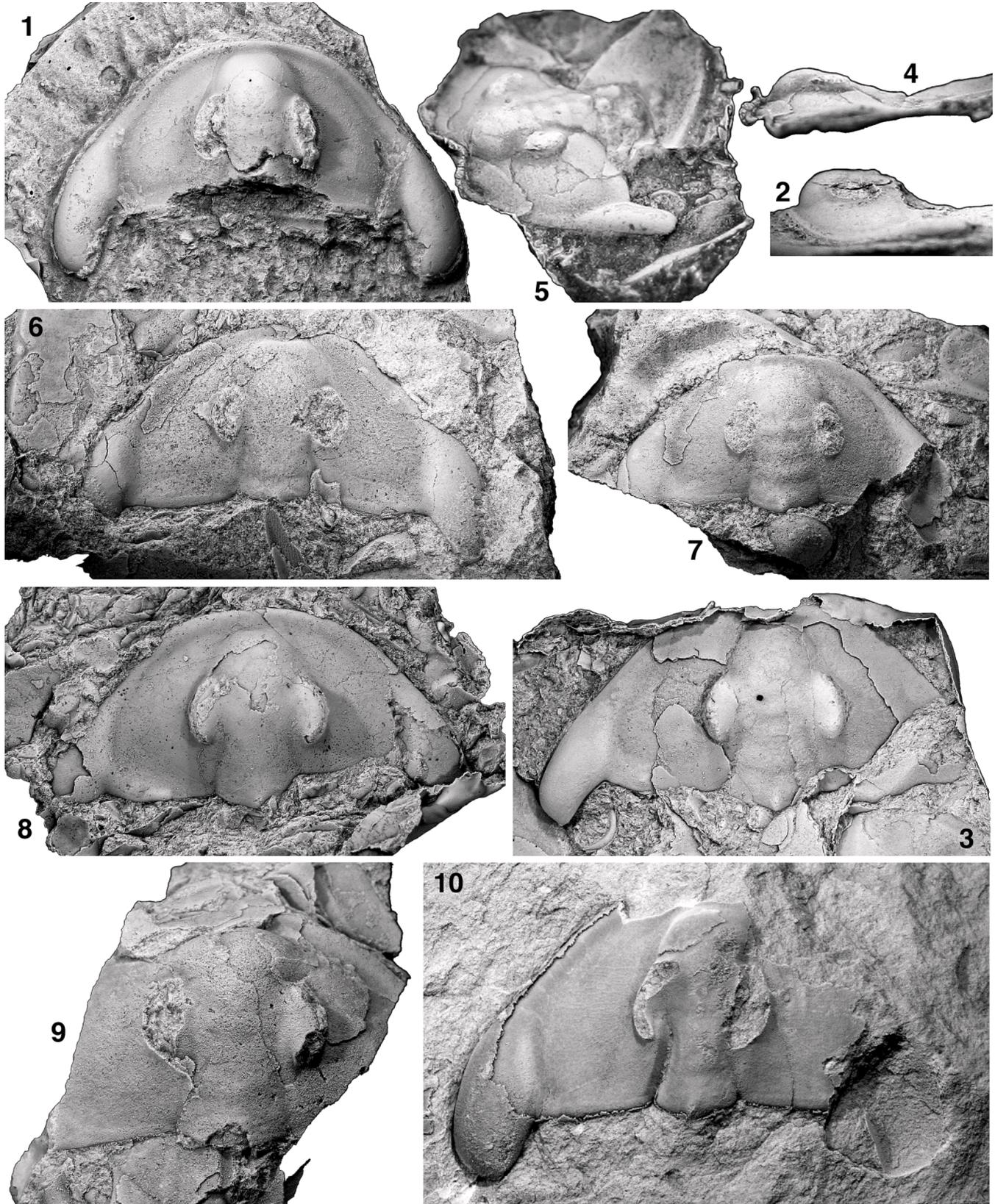


FIGURE 2—Morphologically mature cephalons of *Peachella iddingsi*. 1, 2, holotype cephalon, dorsal ($\times 4$) and left lateral ($\times 3$) views, USNM 15407a; 3–5, cephalon in dorsal ($\times 4$), left lateral ($\times 3$) and oblique dorsoanterolateral ($\times 3$) views, USNM 177241 (latex replica); 6, cephalon, dorsal view, FMNH PE58077, $\times 3$; 7, cephalon, dorsal view, FMNH PE58080, $\times 3$; 8, cephalon, dorsal view, USNM 177242 (latex replica), $\times 4$; 9, incomplete cephalon, dorsal view, FMNH PE58069, $\times 4$; 10, incomplete cephalon, dorsal view, FMNH PE58107, $\times 4$. 1, 2 from USNM locality 52, Prospect Peak, Eureka County, Nevada; 3–5, 8 from USGS collection 3786-CO, Groom Range, Lincoln County, Nevada; 6, 7 from ICS-1069, Big Lime Mountain section, Delamar Mountains, Lincoln County, Nevada; 9 from ICS-1005, Oak Spring Summit section, Delamar Mountains, Lincoln County, Nevada; 10 from ICS-10091, Jaybird Ridge North Canyon section, Spring Mountains, Clark County, Nevada. See text for stratigraphic details.

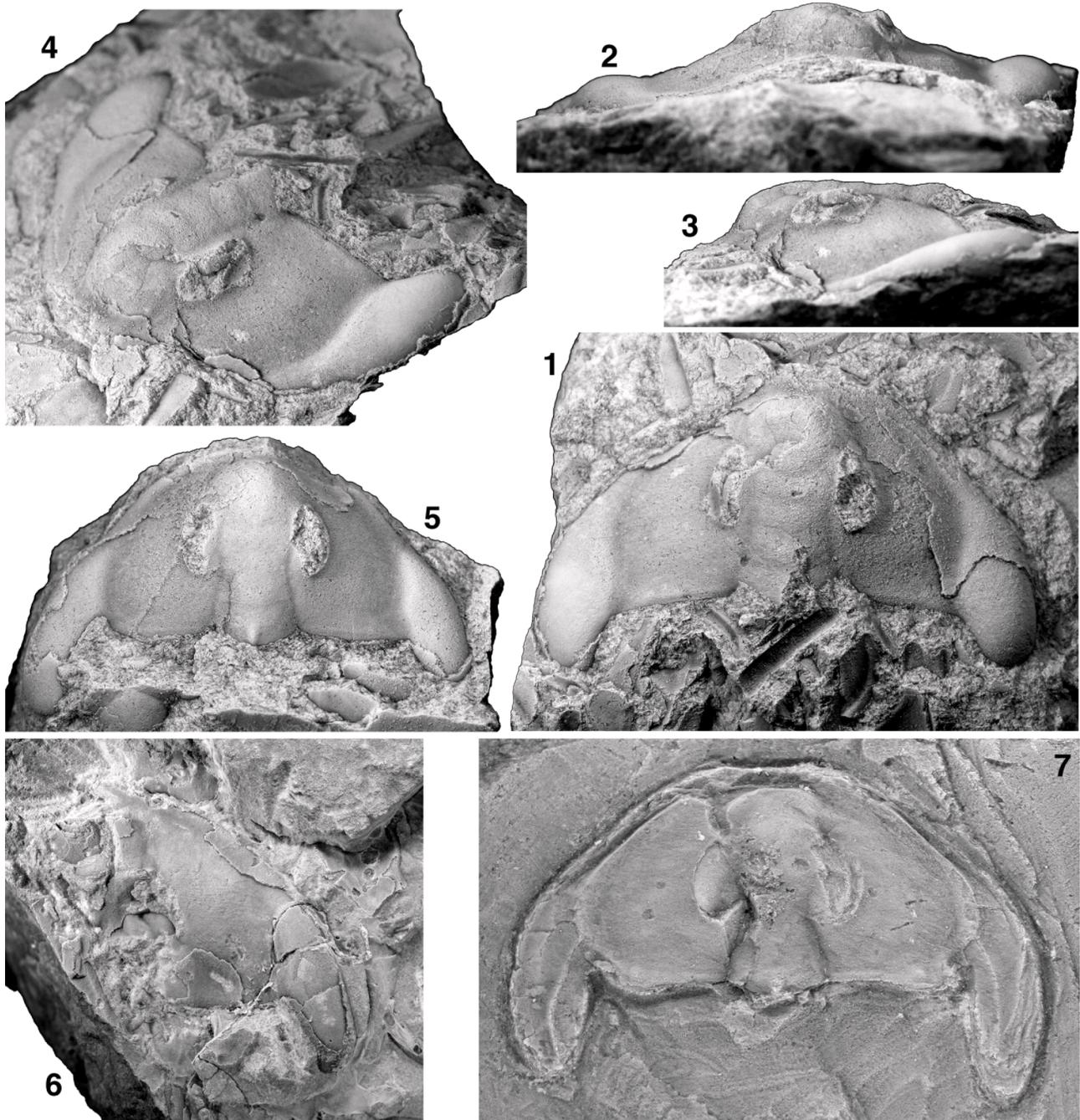


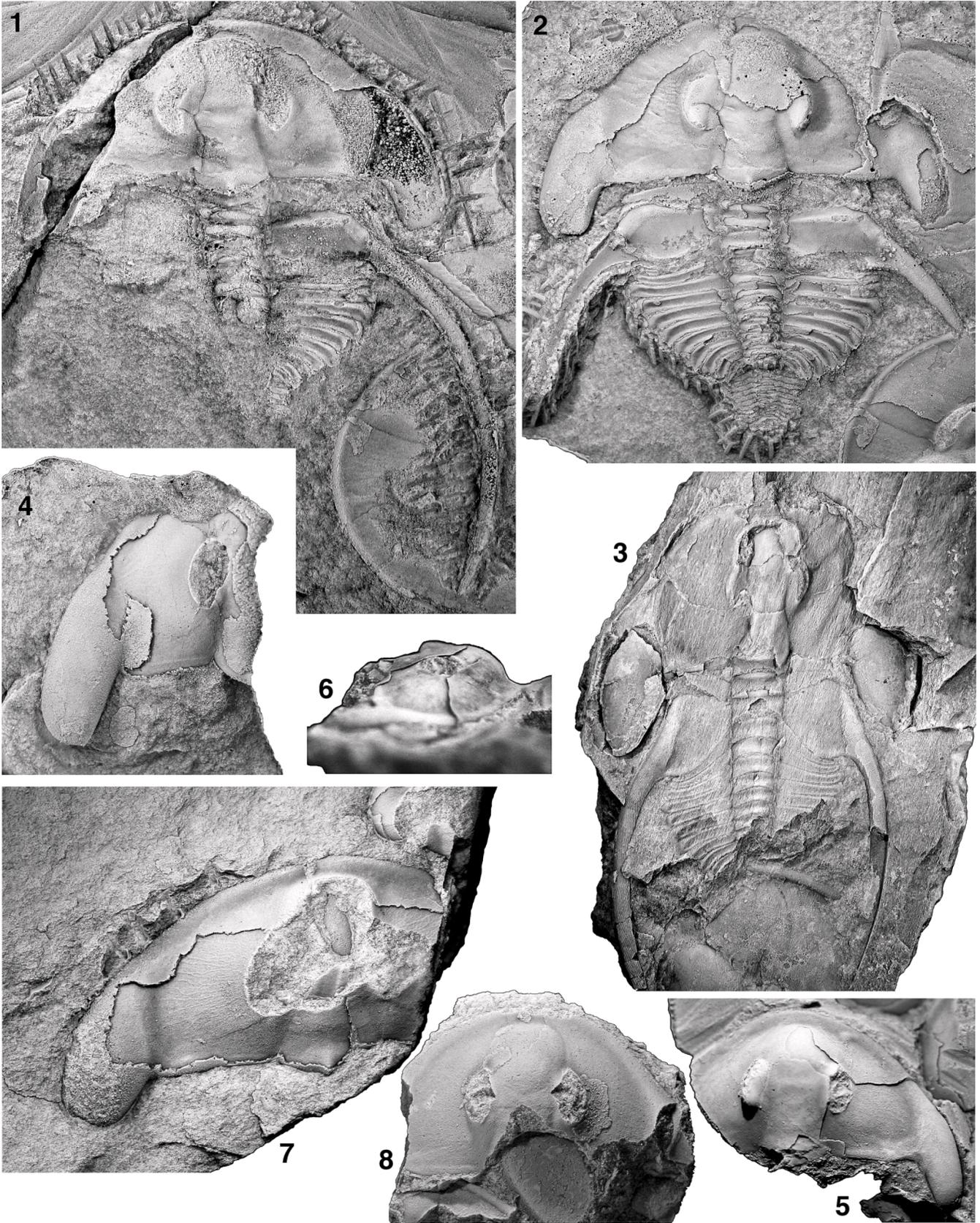
FIGURE 3—Morphologically mature cephalons of *Peachella iddingsi*. 1–4, cephalon in dorsal, anterior, left lateral, and oblique dorsoanterolateral views, FMNH PE58070, $\times 4$; 5, cephalon, dorsal view, FMNH PE58078, $\times 4$; 6, Right side of incomplete cephalon, dorsal view, specimen in lot LACMIP 24908–6, $\times 3$; 7, cephalon, dorsal view, UCR 10.1/14, $\times 6$. This specimen was represented as a line drawing by Mount (1976, fig. 17; 1980a, fig. 17); a photograph of the specimen is shown here for the first time. 1–4 from ICS-1005, Oak Spring Summit section, Delamar Mountains, Lincoln County, Nevada; 5 from ICS-1069, Big Lime Mountain section, Delamar Mountains, Lincoln County, Nevada; 6 from LACMIP locality 24908, Titanother Canyon section, Grapevine Mountains, Inyo County, California; 7 from Marble Mountains, San Bernardino County, California. See text for stratigraphic details.

region of T3 and on distal tips of inner pleural regions of T6 to T9 (Fig. 4.3).

Opisthothorax of at least 11 segments (Fig. 4.2; possibly shows four more but preservation is too poor to be certain). No evidence of axial structures (nodes or spines) on T15 to T25. Inner pleural regions of T15 slightly curved, tapering, divergent; straight, parallel-sided, and roughly transverse on all more posterior segments; distal extremities of pleurae on T15 to T25 taper to blunt end. Axis poorly defined by very weak axial furrow. Pleural furrows effaced. Rest of opisthothorax and pygidium unknown.

Ontogeny.—The smallest known specimen is approximately 2.2 mm in sagittal glabellar length (Fig. 5.1), but is poorly preserved. Better preserved specimens range from approximately 3.0 mm (Fig. 6) to approximately 15.7 mm (Fig. 4.3) in cephalic sagittal length.

On the smallest known cephalon (Fig. 5.1) the glabellar furrows are well incised, deepest abaxially but crossing the glabellar axis. The abaxial portions of SO and S1 are located slightly anterior to the adaxial portions of the furrows; S2 and S3 are roughly transverse. The glabella is parallel-sided anterior to SO; L3 is not



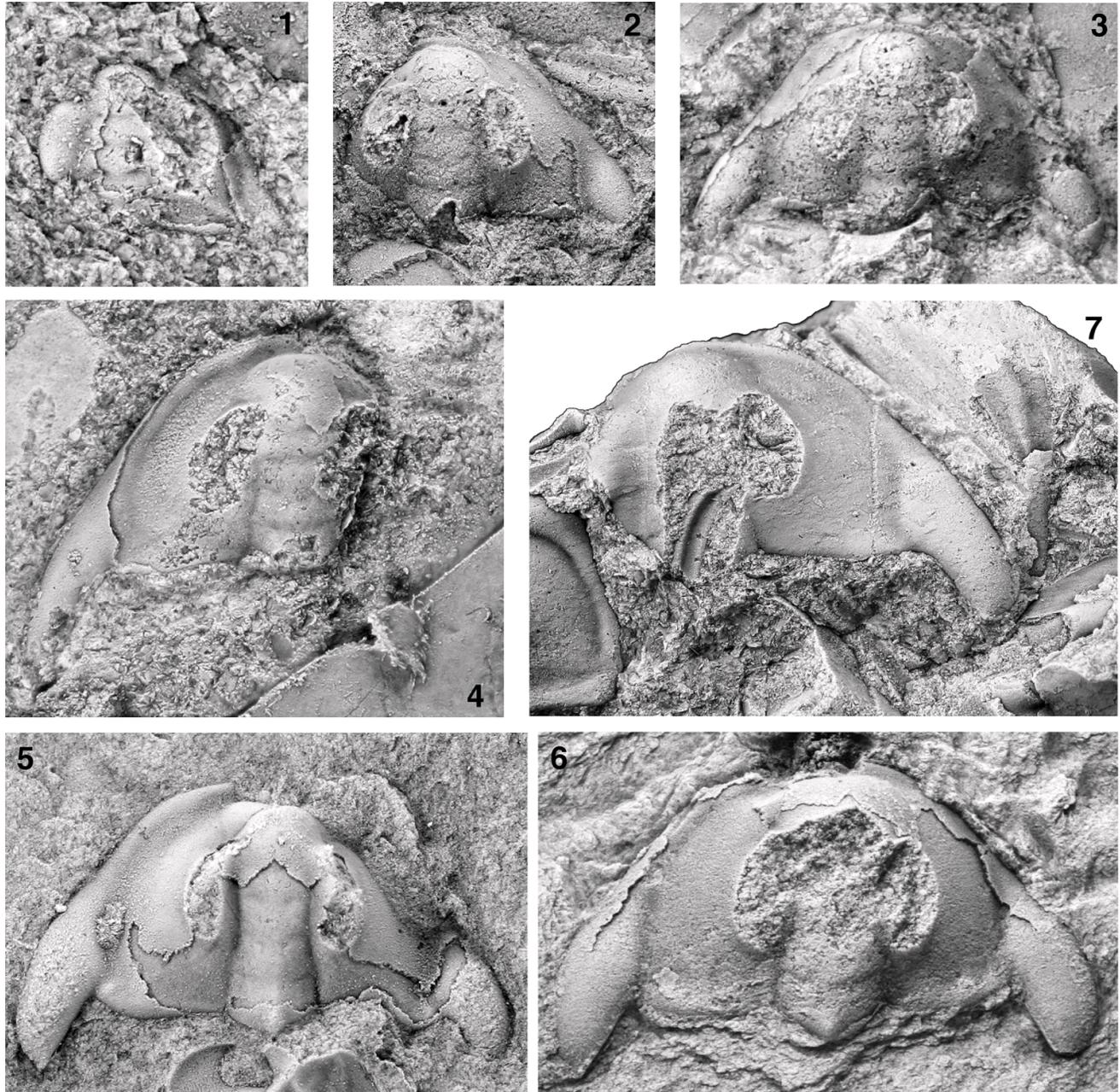


FIGURE 5—1–6, cephalons of *Peachella iddingsi* in phases 3 through 5 of ontogenetic development. 1, partially exfoliated and incomplete cephalon in phase 3 of development, dorsal view, FMNH PE58071, $\times 12$. 2, partially exfoliated and incomplete cephalon in early phase 4 of development, dorsal view, FMNH PE58081, $\times 9$; 3, partially exfoliated cephalon in phase 4 of development, dorsal view, FMNH PE58074, $\times 9$; 4, partially exfoliated and incomplete cephalon in phase 4 of development, dorsal view, USNM 15407c, $\times 10$; 5, partially exfoliated cephalon in early phase 5 of development showing a thorn-like tip to an otherwise inflated genal spine and a small dorsal swelling representing the intergenal spine (immediately adjacent to the left genal spine base), dorsal view, FMNH PE58013, $\times 10$; 6, partially exfoliated and incomplete cephalon in early phase 5 of development, dorsal view, FMNH PE58019, $\times 10$; 7, morphologically mature incomplete cephalon, dorsal view, FMNH PE58095, $\times 7$. 1 and 3 from ICS-1005 and ICS-1046 respectively, both Oak Spring Summit section, Delamar Mountains, Lincoln County, Nevada; 2 from ICS-1069, Big Lime Mountain section, Delamar Mountains, Lincoln County, Nevada; 4 from USNM locality 52, Prospect Peak, Eureka County, Nevada; 5 from ICS-10091, Jaybird Ridge North Canyon section, Spring Mountains, Clark County, Nevada; 6 from Emigrant Pass, Nopah Range, Inyo County, California; 7 from ICS-1364, Toiyabe Range, Lander County, Nevada. See text for stratigraphic details.

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FIGURE 4—Morphologically mature specimens of *Peachella iddingsi*. 1–3, articulated specimens showing details of prothorax and opisthothorax. 1, 2, mostly exfoliated part (1) and latex cast of counterpart (2) of LACMIP 11621, $\times 4$. The photograph published by Palmer and Repina (1993, fig. 4.2; 1997, fig. 257.2) is a composite of these specimens. 3, dorsal view of mildly tectonized specimen, LACMIP 11622, $\times 2$; 4, left side of incomplete and partially exfoliated cephalon, FMNH PE58105, $\times 4$; 5, 6, incomplete and partially exfoliated cephalon, dorsal and right lateral views, USNM 177243, $\times 3$; 7, incomplete and partially exfoliated cephalon, dorsal view, FMNH PE58097, $\times 6$; 8, incomplete cephalon, dorsal view, FMNH PE58076, $\times 3$. 1–3 from Emigrant Pass section, Nopah Range, Inyo County, California; 4, 7 from ICS-10091, Jaybird Ridge North Canyon section, Spring Mountains, Clark County, Nevada; 5, 6 from USGS collection 3786-CO, Groom Range, Lincoln County, Nevada; 8 from ICS-1069, Big Lime Mountain section, Delamar Mountains, Lincoln County, Nevada. See text for stratigraphic details.

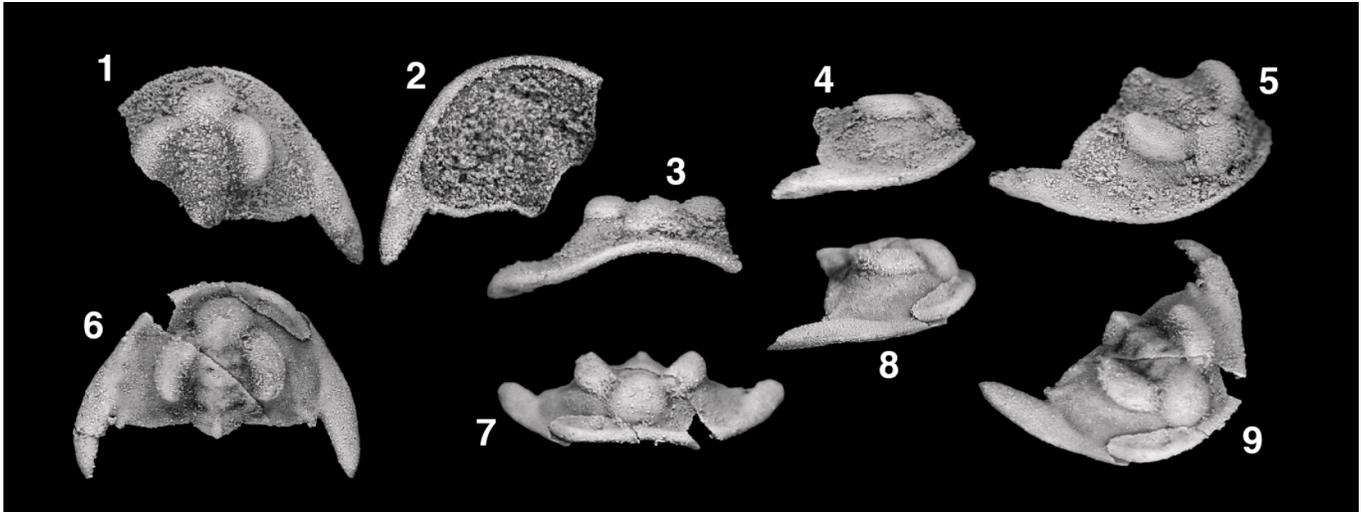


FIGURE 6—Silicified cephalons of *Peachella iddingsi* in early phase 4 of development. 1–5, incomplete and coarsely silicified cephalon, dorsal, ventral, anterior, right lateral, and oblique dorsoanterolateral views, USNM 306569, $\times 7$; 6–9, fractured cephalon, dorsal, anterodorsal, right lateral, and oblique dorsoanterolateral views, USNM 177240, $\times 7$. Both from USGS collection 4144-CO, Titanother Canyon section, Grapevine Mountains, Inyo County, California. See text for stratigraphic details.

noticeably wider (tr.) than L2 and the distal portion of S3 is in contact with the axial furrow near the posterior margin of the base of the ocular lobe; S2 is also in contact with the axial furrow. There are no interocular nodes or obvious axial nodes on glabellar lobes anterior to LO, although the condition on L1 cannot be unequivocally determined. The presence or absence of a preglabellar field cannot be determined. The posterior tip of the ocular lobe is located opposite the midlength of L1. A posterior ocular line or intergenal ridge (incomplete proximal preservation renders precise identification of this structure equivocal) is prominently developed abaxially, crossing the posterior border and running onto a small intergenal spine located distal to a very weak adgenal angle. The base of the genal spine is only slightly inflated and the spine tapers along its length. The glabellar morphology and presence of genal spines indicate that this specimen is in phase 3 of cephalic development (see above). The sagittal glabellar length of this specimen (2.2 mm) is within the range of specimens of *Nephrolenellus multinodus*, *N. geniculatus*, and *Paranephrolenellus besti* also in phase 3 of cephalic development (Webster, 2007b, c).

On slightly larger specimens approximately 3.0 mm in sagittal cephalic length (Fig. 6) the genal spines are more prominently inflated, L3 is slightly wider than L2 (tr.), and S3 is more or less isolated from the axial furrow. The posterior tip of the ocular lobe is still located opposite the midlength of L1. A posterior ocular line crosses the posterior cephalic border onto a small intergenal spine located distal to a weak adgenal angle. A prominent anterior arch is developed. The glabellar morphology indicates that these specimens are in phase 4 of cephalic development (see above). Transition into phase 4 occurred at sagittal cephalic length of approximately 3.2 mm in the two *Nephrolenellus* species (Webster, 2007b).

On cephalons 3.2 to 3.7 mm in sagittal length (Fig. 5.2, 5.3, 5.4) the glabellar furrows are less prominent and weakly incised (particularly over the glabellar axis), S2 still contacts the axial furrow, and the posterior tip of the ocular lobe is located opposite the anterior third of L1. The genal spines are bulbous.

By cephalic length of 3.9 mm (Fig. 5.5) the glabellar furrows are very shallow. The distal margins of L2 and L3 are merged, and S2 is isolated from the axial furrow: the specimen is therefore assigned to phase 5 of olenelloid cephalic development (see above). The genal spines are bulbous but retain a tiny thorn-like projection at the distal tip; the spine is more prominently inflated

on the abaxial side. A posterior ocular line terminates in a small dorsal swelling on the posterior cephalic border. A slightly larger specimen 4.4 mm in sagittal cephalic length (Fig. 5.6) has a similar dorsal swelling on the posterior cephalic border but lacks a posterior ocular line. Larger cephalons in phase 5 of development are essentially morphologically mature and are described above.

Considerable allometry is observed over the sampled portion of cephalic ontogeny (phases 3, 4, and 5) of *Peachella iddingsi*. General trends include the following. (1) LA proportionally elongates longitudinally, increasing from 30% up to 45% of sagittal glabellar length and from 60% up to 95% of maximum width of LA. (2) LO proportionally widens (tr.), especially posteriorly, and LO and L1 become subtrapezoidal, narrowing anteriorly. (3) L2 and L3 proportionally widen (tr.) and shorten (their combined exsagittal length decreases from 20% down to 12% of glabellar length) as they merge distally and isolate S2 from the axial furrow. (4) The ocular lobes proportionally shorten from 50% down to 35% of glabellar length (Fig. 7.3), and the angle between a line drawn from the posterior tip of the ocular lobe to the point where the adaxial margin of the ocular lobe contacts the axial furrow of L3 and the exsagittal axis changes from between 20° and 25° up to between 25° and 40° (Fig. 7.1). However, the abaxial margins of the ocular lobes do not become more divergent (the angle between a line drawn from the abaxial limit of the ocular lobe to the point where the abaxial margin of the ocular lobe contacts the axial furrow of LA and the exsagittal axis varies between 30° and 45° without a distinct trend over the sampled portion of ontogeny; Fig. 7.2). (5) The extraocular area proportionally widens (tr.). (6) The adgenal angle slightly decreases, although with much variation (Fig. 8.1). (7) The genal spines become increasingly inflated (see below) and their bases become progressively less advanced (Fig. 8.3).

Holotype.—USNM 15407a, designated by Walcott (1884; see also Walcott, 1910, caption to pl. 40, fig. 17). A partially restored illustration of this specimen was provided by Walcott (1884, pl. 9, fig. 12) and subsequently copied in later works (Walcott, 1886, pl. 19, fig. 1; Walcott, 1890, pl. 84, fig. 2 [cites USNM catalog number 14510]; Walcott, 1910, pl. 40, fig. 17; Shimer and Shrock, 1944, pl. 254, fig. 17; Poulsen, 1959, fig. 135.6a). An unretouched photograph of the specimen was provided by Palmer and Halley (1979, pl. 5, fig. 4; see also Fig. 2.1, 2.2 herein).

Material examined.—FMNH PE58016; FMNH PE58069-58071; FMNH PE58074; FMNH PE58076-58084; FMNH

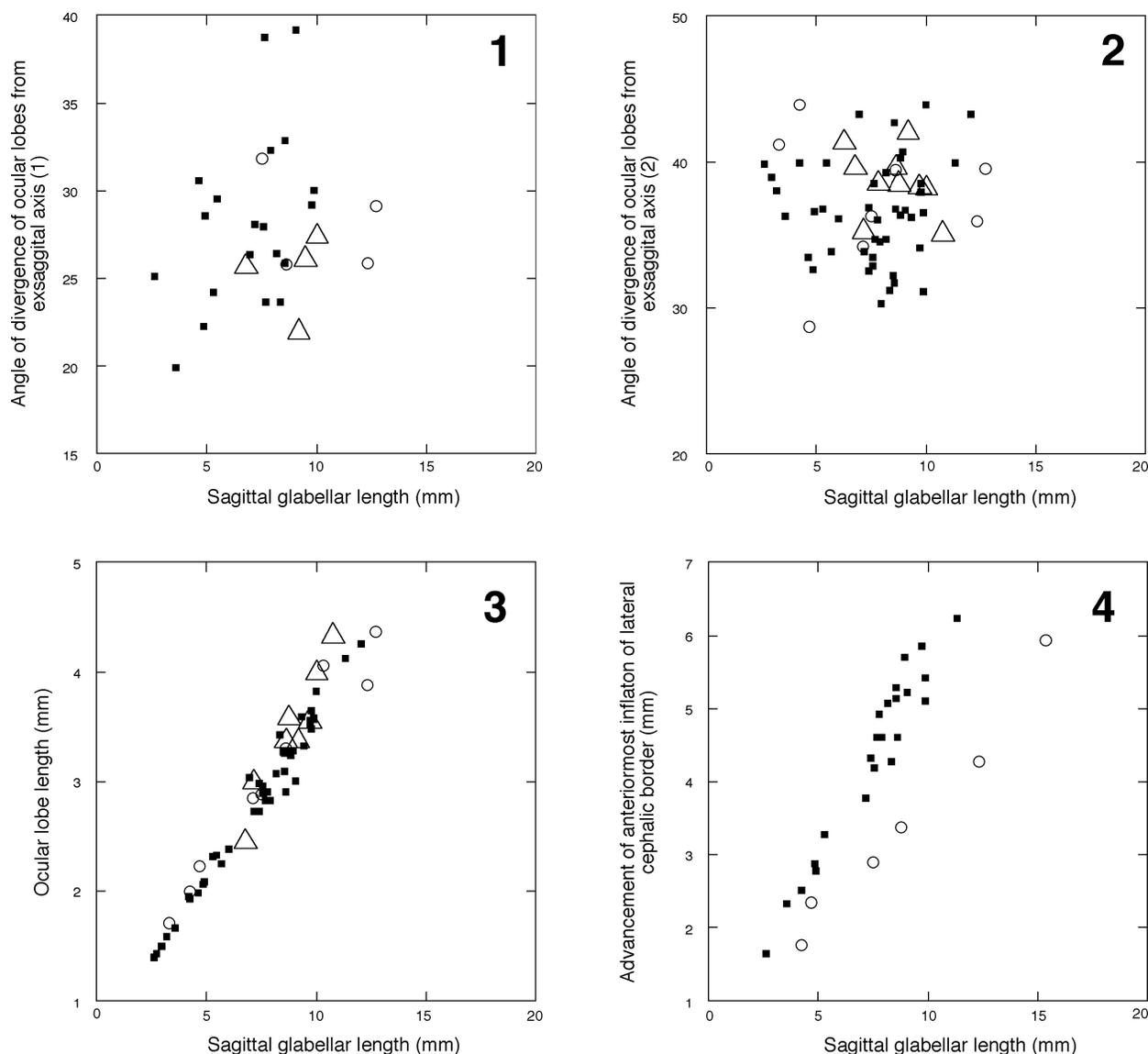
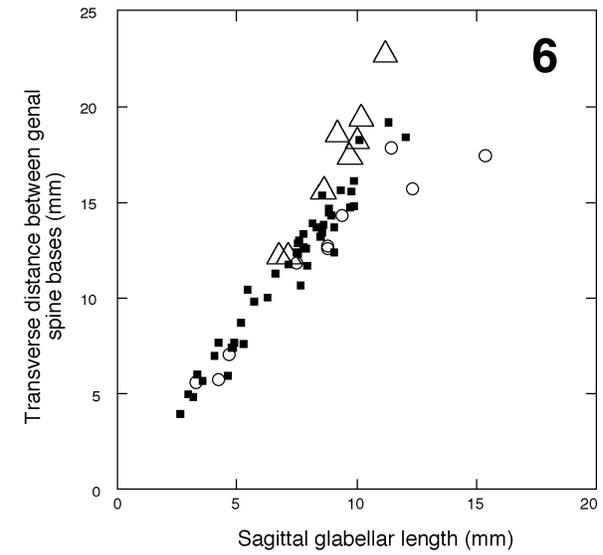
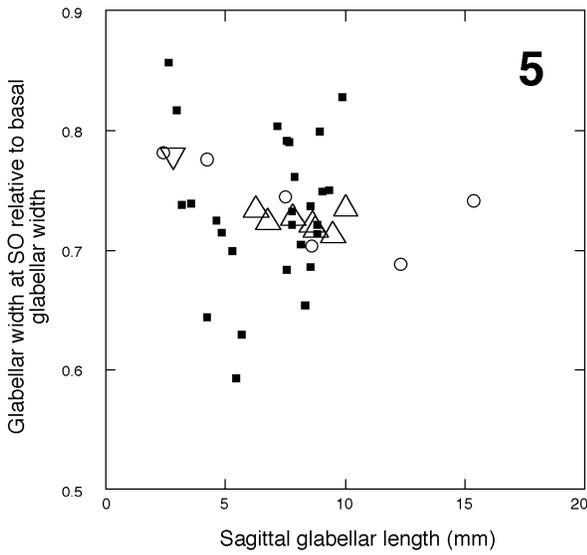
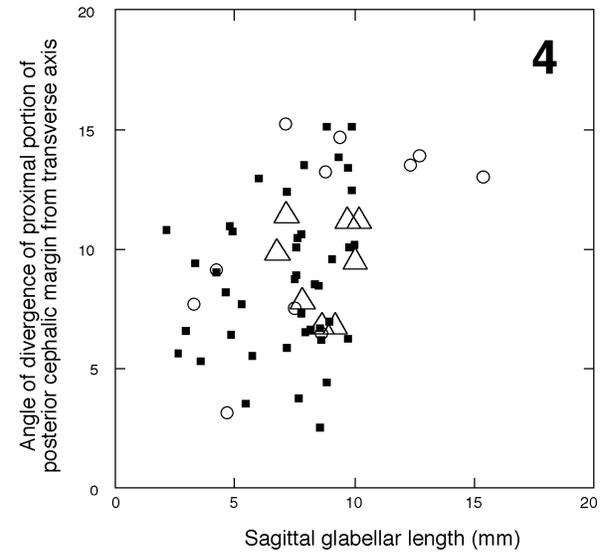
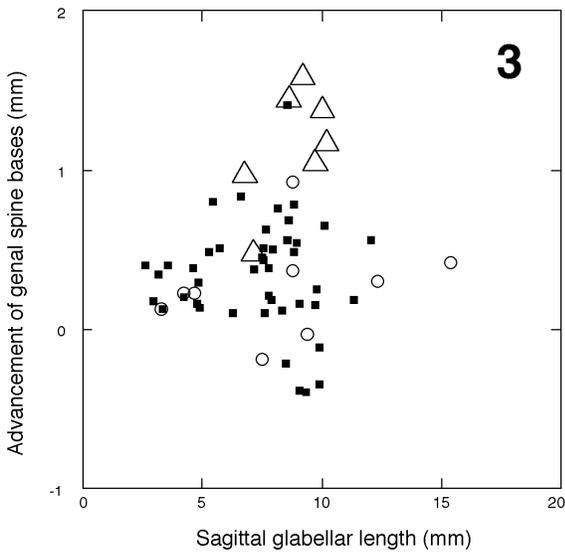
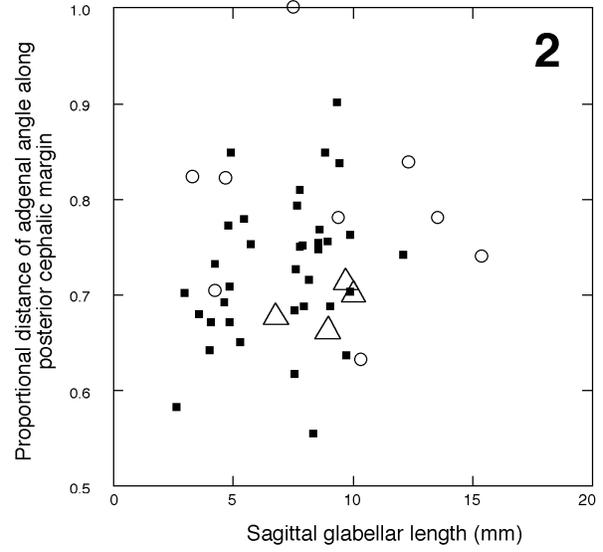
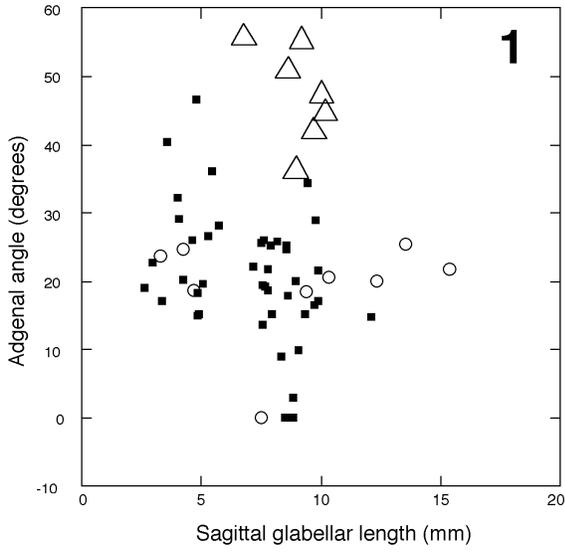


FIGURE 7—Morphometric data for *Peachella iddingsi* (squares), *P. brevispina* (circles), and *Eopeachella angustispina* (triangles), plotted against sagittal glabellar length (mm). 1, angle of divergence of ocular lobes from exsagittal axis, measured as angle between exsagittal axis and line from posterior tip of ocular lobe to contact of adaxial margin of ocular lobe with abaxial margin of L3. 2, angle of divergence of ocular lobes from exsagittal axis, measured as angle between exsagittal axis and line from most abaxial point along ocular lobe to contact of abaxial margin of ocular lobe with abaxial margin of LA. 3, ocular lobe length. 4, advancement of anteriormost inflation of lateral cephalic border, quantified as the distance along the sagittal axis from the posterior margin of the glabella to a transverse line between the anteriormost point of inflation of the lateral cephalic border.

PE58095; FMNH PE58097-58098; FMNH PE58103; FMNH PE58105; FMNH PE58107; FMNH PE58109; ICS-1005.7, 10-14; ICS-1046.5; ICS-1069.2, 4-6, 9-11, 13, 15, 18, 19, 22, 23; ICS-1530.1; ICS-10091.1-3, 9-11; ICS-10110.6, 7, 18; ICS-10116.1; ICS-10129.1, 2; LACMIP 11621; LACMIP 11622; LACMIP 24870; LACMIP 24908-6 (a lot containing 8 specimens); MCZ 154068; UCR 10.1/14; UCR 7003.25, 26, 28, 30, 32-38, 41-48, 51, UCR 7003.d; UCR 7621.1, 3-5; UCR 7914.30; UCR 9724.1; UCR 10001.1; UCR 10081.1, 4, 5; UCR 10083.1 (poor specimen, tentative identification); UCR 10155.1; UCR 10156.1-3; UCR 10523.1; UCR 10218.45; USNM 15407a (the holotype); USNM 15407c; USNM 15407; USNM 177239; USNM 177240; USNM 177241; USNM 177242; USNM 177243; USNM 306569; an unlabelled specimen in the biological collections of the USNM; ICS replica #788 (latex replica of a specimen identified as "MCZ 11"); 116 specimens total.

Other specimens.—Lieberman (1998) assigned LACMIP 4917-5 and UCR 2847.14 to *P. iddingsi*. The former specimen number refers to a fossiliferous platy limestone slab (cataloged as LACMIP 24917-5) bearing many fragments of *Bristolia?* sp. indet. but no *Peachella* specimens, and is here considered a misidentification. The latter specimen could not be located for inclusion in the present study; the catalog number now refers to a small specimen of *Mesonacis fremonti* (Walcott, 1910), and no record could be found of this number having been previously applied to a different specimen (M. A. Kooser, pers. comm., May 2008). Nelson (1976, pl. 8) figured a cephalon of *P. iddingsi* but did not provide a specimen number.

Occurrence.—CALIFORNIA: **Marble Mountains, San Bernardino County:** LACMIP locality 24870 (thin, dark buff to orange weathering limestone interbeds in upper 5 meters of Latham Shale), UCR 10 (bulk collection), UCR 10001 (shale float from



section L-4 on western side of range), UCR 10155 (shale 1.28 to 1.46 meters above base of section L-5 on western side of range, 15.80 to 15.98 meters above base of Latham Shale), UCR 10156 (shale 1.50 to 1.63 meters above base of section L-5 on western side of range, 16.02 to 16.15 meters above base of Latham Shale), UCR 7621 (in uppermost Latham Shale on eastern side of range), UCR 9724 (float from upper Latham Shale on eastern side of range, probably from marker bed 20.40 to 20.44 above base of Latham Shale), UCR 10523 (19.87 meters above the base of the Latham Shale in section on eastern side of range; see LaGrange, 2002); all in the Latham Shale (see also Webster et al., 2003). **Providence Mountains, San Bernardino County:** UCR 7003 (bulk collection), and upper portion of the Latham Shale (Webster et al., 2003). **Grapevine Mountains, Inyo County:** Titanother Canyon section, LACMIP locality 24908, USGS collections 4144-CO and 7183-CO (Palmer and Halley, 1979), in the upper Thimble Limestone Member, Carrara Formation. **Funeral Mountains, Inyo County:** Echo Canyon section, USGS collection 4152-CO (Palmer and Halley, 1979; also personal observation), in the Thimble Limestone Member, Carrara Formation. **Nopah Range, Inyo County:** Emigrant Pass section, 45 meters to 65 meters above base of Carrara Formation (Fowler, 1999; see also Mount, 1980b), including ICS-10110 and UCR 7914 (bulk collections from the Carrara Formation), LACMIP 11621 (approximately 48 meters above base of Carrara Formation), and LACMIP 11622 (approximately 55 meters above base of Carrara Formation). **Eagle Mountain, Inyo County:** 43.5 meters to 47 meters above base of Carrara Formation (E. Fowler, pers. comm., July 2000). **Resting Springs Range, Inyo County:** USGS collection 3675-CO (Palmer and Halley, 1979). **Last Chance Range, Inyo County:** Cucumungo Canyon section, USGS collection 4161-CO (Palmer and Halley, 1979), in the Mule Spring Limestone Formation.

NEVADA: **Groom Range, Lincoln County:** USGS collections 3694-CO, 3786-CO, and 3787-CO (Palmer and Halley, 1979), ICS-10029 (bulk collection), USNM localities 60h and 313g (arenaceous shales and thin, interbedded limestone in the Groom Mining District at the south end of the Timpahute Range; Walcott, 1910); all in the Thimble Limestone Member, Carrara Formation. **Desert Range, Clark County:** USGS collection 7193-CO (Palmer and Halley, 1979), in the upper Thimble Limestone Member, Carrara Formation. **Delamar Mountains, Lincoln County:** Big Lime Mountain section, ICS-1069 (bioclastic limestone block from float); Oak Spring Summit section, ICS-1005 (thin limestone about 50 meters below base of Combined Metals Member) and ICS-1046 (bioclastic limestone block from float); all in the Delamar Member of the Pioche Formation. **Chief Range, Lincoln County:** Klondike Gap section, UCR 10081 (28 meters below base of Combined Metals Member, section C of Webster [2007c]), UCR 10218 (21.2 to 20.9 meters below base of Combined Metals Member, section C of Webster [2007c]), and UCR 10083 (12.5 meters below base of Combined Metals Member, section B of Webster [2007c]), all in the Delamar Member of the Pioche Formation. **Highland Range, Lincoln County:** Happy Face section, ICS-10129 (collection from float); Log Cabin Mine section, ICS-10116 (3.5 to 4.5 meters above base of measured section); USNM locality 30 (arenaceous shales on west

slope of Highland Range, 12.8 km north of Bennett Springs and approximately 12.8 km west of Pioche; Walcott, 1910); all in the Delamar Member of the Pioche Formation. **Spring Mountains, Clark County:** Jaybird Ridge North Canyon section, ICS-10091 (bulk collection); Jaybird Ridge main section, ICS-1530 (bioclastic limestone 63.5 meters above top of Zabriskie Quartzite); both in the Thimble Limestone Member, Carrara Formation. **Toiyabe Range, Lander County:** ICS-1364 (shaly limestone). **Prospect Peak, Eureka County:** USNM locality 52, arenaceous shales above the massive-bedded sandstones of the Prospect Mountain Formation (type locality; Walcott, 1910). Also known from USNM locality 22s (exact provenance uncertain).

All constrained occurrences are in a narrow stratigraphic interval in the upper *Bristolia* Zonule (lower *Peachella iddingsi* Zonule of the developing Dyeran biostratigraphic scheme; Webster, 2003), Dyeran, traditional "Lower Cambrian" of Laurentia, where the species co-occurs with *Bristolia fragilis* Palmer in Palmer and Halley, 1979, *Bristolia* aff. *fragilis* A (see Webster et al., 2003), *Paranephrolenellus besti* Webster, 2007c, *Mesonacis fremonti*, *Olenellus nevadensis* (Walcott, 1910), *Olenellus* aff. *terminatus* (see Webster et al., 2003), and the top of the ranges of *Eopeachella angustispina* and *Bristolia anteros* Palmer in Palmer and Halley, 1979. Taxonomic co-occurrence data from multi-specimen stratigraphically unconstrained slabs are consistent with this range. The first appearance of *Peachella iddingsi* postdates that of *Eopeachella angustispina* and predates that of *P. brevispina*. However, *P. iddingsi* co-occurs with *E. angustispina* in collections ICS-1005 and ICS-1046, and Fowler (1999) noted a single occurrence of *P. iddingsi* above the known range of *P. brevispina* at Emigrant Pass.

Discussion.—The preceding text includes information from recently collected specimens and revises and expands upon the descriptions provided by previous workers. It includes the first formal description of the thorax of *Peachella iddingsi*; a specimen bearing a thorax (LACMIP 11621; Fig. 4.1, 4.2 herein) had been figured without description by Palmer and Repina (1993, fig. 4.2; 1997, fig. 257.2).

Peachella iddingsi is the type species of the genus, and was included as the generic exemplar in a cladistic analysis of olenelloid phylogeny by Lieberman (1998). In that study, the species was apparently coded from examination of 16 specimens (Lieberman, 1998, p. 67; excluding an apparent misidentification [above]). During the course of the present study 116 specimens were examined in detail, representing all museum specimens of which the author is aware plus much newly collected material. This array of specimens yields new insight into the ontogeny and morphology of the species, and reveals previously undocumented intraspecific morphological variation. As a result, several of Lieberman's (1998) character state assignments for *P. iddingsi* must be revised. The ocular lobes gradually decrease in dorso-ventral elevation between the mid-point of the ocular lobes and the axial furrows (character 15, state 0; this had been coded by Lieberman [1998] as being of constant dorso-ventral elevation [state 1]; see Figs. 3.3, 4.6). The ocular lobes are separated from the extraocular area by a prominent shelf (character 16, state 0; this had been coded by Lieberman [1998] as merging smoothly into the extraocular area [state 1]; see Figs. 2.2, 2.4, 4.6). An ocular furrow is

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FIGURE 8—Morphometric data for *Peachella iddingsi* (squares), *P. brevispina* (circles), and *Eopeachella angustispina* (triangles), plotted against sagittal glabella length (mm). 1, strength of the adgenal angle, measured as the angle of anterior deflection of the distal portion of the posterior cephalic margin relative to the proximal portion of the posterior cephalic margin, when traced abaxially. 2, proportional distance of the adgenal angle along the posterior cephalic margin, measured as the ratio between the length of the posterior cephalic margin distal to the adgenal angle (to the base of the genal spine) and the length of the posterior cephalic margin proximal to the adgenal angle (to the axial furrow). 3, advancement of the genal spine bases, quantified as the distance along the sagittal axis from the posterior margin of the glabella to a transverse line between the genal spine bases. 4, angle of divergence of the proximal portion of the posterior cephalic border (between the axial furrow and the adgenal angle) from a transverse line. 5, glabella width at SO (tr.) relative to basal glabella width (tr.). 6, transverse distance between the genal spine bases.

not prominent (character 19, state 1; this had been coded by Lieberman [1998] as being prominent [state 0]); an ocular furrow was seen on just one specimen, and even then was very shallow (Fig. 2.9). At maturity, the ocular lobes diverge from the glabella (character 20) at 25° to 40° (measured as the angle between the exsagittal axis and a line from the posterior tip of ocular lobe to the contact of the abaxial margin of the ocular lobe with the adaxial margin of L3; Fig. 7.1). These observed data fall between Lieberman's (1998) states 0 (10° to 20° angle) and 2 (45° angle), and no state listed by Lieberman (1998) is applicable. Lieberman (1998) had coded this character as being parallel to the sagittal line (state 1). The posterior tips of the ocular lobes are developed opposite the anterior third of L1 (Fig. 3.5), S1 (Fig. 2.7), or rarely the posterior half of L2 (Fig. 4.8; character 23, states 2, 3, and 5; this had been coded by Lieberman [1998] as opposite the medial portion of L1 only [state 2]). S3 is oriented anterolaterally away from the sagittal axis until it contacts the ocular lobes and is therefore carat-shaped on each side of the glabellar axis (Fig. 3.1), and/or is not prominently incised (Fig. 2.6, 2.8); character 27 is therefore polymorphic [states 2 and 3; this had been coded by Lieberman (1998) as straight (state 0)]. S3 crosses the glabellar axis and is therefore conjoined medially (Fig. 3.1, 3.4), and/or is not prominently incised medially (Fig. 2.6, 2.8); character 28 is therefore polymorphic [states 0 and 2; this had been coded by Lieberman (1998) as not prominently incised medially (state 2) only]. Similarly, the middle sector of S3 is sometimes not prominently incised (Fig. 2.6, 2.8), and character 29 is also polymorphic [states 0 and 2; this had been coded by Lieberman (1998) as linear (state 0) only]. L1, L2, and L3 are gently convex in transverse convexity (character 30, state 0; Fig. 3.2; this had been coded by Lieberman [1998] as strongly convex [state 1]). S2 is sometimes not prominently incised medially (Figs. 2.6, 2.8, 3.5); it is therefore polymorphic for its orientation [character 31, states 1 and 2; this had been coded by Lieberman (1998) as transverse (state 1) only], its depth over the sagittal axis [character 33, states 0 and 2; this had been coded by Lieberman (1998) as conjoined medially (state 0) only], and its medial orientation [character 34, states 0 and 2; this had been coded by Lieberman (1998) as straight (state 0) only]. Extraocular genal caeca, anterior ocular lines, intergenal ridges, and genal ridges were present on some individuals but not on others (see above), and characters 45, 46, 47, and 48 are all therefore polymorphic (states 0 and 1; these had been coded by Lieberman [1998] as absent, not visible, prominently developed, and visible as a trace, respectively). An adgenal angle (intergenal angle of previous authors; see Webster, 2007b) can be located close to the base of the genal spine (character 53, state 0; as coded by Lieberman [1998]; Fig. 4.4), but is absent on some specimens (state 3, Fig. 3.1, 3.4); character 53 is therefore polymorphic (states 0 and 3). At maturity, the strength of the adgenal angle ranged from 0° (absent) up to 34° (Fig. 8.1; character 55, equivalent to states 0 and an undefined state between states 0 and 1; this had been coded by Lieberman [1998] as state 0 only). An intergenal spine is either not developed (Fig. 2.6) or is represented by a distinct dorsal swelling or node (Figs. 4.5, 5.5, 5.6; character 54, states 0 and 1; this had been coded by Lieberman [1998] as being a small pointed spine [state 2]). Thoracic segments T5 to T8 are blunt-tipped and pleural spines are not obviously developed (Fig. 4.1, 4.2, 4.3; Lieberman (1998, character 63) coded the length of the pleural spines as extending two thoracic segments back (state 1), but a coding of state 2 ("do not sweep significantly back") might be more appropriate. Similarly, because thoracic pleural spines are not obviously developed, the pleural furrows terminate on the inner pleural region (character 67, state 0; this had been coded by Lieberman [1998] as extending onto the pleural spines [state 1]) and the width of the pleural spines on T5 to T8 (character 72) cannot be determined; neither state for character 72 is appropriate (Lieberman [1998] coded this as state 0 [spine width more than two-thirds length of medial part

of inner pleural region]). Whether considered individually or as a group, the lateral margins of the prothoracic axial rings either converge posteriorly or diverge then converge posteriorly (character 65, state 1; this had been coded by Lieberman [1998] as being sub-parallel [state 0]; Fig. 4.2, 4.3). Axial nodes are present on T1 to at least T9 (character 66, state 0; this had been coded by Lieberman [1998; see also Sundberg, 2000] as absent [state 1]; Fig. 4.3). The effects of these revised character state assignments on Lieberman's (1998) cladogram topology will be discussed elsewhere in a full systematic revision of the Olenelloidea. The high degree of morphological variation exhibited within *P. iddingsi* is typical of stratigraphically old, phylogenetically basal trilobites (Webster, 2007a).

Features distinguishing *Peachella iddingsi* from *P. brevispina* and *E. angustispina*, the two most similar species, are discussed under those species.

PEACHELLA BREVISPINA Palmer in Palmer and Halley, 1979
Figures 9, 10, 11

Peachella brevispina PALMER AND HALLEY, 1979, pp. 13, 75, pl. 5, figs. 1–3; MOUNT, 1980b, pp. 79, 80; STITT AND CLARK, 1984, pp. 145, 146–150, figs. 2a, b, 3; WHITTINGTON, 1989, pp. 131, 132, 133, 137 [often as *Peachella*]; HAHN, HAHN, AND BRAUCKMANN, 1992, p. 93; FOWLER, 1999, pp. 48, 49; LIEBERMAN, 1999, pp. 141, 143; SMITH AND LIEBERMAN, 1999, pp. 461, 462; LIEBERMAN, 2002, p. 699; LIEBERMAN, 2003, p. 63.

Description (mature morphology).—Cephalon semicircular in outline; proximal portion of posterior cephalic margin angled slightly posteriorly away from axial furrow, straight (Fig. 9.1) or with distal portion flexing anteriorly by 15° to 25° relative to proximal portion at rounded adgenal angle located three-fifths to four-fifths of distance along posterior margin from axial furrow to base of genal spine (Fig. 9.7, 9.8). Greatest observed cephalic length approximately 15 mm (sag.). Genal spines wide, bluntly rounded, bulbous and inflated in relief; posterolaterally oriented; base opposite or posterior to LO; length less than half cephalic length (sag.). Proximal portion of ventral surface of genal spine not inflated, contiguous with cephalic doublure, clearly demarcated from inflated portion of genal spine (Fig. 9.6, 9.10). Intergenal spine typically absent; rarely represented by small dorsal swelling on posterior cephalic border between adgenal angle and base of genal spine (Fig. 9.7, 9.8). Cephalic border poorly defined by an extremely weak cephalic border furrow which is virtually absent posterolaterally on some specimens (Fig. 9.1, 9.9) or by a break in slope only; evenly or acutely rounded dorsally anteriorly, steeply sloping to cephalic margin, gently sloping into cephalic border furrow; width of anterior border opposite junction of ocular lobes with LA approximately half length (exsag.) of LO; posterior border not defined or defined by extremely weak border furrow (Fig. 9.7, 9.10), narrows adaxially and poorly defined or absent at base of genal spine. Lateral cephalic border at base of genal spine distinctly broadened laterally and slightly inflated dorsally posterior to point opposite lateral margin of L2 or L1, merging into swollen genal spine. Glabella extends to anterior border furrow, 88% to 95% of cephalic length (sag.), hourglass-shaped, constricted at S1. Maximum width of LA up to 30% wider (tr.) than basal glabellar width. Posterior margin of glabella strongly convex posteriorly. Axial furrow very shallow. SO effaced or extremely shallow, when evident deepest abaxially, abaxial end slightly anterior to adaxial end (Fig. 9.2). S1 effaced or extremely shallow, when evident deepest abaxially, oriented strongly anterolaterally abaxially (Fig. 9.2). LO and L1 subtrapezoidal, narrowing anteriorly. S2 effaced or extremely shallow, when evident deepest in slot position, isolated from axial furrow, abaxial end slightly anterior to adaxial end (Fig. 9.2). L2 and L3 merged distally, widening (tr.) anteriorly until contact with ocular lobes.

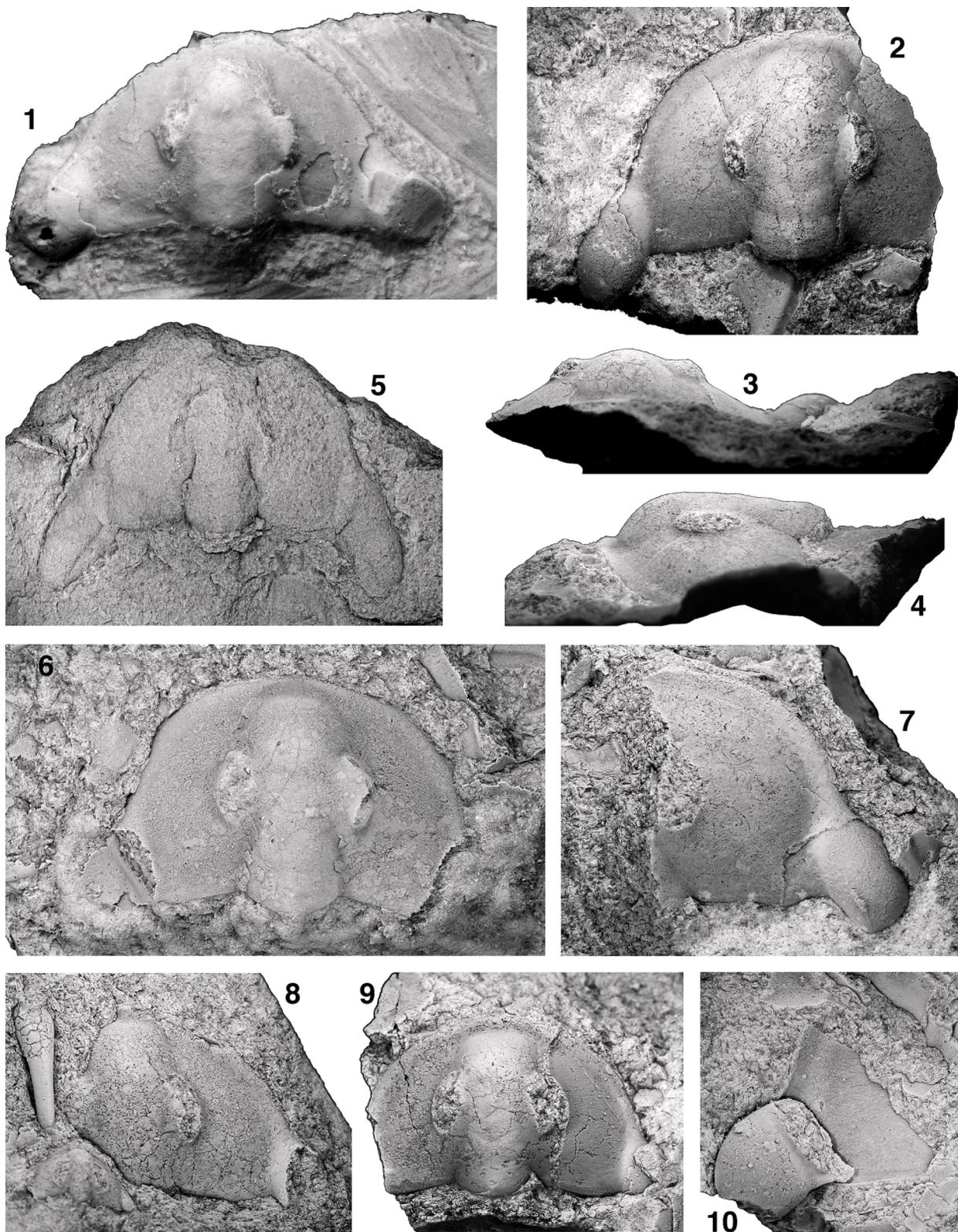


FIGURE 9—Morphologically mature cephalons of *Peachella brevispina*. 1, holotype cephalon, dorsal view, USNM 177236 (latex replica), $\times 4$; 2–4, mostly exfoliated cephalon in dorsal, anterior, and left lateral views, FMNH PE58085, $\times 3$; 5, large, compacted cephalon preserved in siltstone, dorsal view, FMNH PE58114, $\times 2$; 6, incomplete cephalon with doublure at genal spine base exposed, dorsal view, FMNH PE58093, $\times 3$; 7, partial cephalon, dorsal view, FMNH PE58087, $\times 3$; 8, partial cephalon, dorsal view, FMNH PE58089, $\times 3$; 9, cephalon, dorsal view, FMNH PE58088, $\times 4$; 10, fragmentary cephalon showing ventral surface of genal spine and doublure, ventral view, FMNH PE58091, $\times 3$. 1 from USGS collection 4167-CO, Dublin Hills, Inyo County, California; 2–4 and 6–10 from ICS-1073, Ruin Wash section, Chief Range, Lincoln County, Nevada; 5 from ICS-10113, Log Cabin Mine section, Highland Range, Lincoln County, Nevada. See text for stratigraphic details.

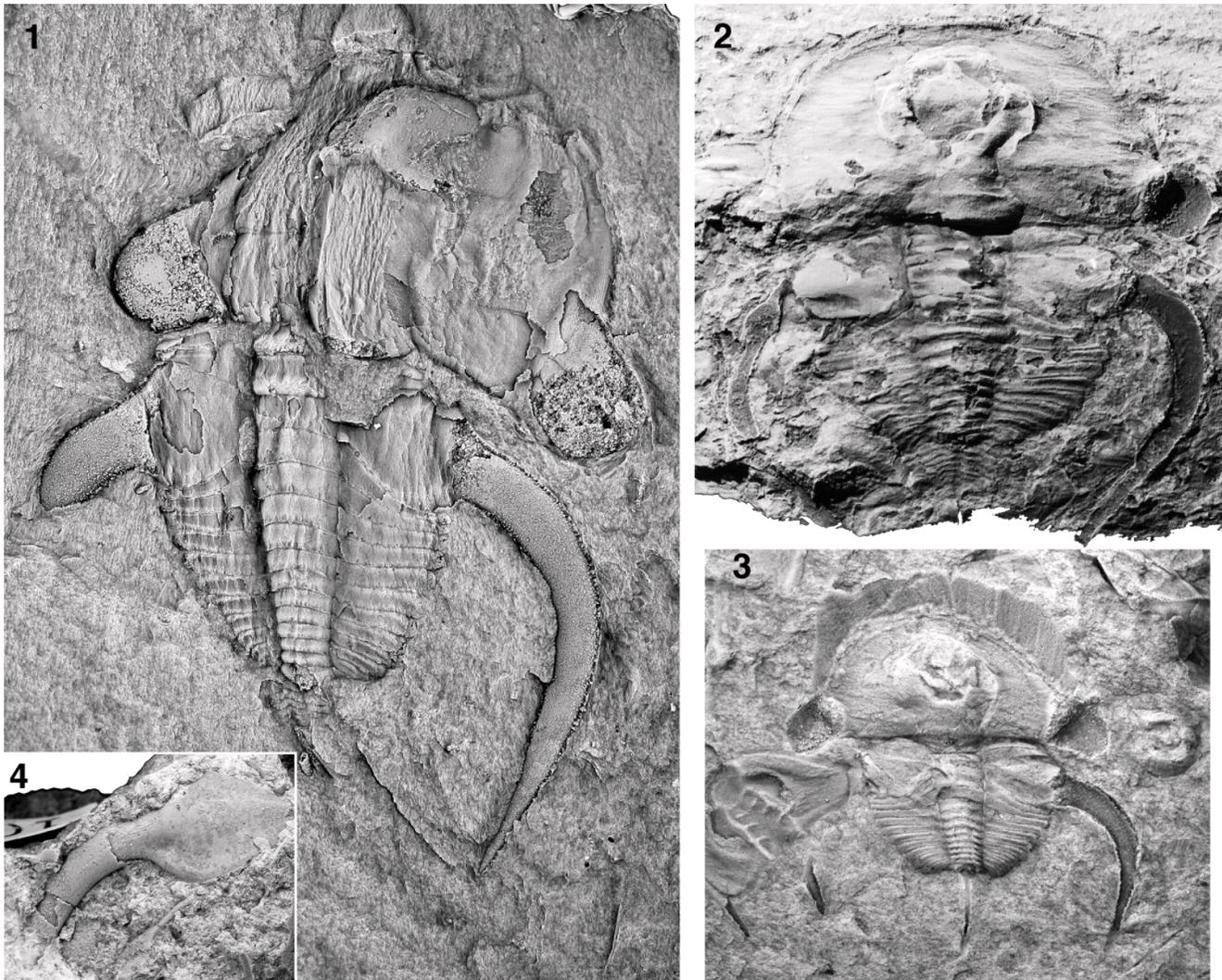


FIGURE 10—Morphologically mature specimens of *Peachella brevispina*. 1–3, articulated specimens showing details of prothorax and opisththorax; 1, tectonized specimen, dorsal view, SDNHM 24548 (latex of counterpart), $\times 4$; 2, tectonized specimen, dorsal view, NSB 3931a, $\times 2$; 3, mildly tectonized specimen, dorsal view, NSB 3932c, $\times 4$; 4, isolated left pleura and pleural spine of third thoracic segment, dorsal view, FMNH PE58092; $\times 3$. 1–3 from Emigrant Pass section, Nopah Range, Inyo County, California; 4 from ICS-1073, Ruin Wash section, Chief Range, Lincoln County, Nevada. See text for stratigraphic details.

S3 effaced or extremely shallow, when evident oriented anterolaterally away from axis until contact with ocular lobes (Fig. 9.1, 9.6). LA slightly wider (tr.) than long (sag.), 30% to 45% of glabellar length (sag.), slightly inflated dorsally above extraocular area (Fig. 9.3), summit barely higher than posterior glabellar lobes (Fig. 9.4); widest point slightly anterior to contact with anterior margin of ocular lobes. Small to tiny axial node on LO. Ocular lobes divergent from exsagittal axis by 25° to 32° (measured as angle between exsagittal axis and line from posterior tip of ocular lobe to contact of adaxial margin of ocular lobe with abaxial margin of L3; Fig. 7.1), or 28° to 44° (measured as angle between exsagittal axis and line from most abaxial point along ocular lobe to contact of abaxial margin of ocular lobe with abaxial margin of LA; Fig. 7.2), crescentic, posterior tip close to axial furrow and opposite anterior half of L1 (Fig. 9.8) or S1 (Fig. 9.2, 9.6), convex dorsally; ocular furrow not developed. Interocular area sloping down from ocular lobes to axial furrow (can appear flat and shelf-like on compacted specimens), slightly narrower than width (tr.) of ocular lobes and approximately 20% to 30% width (tr.) of extraocular area opposite L2. Extraocular area sloping relatively steeply down to cephalic border (Fig. 9.3). Weak posterior

ocular line present on some individuals (Fig. 9.7, 9.9). Genal caeca occasionally weakly developed on extraocular area (Fig. 9.6, 9.9). Terrace lines on cephalic doublure and rostral plate (Fig. 10.2). Bertillon markings sometimes developed on dorsal surface of base of genal spine (Fig. 10.1), rarely on dorsal surface of anterior and lateral cephalic border (Fig. 10.1), and questionably rarely on anterior portion of ocular lobes. Hypostome unknown.

Prothorax of 14 segments (Fig. 10.1, 10.2, 10.3); width (tr.) of axis approximately equal to width (tr.) of inner pleural region on T1, gently tapering posteriorly. Axial nodes developed on all segments (Fig. 10.1). Inner pleural regions of T1 and T2 transverse, tapering distally, with straight margins; tips blunt. T3 hyperpleural; pleural spine robust, dolichospinous, sharp-tipped. Inner pleural region of T4 and to progressively lesser extent T5 and T6 tapering, divergent relative to transverse line proximally, curving to more transverse orientation distally. Inner pleural regions of T6 to T10 transverse, parallel-sided, with straight margins. Inner pleural regions of T11 to T14 increasingly divergent, parallel-sided, margins increasingly curved on more posterior segments. Pleurae of T4 to T14 blunt-tipped or with very small sentate pleural spines, progressively longer on more posterior segments. Pleural furrows barely extend onto base of pleural spines of T3 and

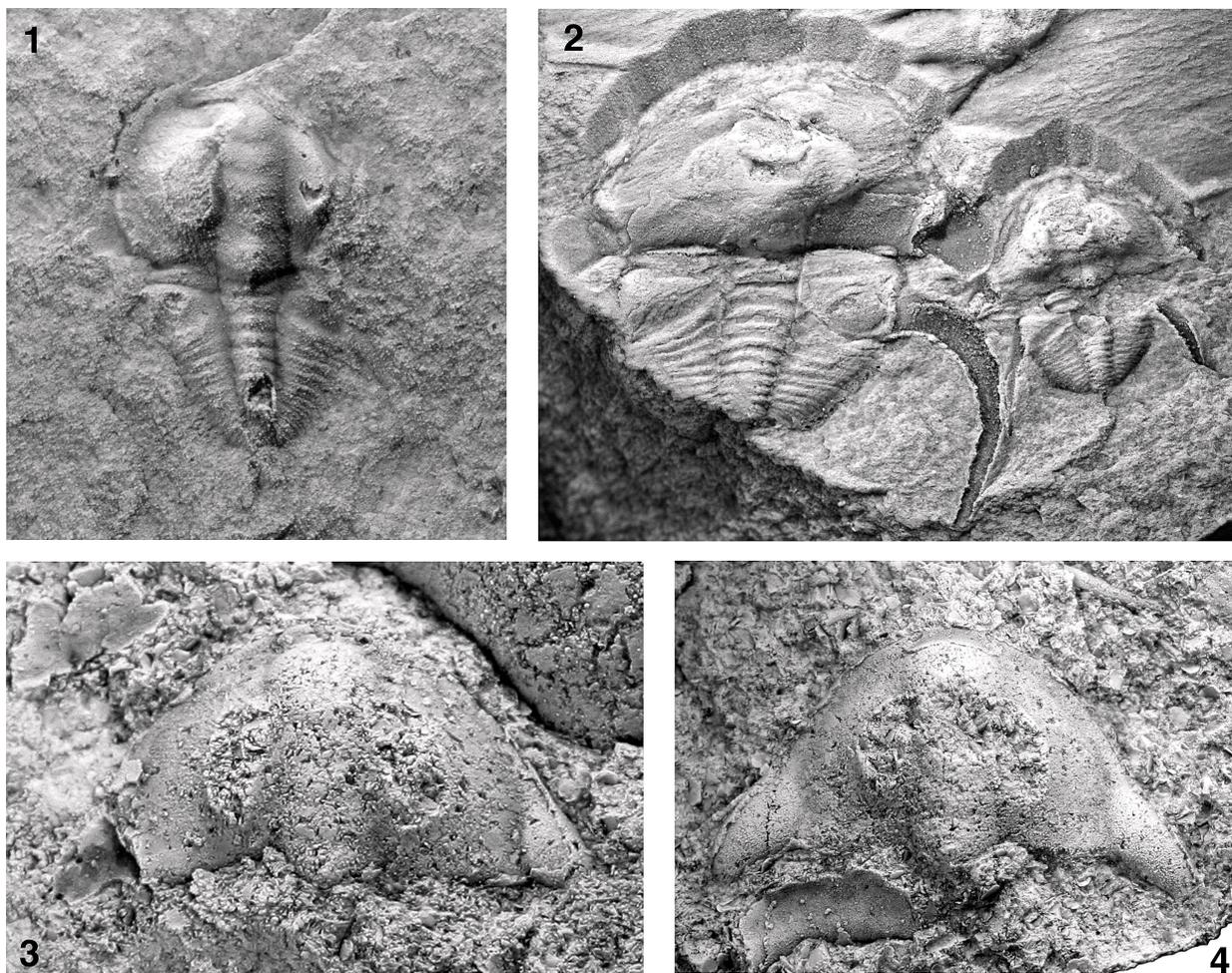


FIGURE 11—Specimens of *Peachella brevispina* in phases 4 and 5 of ontogenetic development of the cephalon. 1, articulated specimen in phase 4 of cephalic development, dorsal view, FMNH PE58108, $\times 10$; 2, articulated specimen in phase 4 of cephalic development (NSB 3932a, right), and another in phase 5 of cephalic development (NSB 3932b, left), dorsal view, $\times 6$; 3, exfoliated cephalon in late phase 4 or early phase 5 of cephalic development, dorsal view, FMNH PE58090, $\times 10$; 4, exfoliated cephalon in late phase 4 or early phase 5 of cephalic development, dorsal view, FMNH PE58086, $\times 7$. 1, 2 from Emigrant Pass section, Nopah Range, Inyo County, California; 3, 4 from ICS-1073, Ruin Wash section, Chief Range, Lincoln County, Nevada. See text for stratigraphic details.

T9 to T14 when spines are developed. Base of pleural spine of T3 may bear terrace lines or bertillon markings, distally grading into granulations on pleural spine (Fig. 10.1, 10.4).

Opisthothorax of at least 9 segments (Fig. 10.1). Long axial spine on T15; presence of axial structures on T16 and more posterior segments unclear. Inner pleural regions of T15 slightly curved, tapering, divergent; straight, parallel-sided, and divergent on all more posterior segments; tips of pleurae of T15 to T21 pointed, tips of more posterior segments unclear. Axis poorly defined by weak axial furrow on T15 to T19; defined by break in slope on more posterior segments. Pleural furrows effaced. Rest of opisthothorax and pygidium unknown.

Ontogeny.—Known specimens range from approximately 2.6 mm (Fig. 11.1, 11.2) to approximately 15 mm in cephalic sagittal length (Figs. 9.5, 9.7, 10.2).

On the smallest known cephalata the axial and glabellar furrows are moderately well incised (Fig. 11.1, 11.2). L2 and L3 barely widen anteriorly, L3 is only marginally wider (tr.) than L2, and the ocular lobes barely contact the anterolateral corner of L3. These are characteristics of the earliest stages of phase 4 of olenelloid cephalic development (above). Transition into phase 4 of cephalic development evidently took place at smaller cephalic size in *P. brevispina* (approximately 2.6 mm sag. length) than in *P. iddingsi* (3.0 mm in sagittal cephalic length; above) and in the

two *Nephrolenellus* species (approximately 3.2 mm sag. length; Webster, 2007b).

During subsequent development in *P. brevispina*, the posterior portion of LO proportionally widened and, as in *Nephrolenellus*, L1 progressively proportionally narrowed (tr.) anteriorly, L2 and L3 proportionally widened (tr.) and shortened (exsag.), and LA proportionally elongated (sag.) and widened (tr.), resulting in the hourglass-shaped glabella typical of morphologically mature individuals. Proportional anterolateral expansion and ultimate merger of the distal portions of L2 and L3 with consequent isolation of S2 from the axial furrow evidently occurred at cephalic lengths somewhere between 2.7 mm and 5 mm: this merger of L2 and L3 defines entry into phase 5 of olenelloid cephalic development (above). In contrast to *Nephrolenellus* species (Webster, 2007b), there is no indication of axial nodes on glabellar lobes anterior to LO over the known portion of *P. brevispina* ontogeny. The axial and glabellar furrows are less well incised on cephalata 3.5 mm and 4.5 mm in sagittal length (Fig. 11.3, 11.4), and are extremely shallow or effaced on cephalata longer than 5 mm (sag.).

Other morphological changes over the sampled portion of ontogeny in *P. brevispina* included considerable modification to cephalic outline: the extraocular area progressively widened (tr.), the posterior cephalic margin progressively became oriented more strongly posteriorly when traced abaxially (trending from 5° to

15° relative to a transverse line; Fig. 8.4), the base of the genal spines became progressively less anteriorly advanced (Fig. 8.3), and the anteriormost point of inflation of the lateral cephalic border became more posteriorly located during phases 4 and 5 of cephalic development (Fig. 7.4). There is no pronounced change in the strength or relative location of the adgenal angle along the posterior cephalic margin over the sampled portion of ontogeny (Fig. 8.1, 8.2). The ocular lobes proportionally shortened (from approximately 47% to just over 30% of sagittal cephalic length), associated with an anterior migration of the posterior tips of the ocular lobes from a point opposite the midpoint of L1 (Figs. 7.3, 11.1).

The shape of the genal spine is unclear on the smallest known specimens, but on a cephalon 4.5 mm in sagittal length (Fig. 11.4) the spines are more elongate and less bulbous at the distal end relative to the morphologically mature condition. On this small specimen the inflation of the genal spine does not extend to the very tip of the spine, which can be seen as a tiny, thorn-like projection extending posteriorly from the posterolaterally oriented inflated portion of the spine. The transition from the swollen to the non-swollen portion of the spine is abrupt. The spine tip is located slightly posterior to the midline of the swollen part of the spine, suggesting that inflation of the genal spine was more pronounced on the outside (abaxial) margin of the spine. This spine tip is absent on all larger specimens, presumably having been either resorbed or inflated so as to be continuous in relief with the rest of the genal spine (see below).

A thorax bearing at least twelve segments is preserved on one of the smallest known specimens (Fig. 11.1). This smallest known thorax is qualitatively similar in all preserved features to the morphologically mature condition (described above) except that it is proportionally narrower (tr.) relative to its length, it is more evenly posteriorly tapered in outline, and the pleurae of all segments posterior to T3 are divergent relative to a transverse line (becoming increasingly so posteriorly). The proportional widening (tr.) of the thorax mirrors the proportional widening (tr.) of LO and the extraocular area during phase 4 of cephalic development.

Holotype.—USNM 177236, designated by Palmer in Palmer and Halley (1979, pl. 5, fig. 1; Fig. 9.1 herein).

Material examined.—USNM 177236 (the holotype); USNM 177237; USNM 177238 (slab bearing three specimens); FMNH PE58085-58094; FMNH PE58108; FMNH PE58114; ICS-1073.3, 6-8, 11, 15; ICS-1197.1, ?; ICS-10110.2; ICS-10113.2; ICS-10129.8; SDNHM 24548; UCR 7914.25; ICS replica collection #1889; four specimens in the private collection of Norm Brown; two specimens in the private collection of Ed Fowler; 37 specimens total.

Occurrence.—CALIFORNIA: **Dublin Hills, Inyo County:** USGS collection 4167-CO, platy limestone in Carrara Formation (type locality; Palmer and Halley, 1979; see also Bates, 1965). **Eagle Mountain, Inyo County:** USGS collection 3679-CO, limestone in Thimble Limestone Member, Carrara Formation (Palmer and Halley, 1979; see also Bates, 1965). **Nopah Range, Inyo County:** Emigrant Pass section, shale and limey shale 59 meters to 64 meters above base of Carrara Formation (Fowler, 1999); bulk, float, and/or unconstrained collections ICS-10110, SDNHM locality no. 3169 (Stitt and Clark, 1984; see also Mount, 1980b), and UCR 7914; UCR 7923, 76.8 meters above base of Carrara Formation (this occurrence has not been confirmed by the author).

NEVADA: **Chief Range, Lincoln County:** Ruin Wash section, ICS-1073, bioclastic limestone above *Bristolia insolens* beds in the upper Delamar Member, Pioche Formation. **Highland Range, Lincoln County:** Happy Face section, ICS-10129; Log Cabin Mine section, ICS-1197 and ICS-10113; all float collections from siltstones and sandstones upper Delamar Member, Pioche Formation. Occurrences in Nevada are documented here for the first time: all previous records of the species were in the Carrara Formation of California. All constrained occurrences are in the upper

Bristolia Zonule (upper *Peachella iddingsi* Zonule of the developing Dyeran biostratigraphic scheme; Webster, 2003), Dyeran, traditional “Lower Cambrian” of Laurentia, where the species co-occurs with *Bristolia fragilis* and *Olenellus nevadensis*. Taxonomic co-occurrence data from multi-specimen stratigraphically unconstrained slabs are consistent with this range. The first appearance of *Peachella brevispina* postdates that of *Eopeachella angustispina* and *P. iddingsi*. The range of *P. iddingsi* may entirely encompass that of *P. brevispina* at Emigrant Pass (see Fowler 1999).

Discussion.—This description includes information from recently collected specimens, and revises and expands upon the descriptions provided by Palmer in Palmer and Halley (1979) and Stitt and Clark (1984). Features of ornament are documented for the first time, as are details of glabellar segmentation, the presence of an occipital node, and the condition of the posterior cephalic border. Several aspects of the original description of the thorax (Stitt and Clark, 1984) must also be revised: axial nodes are present on all prothoracic segments (not just T10–T14; Fig. 10.1), and the tips of the thoracic pleurae sometimes bear tiny setate spines. T15 is considered part of the opisthothorax rather than the prothorax (contra Stitt and Clark, 1984); the prothorax therefore consists of 14 segments. Stitt and Clark (1984) identified a possible pygidium on SDNHM 24548. The structure to which they refer is too poorly preserved and enigmatic to be interpreted and described as a pygidium (Fig. 10.1).

At morphological maturity, *Peachella brevispina* differs from *P. iddingsi*, the only other congeneric species and presumed sister-taxon (Lieberman, 1999), most obviously by possessing shorter, more posterolaterally-oriented genal spines. The anteriormost limit of inflation of the lateral cephalic border is located more posteriorly in *P. brevispina* than in *P. iddingsi* (Fig. 7.4). The degree of cephalic effacement is also typically higher in *P. brevispina*. Other differences are more subtle: the ocular lobes tend to be slightly longer relative to glabellar length in *P. brevispina* than in *P. iddingsi*, although with much overlap in variation (Fig. 7.3); the occipital node is typically smaller in *P. brevispina* than in *P. iddingsi*; and anterior ocular lines, intergenal ridges, and genal ridges are present on some specimens of *P. iddingsi*, but have not been observed on *P. brevispina*. Palmer in Palmer and Halley (1979) noted that the glabella was narrowest at about its mid-length in *P. iddingsi*, but was of nearly constant breadth in *P. brevispina*. This potential interspecific difference is not supported here (Fig. 8.5). Differences from *Eopeachella angustispina* are discussed under that species.

Genus EOPEACHELLA new genus

Type species.—*Eopeachella angustispina* n. sp., by monotypy.

Diagnosis.—Biceratopsids of relatively small size (sagittal length of cephalon rarely exceeds 11 mm). Glabella hourglass-shaped, constricted at S1, transverse width of L1 less than width of LO; glabellar furrows very shallow; preglabellar field absent. Ocular lobes short, posterior tips located close to glabella opposite anterior third of L1 or S1. Distal portion of posterior margin of cephalon flexing anteriorly by 35° to 55° relative to proximal portion at rounded adgenal angle located approximately two-thirds of distance along posterior margin from axial furrow to base of genal spine. Intergenal spines absent or represented by tiny swelling. Genal spines just less than half cephalic length (sag.), moderately stout, taper along length to blunt tip, base opposite LO. Lateral cephalic border and base of genal spine distinctly broadened laterally and slightly inflated dorsally posterior to point opposite lateral margin of L2 or L3, maximum inflation at base of genal spine.

Occurrence.—Upper Dyeran, *Bristolia* Zonule of Palmer and Halley (1979); U.S.A. (Nevada).

Etymology.—Named for the lower stratigraphic first appearance and inferred sister-taxon relationship to *Peachella*.

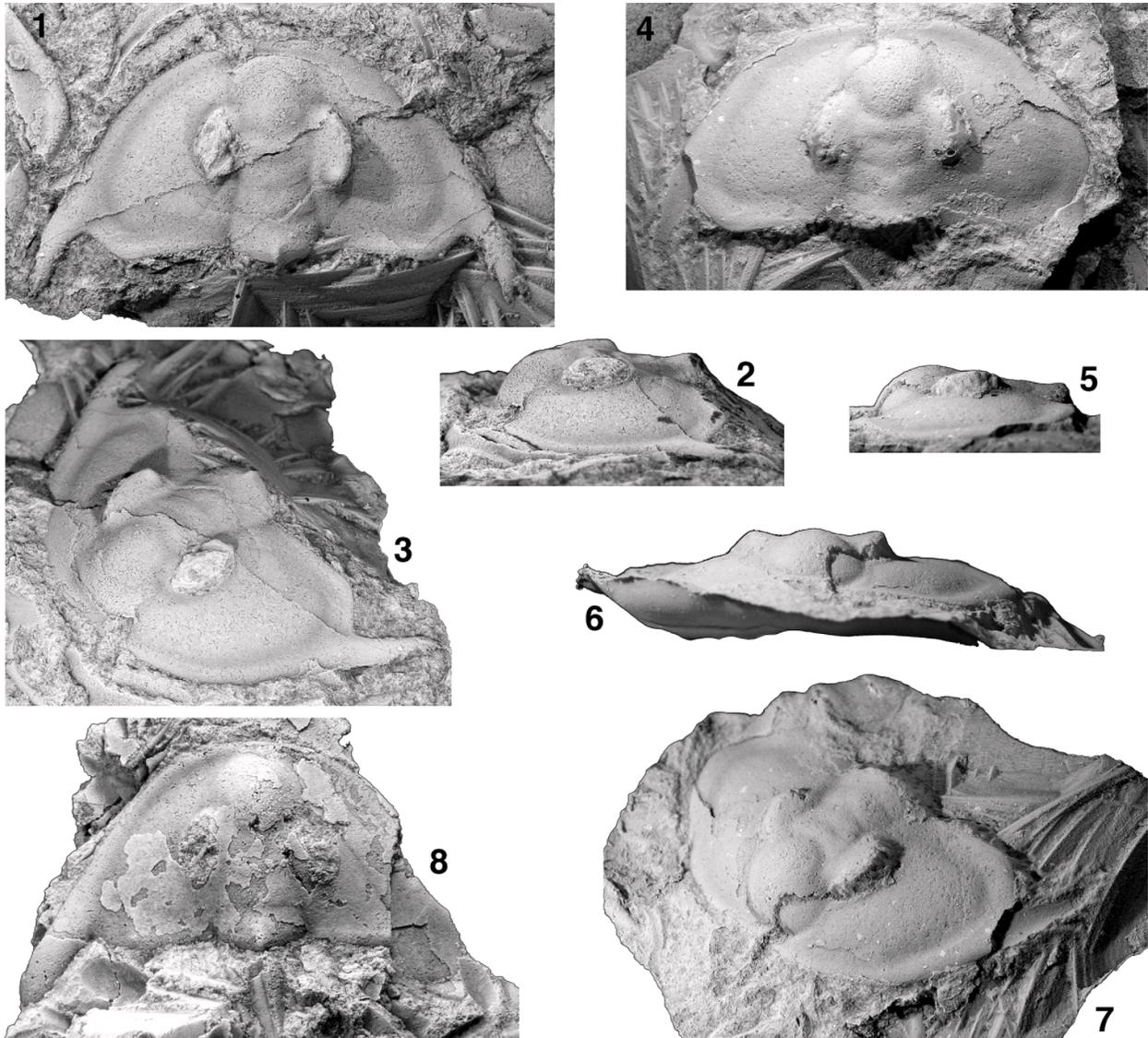


FIGURE 12—Morphologically mature cephalons of *Eopeachella angustispina*. 1–3, holotype cephalon in dorsal, left lateral, and oblique dorsoanterolateral views, FMNH PE58061, $\times 3$; 4–7, Cephalon in dorsal, left lateral, anterior, and oblique dorsoanterolateral views, FMNH PE58060, $\times 3$; 8, partially exfoliated cephalon, dorsal view, FMNH PE58073, $\times 4$. 1–7 from ICS-1003, 8 from ICS-1046, all from Oak Spring Summit section, Delamar Mountains, Lincoln County, Nevada. See text for stratigraphic details.

Discussion.—Based on their very similar oculo-glabella morphology (including general effacement), *Eopeachella* is hypothesized to be the sister-taxon to *Peachella*. The genera are most easily distinguished by the development in *Eopeachella* of moderately stout, blunt-tipped, genal spines which taper along their length, as opposed to the grossly bulbous, inflated genal spines in both *Peachella* species. It is deemed more appropriate to recognize *Eopeachella* as a distinct genus rather than expand the diagnosis of *Peachella* to include *E. angustispina* and lose the historical association of *Peachella* with bulbous genal spines. The relationship of *Biceratops* to this hypothesized *Eopeachella* + *Peachella* clade/grade has yet to be resolved, and will be fully explored in a comprehensive cladistic analysis to be presented elsewhere.

EOPEACHELLA ANGUSTISPINA new species
Figures 12, 13

Peachella n. sp. WEBSTER, 2007c, p. 51.

Description (mature morphology).—Cephalon semicircular in

outline; proximal portion of posterior cephalic margin angled slightly posteriorly away from axial furrow, distal portion flexing anteriorly by 35° to 55° relative to proximal portion at rounded adgenal angle located approximately two-thirds of distance along posterior margin from axial furrow to base of genal spine. Greatest cephalic length estimated to exceed 11 mm (sag.). Genal spine moderately stout, tapers along length to blunt tip, base opposite LO; length just less than half cephalic length (sag.). Intergenal spine typically absent, rarely represented by tiny swelling located midway between adgenal angle and base of genal spine (Figs. 12.8, 13.6). Cephalic border defined by very shallow cephalic border furrow which weakens posterolaterally on some specimens (Fig. 12.8); rounded dorsally anteriorly, steeply sloping to cephalic margin, gently sloping into cephalic border furrow; width of anterior border opposite junction of ocular lobes with LA approximately half length (exsag.) of LO; posterior border narrows adaxially. Lateral cephalic border and base of genal spine distinctly broadened laterally and slightly inflated dorsally posterior to point opposite lateral margin of L2 or L3, maximum inflation

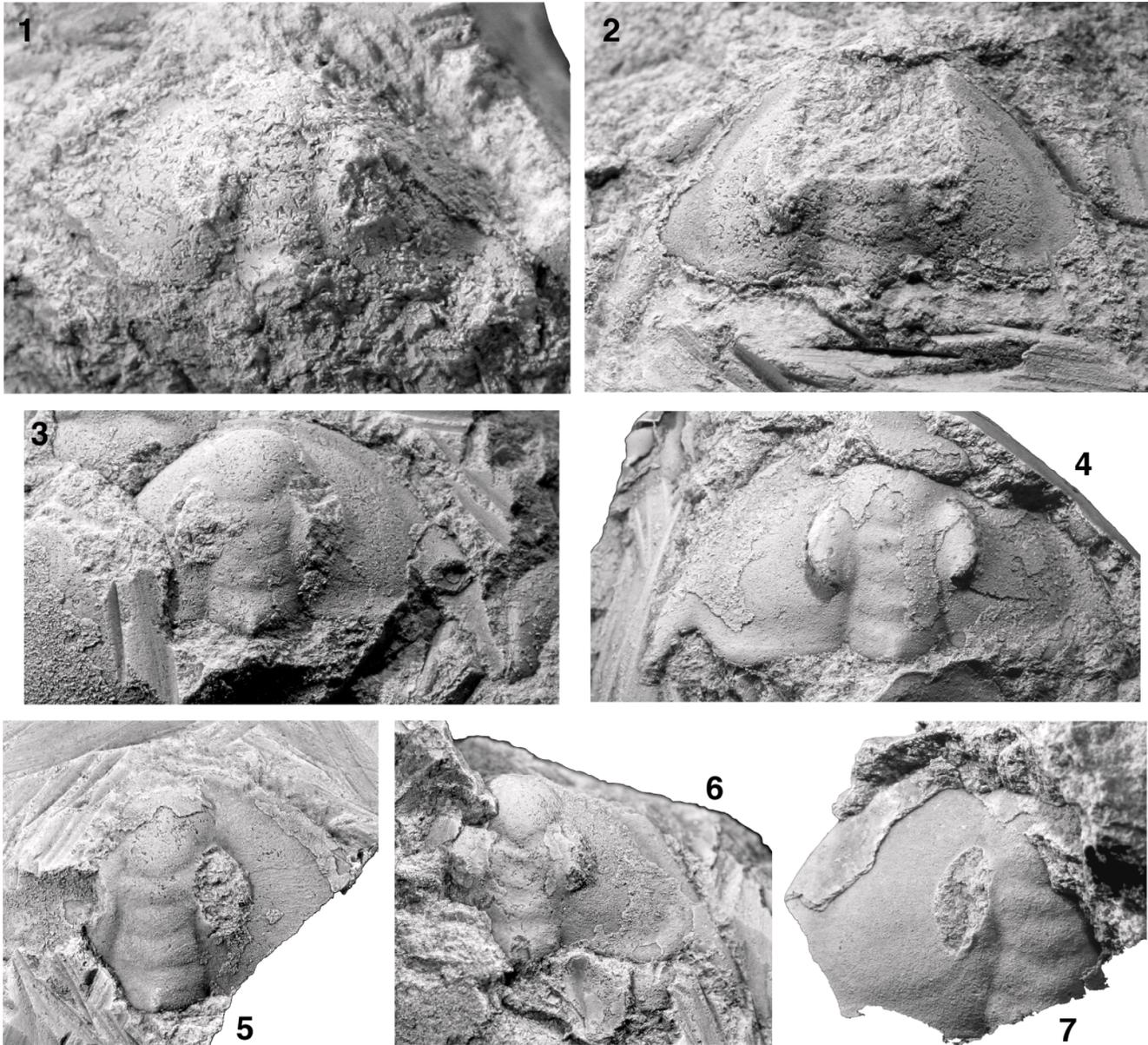


FIGURE 13—Morphologically mature cephalons of *Eopeachella angustispina*. 1, poorly preserved, exfoliated cephalon in early phase 5 of development, dorsal view, FMNH PE58066, $\times 10$; 2, incomplete and exfoliated cephalon, dorsal view, FMNH PE58065, $\times 7$; 3, exfoliated cephalon, dorsal view, FMNH PE58064, $\times 5$; 4, mostly exfoliated cephalon, dorsal view, FMNH PE58063, $\times 5$; 5, incomplete and exfoliated cephalon, dorsal view, FMNH PE58067, $\times 4$; 6, mostly exfoliated cephalon, dorsal view, FMNH PE58062, $\times 3$; 7, incomplete and mostly exfoliated cephalon, dorsal view, FMNH PE58068, $\times 4$. All specimens from ICS-1003, Oak Spring Summit section, Delamar Mountains, Lincoln County, Nevada. See text for stratigraphic details.

at base of genal spine; width (tr.) of border at point of maximum inflation approximately 1.5 times length (exsag.) of LO. Glabella extends to anterior border furrow, 90 to 95% of cephalic length (sag.), hourglass-shaped, constricted at S1. Maximum width of LA up to 17% wider (tr.) than basal glabellar width. Posterior margin of glabella convex posteriorly. Axial furrow and all glabellar furrows very shallow. SO deepest abaxially, abaxial end slightly anterior to adaxial end. S1 deepest abaxially, oriented strongly anterolaterally abaxially. LO and L1 subtrapezoidal, narrowing anteriorly. S2 deepest in slot position, isolated from axial furrow, abaxial end slightly anterior to adaxial end. L2 and L3 merged distally, widening (tr.) anteriorly until contact with ocular lobes. S3 oriented anterolaterally away from axis until contact with ocular lobes; very shallow over axis. LA slightly wider (tr.) than long (sag.), 35% to 45% of glabellar length (sag.), slightly

inflated dorsally above extraocular area (Fig. 12.6), summit slightly higher than posterior glabellar lobes (Fig. 12.2, 12.5); widest point slightly anterior to contact with anterior margin of ocular lobes. Large axial node on LO; L1 typically with low, broad swelling axially (Figs. 12.1, 12.4, 12.7, 13.2, 13.3, 13.4, 13.6, 13.7). Ocular lobes divergent from exsagittal axis by 22° to 28° (measured as angle between exsagittal axis and line from posterior tip of ocular lobe to contact of adaxial margin of ocular lobe with abaxial margin of L3; Fig. 7.1) or 35° to 42° (measured as angle between exsagittal axis and line from most abaxial point along ocular lobe to contact of abaxial margin of ocular lobe with abaxial margin of LA; Fig. 7.2), crescentic, posterior tip close to axial furrow and opposite anterior third of L1 (Fig. 13.3, 13.4) or S1 (Fig. 12.1, 12.4, 12.7), convex dorsally; ocular furrow not developed. Interocular area sloping down from ocular lobes to

axial furrow (Fig. 12.6), slightly narrower than width (tr.) of ocular lobes and approximately one-sixth width (tr.) of extraocular area opposite L2. Extraocular area gently vaulted (Fig. 12.6). Genal caeca occasionally developed on extraocular area (Fig. 13.5). Very weak ridge representing either intergenal ridge or posterior ocular line present on some individuals (Figs. 12.1, 12.4, 13.4, 13.5, 13.7). Hypostome, thorax, and pygidium unknown.

Ontogeny.—Known cephala range from approximately 3.9 mm (Fig. 13.1) to more than 11 mm sagittal length. On all these specimens the anterolateral margins of L3 are in contact with the adaxial margins of the ocular lobes, and L3 is wider (tr.) than L2; the distal portions of L2 and L3 are also merged, and S2 is therefore isolated from the axial furrow. This glabellar morphology is characteristic of phase 5 of ontogenetic development of the olenelloid cephalon (see above). Similar-sized specimens of *P. iddingsi* and *P. brevispina* are also in phase 5 of cephalic development. Morphological changes in *E. angustispina* over this ontogenetic interval were very slight: the ocular lobes slightly shortened such that the posterior tips migrated from a position opposite the mid-length of L1 (Fig. 13.1, 13.2) to opposite the anterior third of L1 or S1. The low, broad swelling on the axis of L1 (also seen on some *P. iddingsi* cephalia; see above) may represent a remnant axial node, although this homology must remain speculative in the absence of knowledge of earlier ontogenetic stages. Ontogenetic loss of axial nodes on glabellar lobes anterior to LO is typical of other biceratopsid taxa (e.g., *Nephrolenellus*, *Biceratops*; Webster, 2007b, in preparation). Effacement of glabellar and axial furrows during phases 4 and 5 of cephalic development (see below) is a presumed synapomorphy of *Eopeachella*, *Peachella*, and *Biceratops* (see also Lieberman, 1998). In *E. angustispina* the effacement took place prior to attaining a cephalic length of 3.9 mm.

Holotype.—FMNH PE58061, designated herein (Fig. 12.1–12.3).

Material examined.—FMNH PE58060–58068; FMNH PE58073; ICS-1003.1, 4, 6, 10, 13, 14; ICS-1005.4–6; 19 specimens total.

Occurrence.—NEVADA: **Delamar Mountains, Lincoln County:** Oak Spring Summit section, ICS-1003 (platy bioclastic limestone approximately 35 m above top of Zabriskie Quartzite), ICS-1005 (thin limestone about 50 meters below base of Combined Metals Member), and ICS-1046 (bioclastic limestone block from float); all in the Delamar Member of the Pioche Formation. All constrained occurrences are in the *Bristolia* Zonule (in and below the *Peachella iddingsi* Zonule of the developing Dyeran biostratigraphic scheme; Webster, 2003), Dyeran, traditional “Lower Cambrian” of Laurentia, where the species co-occurs with *Olenellus nevadensis* and *Bristolia* sp. *Peachella iddingsi* also co-occurs with *E. angustispina* in the higher stratigraphically constrained collection (ICS-1005) and in ICS-1046.

Etymology.—Named for the condition of the genal spines, which are relatively narrow in comparison to those of the two *Peachella* species.

Discussion.—*Eopeachella angustispina* most obviously differs from *P. iddingsi* and *P. brevispina* in lacking bulbous, prominently inflated genal spines. Although the lateral cephalic border at the base of the genal spines distinctly broadens and the tips of the genal spines are blunt in *E. angustispina*, the spines are tapered along their length. In this sense, *E. angustispina* represents a morphological intermediate between biceratopsid taxa possessing “normal” genal spines and the two *Peachella* species. The cephalic (including glabellar) furrows of *E. angustispina* are very shallow but nevertheless typically more prominently incised than in *P. iddingsi* and particularly *P. brevispina*. *Eopeachella angustispina* also subtly differs in cephalic outline from the *Peachella* species: the adgenal angle is greater in *E. angustispina* than in *P. iddingsi* and *P. brevispina* (Fig. 8.1); the range of variation in location of the adgenal angle along the posterior cephalic margin

is much greater in *P. iddingsi* and *P. brevispina* than in *E. angustispina* (in *E. angustispina* it has not been observed to lie as close to the base of the genal spine as it can in either *Peachella* species; Fig. 8.2); the bases of the genal spines are more anteriorly located in *E. angustispina* than in *P. iddingsi* and *P. brevispina* (Fig. 8.3); and the cephalon is typically wider (tr.) between the adaxial margins of the genal spine bases relative to glabellar length (sag.) in *E. angustispina* than in *P. iddingsi* and particularly *P. brevispina* (Fig. 8.6).

In general cephalic outline, in the inflation of the lateral cephalic border at the base of the genal spines, and in the tapering of the genal spines, *E. angustispina* closely resembles *Paranephrolenellus inflatus*. However, in *Paranephrolenellus inflatus* the glabellar, axial, and cephalic border furrows are prominently incised, the genal spines taper to a sharp point, L2 and L3 do not merge distally, LA is wider and much more prominently inflated dorsally, and the ocular lobes are more strongly divergent. Cladistic analysis (to be presented elsewhere) suggests that the similarity in morphology of the lateral cephalic border and base of genal spines between these taxa is convergent.

The first appearance of *Eopeachella angustispina* is stratigraphically lower than that of either *Peachella* species, although the top of its range overlaps with *P. iddingsi* (collections ICS-1005 and ICS-1046). The previously undocumented occurrence of *E. angustispina* and of *P. brevispina* (above) in the Delamar Member raises the diversity of olenelloid trilobites in that unit to 20 species (see also Webster, 2007c), exceeding that in all other coeval units.

ON THE ORIGIN OF THE DERIVED FEATURES OF PEACHELLA

Peachella has long been diagnosed by its general cephalic effacement and its prominently inflated, bulbous genal spines. However, the ontogenetic and phylogenetic origins of these derived features have remained enigmatic. The material examined and described above permits insight into these issues.

As discussed above, *Eopeachella angustispina* is considered to be the sister-taxon to *Peachella*. The stratigraphic order of first appearances of the species (*E. angustispina* below *P. iddingsi* below *P. brevispina*) cannot be interpreted in terms of a simple anagenetic evolutionary lineage: the fact that *E. angustispina* co-occurs with *P. iddingsi* and that the stratigraphic range of *P. brevispina* may be contained within that of *P. iddingsi* (above) demonstrates that *Eopeachella* and *Peachella* evolution involved cladogenetic speciation.

Cephalic effacement.—In both *Peachella* species the effacement of cephalic furrows occurred progressively during relatively late stages of ontogeny (phases 4 and 5 of cephalic development). In *Peachella iddingsi*, the axial and glabellar furrows are well incised on a cephalon 2.2 mm in sagittal glabellar length (Fig. 5.1); the furrows are less prominent on cephalia 3.2 to 3.7 mm in sagittal length (Fig. 5.2, 5.3, 5.4), and are very shallow on cephalia 3.9 mm in sagittal length (Fig. 5.5). Traces of glabellar furrows can often be seen even on large cephalia (Figs. 2.7, 3.1). In *Peachella brevispina*, the axial and glabellar furrows are moderately well incised on cephalia 2.6 mm in sagittal cephalic length (Fig. 11.1, 11.2); the furrows are less prominent on cephalia 3.5 mm and 4.5 mm in sagittal length (Fig. 11.3, 11.4), and are extremely shallow or effaced on cephalia longer than 5 mm (sag.). Cephalic effacement is similarly ontogenetically dynamic in *Biceratops* (unpublished data). It is presently unknown whether cephalic effacement also progressively occurred during the ontogeny of *Eopeachella*: the smallest known specimen of *E. angustispina* (approximately 3.9 mm in sagittal cephalic length; Fig. 13.1) bears very shallow cephalic furrows. Other biceratopsid taxa such as *Nephrolenellus* spp. (Webster, 2007b) and *Bristolia* spp. (Palmer and Halley, 1979) possess well incised cephalic furrows throughout ontogeny. It therefore seems parsimonious to interpret

progressive cephalic effacement during ontogeny as a characteristic which evolved in the last common ancestor of *Biceratops*, *Eopeachella*, and *Peachella*.

This ontogenetic trend towards cephalic effacement is mirrored by a general stratigraphic and phylogenetic trend. The degree of cephalic effacement is typically somewhat less in *Eopeachella angustispina* than in *Peachella iddingsi*, and effacement is most extreme in *P. brevispina*. Such a coupling between an ontogenetic and a stratigraphic/phylogenetic trend could be achieved through evolutionary rate and/or timing modifications to development (Webster and Zelditch, 2005).

McNamara (1986) suggested that effacement of glabellar furrows was associated with peramorphic development of the glabella from the "expansion stage" (roughly equating to phases 3, 4 and 5 of cephalic development as defined above) into the "development stage" (equating to phase 5 of cephalic development as defined above) in Cambrian trilobites. This purported association is not tenable for olenelloid trilobites, however. In terms of glabellar shape and segmentation (which define the various stages in McNamara's [1986] divisions of glabellar ontogeny and the various phases of cephalic development used here), the condition in morphologically mature (phase 5) *Biceratops*, *Eopeachella*, and *Peachella* (which are effaced) is no more ontogenetically "advanced" than in morphologically mature (phase 5) *Bristolia* or *Olenellus* species (which are not effaced). Furrow effacement in olenelloids is a progressive ontogenetic feature superimposed upon and independent of a phylogenetically conserved pattern of ontogenetic shape change in the glabella.

Furrow effacement similar to that observed in *Peachella* convergently evolved in many other trilobite groups (e.g., "illaeni-morph" trilobites and many agnostine and styginid genera; see Shergold, 1977; Lane and Thomas, 1983; Fortey and Owens, 1990, 1997). As in *Peachella* (above), the effacement is ontogenetically dynamic in at least some of these other cases (e.g., the olenid *Leurostega aphelix* Robison and Pantoja-Alor, 1968; see Robison and Pantoja-Alor, 1968, pl. 103, figs. 1–4, 7–9). Comparative morphology at early (pre-effacement) ontogenetic stages may therefore be useful in resolving phylogenetic placement of effaced taxa within otherwise non-effaced clades.

The functional significance of effacement is unknown, and there is no consistent correspondence between effacement and environment or exoskeletal thickness among other effaced trilobites (Fortey and Owens, 1997). Lane and Thomas (1983) noted that effacement in styginids and illaenids was often associated with an increase in dorsal convexity of the exoskeleton and an increase in width of the axis. The *Peachella* cephalon is moderately strongly vaulted for an olenelloid (Figs. 3.2, 9.3), supporting a relationship between convexity and effacement (although the non-effaced cephalon of *Nephrolenellus* is even more strongly convex; Webster, 2007b). However, the axis of *Peachella* is of typical proportions for an olenelloid, and there is no apparent association between axis width and effacement in these trilobites. In terms of environment, *Peachella* ranged across the Cordilleran shelf (Fig. 1) and is found in a variety of lithologies. In *P. iddingsi* there is variation in degree of effacement among similar sized specimens within single collections (e.g., compare Fig. 2.6 and 2.7; or Fig. 2.8 and 2.3 or 2.5). When this within-collection variation is taken into account, there are no obvious differences among localities in the degree of effacement. This suggests that degree of effacement was not an ecophenotypic response to environmental heterogeneity, at least within species on the geographic scale sampled here. There is similarly little support for ecophenotypy as an explanation for interspecific differences in degree of effacement. *Peachella* is restricted to a time of general relative shallowing (Webster, 2007c), but the lowest occurrence of *Eopeachella* (and the inferred phylogenetic origin of effacement in the clade) is in the lower portion of the Delamar Member in an interval of relative deepening (Webster, 2007c). *Eopeachella*

and *Peachella* (and also the stratigraphically younger *Biceratops*) co-occur with many other trilobites which do not show analogous ontogenetic or stratigraphic trends toward effacement.

Genal spine inflation.—The present study reveals that the characteristic bulbous, inflated, blunt-tipped genal spine morphology of morphologically mature *Peachella* specimens was also progressively attained during ontogeny. At phase 3 of cephalic development in *P. iddingsi* the base of the genal spine is only slightly inflated, and the spine tapers along its length in the style of a "typical" trilobite (Fig. 5.1). During phase 4 of cephalic development the genal spines become progressively more inflated (compare Fig. 6.1 and 6.6 to Fig. 5.2, 5.3, and 5.4), and by early phase 5 of cephalic development the genal spines are essentially of mature morphology (Fig. 5.5, 5.6). Some specimens in phase 5 of cephalic development retain a tiny thorn-like projection at the distal tip of the genal spine (Figs. 2.3, 2.10, 4.4, 5.5, 5.7). Assuming that this projection represents the true tip of the genal spine, this suggests that the inflation of the spine progressed in a proximal-to-distal direction down the spine during phases 3, 4, and 5 of ontogeny (in a crudely similar fashion to the pattern of inflation of an elongate party balloon). The location of this projection indicates that the spine is more prominently inflated on its abaxial side.

The same ontogenetic pattern of spine inflation apparently also holds for *P. brevispina*. Small cephalons of *P. brevispina* exhibit a genal spine morphology strikingly similar to that of *P. iddingsi* in phase 4 of cephalic development (compare Fig. 11.4 with Fig. 5.3). The small thorn-like projection on the distal tip of the genal spine can also be seen on Fig. 11.4. All known specimens of *Eopeachella angustispina* are in phase 5 of cephalic development and have an essentially mature genal spine morphology which is, at least in the sense of being broad and inflated proximally and tapering to the tip, coarsely similar to the early stage of ontogenetic inflation of the genal spine of *Peachella*. It therefore seems parsimonious to interpret progressive genal spine inflation during ontogeny as a characteristic which evolved in the last common ancestor of *Eopeachella*, and *Peachella*. (*Biceratops* lacks genal spines, and the condition of the last common ancestor of the hypothesized *Eopeachella* + *Peachella* + *Biceratops* clade is therefore unknown.)

The degree of spine inflation is markedly greater in *Peachella* than in the stratigraphically older *Eopeachella*. Mirroring the pattern of cephalic effacement, this crude parallelism between ontogenetic and phylogenetic change in spine inflation could be achieved through evolutionary rate and/or timing modifications to development (Webster and Zelditch, 2005).

Also like cephalic effacement, genal spine inflation convergently evolved (although not to the degree found in *Peachella*) in several trilobite lineages (e.g., the Carboniferous *Cystispina* Richter and Richter, 1939, *Tawstockia* Brauckmann, 1974, and *Spatulina* Osmólska, 1962; see Hahn et al., 1992; Owens and Tilsley, 1995). As in *Peachella* (above), the inflation of the spine in at least some of these taxa did not extend to the tip and, although their early ontogenies are unknown, it is possible that progressive inflation during development also occurred. These phillipsiid taxa inhabited deep-water facies, and are characterized by moderate effacement of glabellar furrows and a reduction or loss of eyes. The spine inflation and effacement of the inferred *Eopeachella* and *Peachella* clade initiated during a time of relative sea-level deepening, but was maintained during subsequent shallowing. *Peachella* is found in a range of lithologies (carbonates, mudstones, and sandstones), rendering an explanation of the spine morphology in terms of adaptation to a particular substrate type (e.g., for support) poorly substantiated. Thus, although study of *Eopeachella* and *Peachella* offers insight into the evolution and development of genal spine inflation that may be general to convergent cases in other trilobite clades, the functional significance of this morphology remains unknown.

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