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Continuous character variation within the *Glossopleura-Anoria-Sonoraspis* plexus: Dolichometopid trilobites from the Cadiz Formation (Cambrian: Miaolingian, Wuliuan), California

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ABSTRACT

Restudy of type, referred, and new material of the dolichometopid trilobites belonging to *Anoria, Glossopleura,* and *Sonoraspis* from the middle Cambrian Cadiz Formation of California, USA, along with material from other formations of the *Glossopleura* Assemblage Biozone in western North America, demonstrates that only two dolichometopid species are present in the Cadiz Formation: *Glossopleura mohavensis* and *G. lodensis. Sonoraspis californica* is confirmed as a junior subjective synonym of *G. mohavensis*, and *Sonoraspis* in general is a junior synonym of *Glossopleura*, as proposed previously. *Anoria* is valid but should be restricted to the species *A. tontoensis. Anoria baton* should be within *Glossopleura*, and the generic position of *Anoria bessus* is unresolved. Most of the qualitative characters used in the past to separate *Anoria, Glossopleura,* and *Sonoraspis* (e.g., palpebral lobe, glabella) prove to be continuously variable with no statistical separation to allow discrete character assignment. Similarly, postcranidial characters, such as thoracic segment numbers, axial spine presence or absence, and enlarged or normal T5 pleural spines, are so variable between genera and within samples as to be unreliable for generic separation, although some characters may assist species diagnoses as non-autapomorphic, "character combination" descriptive elements.

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INTRODUCTION

The Cadiz Formation is a lower-middle (Stage 4–Wuliuan) Cambrian unit exposed in the Marble, Providence, Bristol, and Ship mountains of the Mojave Desert in southeastern California, USA (Hazzard and Crickmay, 1933; Hazzard and Mason, 1936; Fuller, 1980; Foster, 1994, 2011a; Kenney, 2011; Stone et al., 2017). Among the middle Cambrian fossils previously reported from the formation are several species of the dolichometopid trilobite genera *Glossopleura, Anoria,* and *Sonoraspis* (Resser, 1928, 1935; Stoyanow and Susuki, 1955). These genera have been regarded as separate by some (Walcott, 1924; Poulsen, 1927; Resser, 1935; Stoyanow, 1952; Stoyanow and Susuki, 1955) but Lochman (in Cooper et al. 1952) and Palmer (1954) regarded *Sonoraspis* as a junior subjective synonym of *Glossopleura*.

Anoria was named by Walcott (1924) from the Bright Angel Formation of Grand Canyon. Poulsen (1927) named *Glossopleura* based on *Dolichometopus boccar* from the Stephen Formation, plus the new species *G. walcotti* from the Cape Wood Formation, Greenland. *Glossopleura* was differentiated from *Anoria* based on longer eyes and a lack of axial nodes (i.e., “median tubercles” or spine bases) on the thoracic segments or pygidium, plus the lack of an enlarged T5 pleural spine (Poulsen, 1927). *Sonoraspis* was named by Stoyanow (1952) based on material from the Arrojo Formation of Mexico, with a purported mix of *Anoria*- and *Glossopleura*-like characters. Including the dolichometopid *Bathyuriscus*, which is outside the dolichometopid plexus being studied here, at least 10 genus-species combinations have been assigned to what are probably a total of only three species of dolichometopids from the Cadiz Formation.

This study seeks to: 1) determine the validity of *Sonoraspis* and *Anoria*, relative to the more widely reported *Glossopleura*, by quantitatively testing characters used historically to separate the genera; and 2) determine which genera and species of dolichometopids are then actually present in the Cadiz Formation, based on historic type and referred specimens, plus new material collected in recent years. These results will have implications for other species of these genera from other formations as well.

MATERIALS AND METHODS

Materials studied included type material from numerous institutions, plus published specimens, and newly collected field specimens from the Cadiz Formation (UCR locality 7359). Specimens were identified using type specimens of *Glossopleura boccar* (Walcott); *G. mckeei* Resser, 1935; *G. mohavensis* Resser, 1935; *Anoria tontoensis* Walcott, 1924; and *A. lodensis* (Resser, 1935) from the USNM, and *Sonoraspis californica* Stoyanow and Susuki, 1955, from the LACM, plus a number of other specimens (total N=60; Table 1) and additional references such as Oldroyd (1973), Schwimmer (1973), and Campbell (1974). Based on data in Poulsen (1964), all specimens studied were holaspid stage.

As noted above, qualitative characters used historically to separate the genera *Glossopleura*, *Anoria*, and *Sonoraspis* (and sometimes species of *Glossopleura*) were tested to help determine the relationships of specimens from the Cadiz Formation. These analyses involved other species from other formations, and in some cases the results had implications for these taxa and units as well.

To test the distinction between long and short eyes, and between more anteriorly positioned and posteriorly positioned eyes, in *Glossopleura, Anoria,* and *Sonoraspis*, 46 complete or nearly complete specimens and several isolated cranidia were examined (Table 1). Three aspects were measured for these specimens: 1) eye length (EL), more specifically as a proxy for palpebral lobe length; 2) glabella length (GL); and 3) mid-ocular distance (MOD), anterior-posterior distance between level of mid-point of eye length and front edge of glabella, measured parallel to long axis of glabella (Figure 1; Appendix Table 1). Relative eye length (EL/GL) and relative eye position (MOD/GL) were plotted. Total-sample specimen size range was limited and meraspids were not identified; according to criteria of Poulsen (1964), and as noted above, the specimens examined were holaspids, so ontogenetic change in relative eye size or position was not a significant factor. Additionally, there is no indication of ontogenetic change in at least two of the aspects studied.

Relative expansion of the anterior glabella was assessed by measuring and comparing the width of the anterior glabella (AGW) versus the mid-glabella width (MGW) and versus the posterior glabella width (PGW) (Figure 1). The cephalon width (CW) of specimens with articulated librigenae was also measured. The relative width of the glabella was assessed by comparing the ratio of PGW/CW.

Analysis of the results included calculation of means, standard deviations, 95% confidence

TABLE 1. Data for dolichometopid specimens used in this study. Abbreviations: AGW, anterior glabella width; CW, cephalon width; EL, eye length; GL, glabella length; MGW, mid-glabella width; MOD, mid-ocular distance; PGW, posterior glabella width.

	Specimen Number	Formation	Number of Thoracic Segments	5th Thoracic Pleural Spines	Axial Spine Bases	Eye Length (EL/GL)	Eye Position (MOD/GL)	AGW/ MGW	AGW/ PGW	PGW/ CW	Historic Identification	Identification Source	Taxonomic Assignment Here
1	USNM 78400a	Cadiz	8	Elongate	None preserved	0.476	0.555	1.23	1.15	0.252	*Glossopleura lodensis*	Resser, 1935	*G. lodensis*
2	USNM 78400b	Cadiz	8	Short, typical	None preserved	0.402	0.487	1.40	1.08	0.308	*Glossopleura mohavensis*	Resser, 1935	*G. mohavensis*
3	LACM 10785	Cadiz	8	Short, typical	T1–T8	0.424	0.436	1.09	0.97	?	*Sonoraspis californica*	Stoyanow & Susuki, 1955	*G. mohavensis*
4	LACMIP 10786	Cadiz	8	Short, typical	T3–T8	0.397	0.460	1.15	0.94	?	*Sonoraspis californica*	Stoyanow & Susuki, 1955	*G. mohavensis*
5	LACMIP 2471-11	Cadiz	8?	Elongate	?	0.500	0.628	1.10	1.05	0.233	*Anoria lodensis*	Resser, 1935	*G. lodensis*
6	MWC 7779	Cadiz	8?	?	None preserved	?	?	?	?	?	New specimen	–	*G. mohavensis*
7	MWC 7769	Cadiz	8	Short, typical	None preserved	?	?	?	?	?	New specimen	–	*G. mohavensis*
8	USNM 62714	Bright Angel	7	Short, typical	T4–T7	0.459	0.676	1.33	1.20	0.286	*Glossopleura mckeei*	Resser, 1935	*G. boccar;* Sundberg, 2005
9	USNM 62713	Bright Angel	7	Short, typical	None preserved	0.587	0.601	1.40	1.17	0.310	*Glossopleura mckeei*	Resser, 1935	*G. boccar;* Sundberg, 2005
10	USNM 108592a	Bright Angel	7	Short, typical	T3–T7	0.524	0.571	1.30	1.25	?	*Glossopleura mckeei*	Resser, 1935	*G. boccar;* Sundberg, 2005
11	USNM 108592b	Bright Angel	7	Short, typical	None preserved	0.476	0.476	1.31	1.21	?	*Glossopleura mckeei*	Resser, 1935	*G. boccar;* Sundberg, 2005
12	USNM 108592c	Bright Angel	7	Short, typical(?)	T3–T7	0.543	0.543	1.42	1.21	0.280	*Glossopleura mckeei*	Resser, 1935	*G. boccar;* Sundberg, 2005
13	USNM 62685	Bright Angel	7	Elongate	T2–T7	0.333	0.385	1.16	1.02	0.338	*Anoria tontoensis*	Walcott, 1924	*Anoria tontoensis*
14	GRCA 123303	Bright Angel	?	?	?	0.327	0.537	1.22	1.11	0.293	New specimen	–	*Anoria tontoensis*
15	GRCA 123304	Bright Angel	?	?	None preserved	0.371	0.498	?	?	0.272	New specimen	–	*Anoria tontoensis*
16	DMNH EPI.42917	Bright Angel	7	Short, typical	None preserved	0.294	0.456	?	?	?	New specimen	–	*Anoria tontoensis*
17	DMNH EPI.42915	Bright Angel	7	Medium, all	None preserved	0.446	0.465	1.19	1.01	0.325	New specimen	–	*Anoria? bessus*
18	DMNH EPI.42916	Bright Angel	7	Medium, all	T4(?)–T7	?	?	?	?	?	New specimen	–	*Anoria? bessus*
19	GRCA 11520	Bright Angel	7	Short, typical	None preserved	0.370	0.518	1.20	1.13	?	*Anoria tontoensis*	Foster, 2011b; catalog	*Anoria tontoensis*
20	USNM 62686	Bright Angel	7	?	T1–T6(T7?)	?	?	1.26	1.10	?	*Anoria tontoensis*	McKee & Resser, 1945	*Anoria tontoensis*
21	GRCA 2797	Bright Angel	?	?	T2–T7	0.353	0.647	1.05	1.02	0.275	*Anoria tontoensis*	Foster, 2011b; catalog	*Anoria tontoensis*
22	USNM 123356	Ophir	7	Short, typical	None preserved	?	?	?	?	?	*Glossopleura producta*	Palmer, 1954	*G. producta*
23	USNM 15459	Ophir	7	Short, typical	None preserved	0.500	0.500	1.33	1.14	0.250	*Glossopleura producta*	Resser, 1935	*G. producta*
24	FHPR 16738	Ophir	7?	?	T4–T7	0.484	0.377	1.13	1.00	0.205	New specimen	–	*G. producta*

TABLE 1 (continued).

	Specimen Number	Formation	Number of Thoracic Segments	5th Thoracic Pleural Spines	Axial Spine Bases	Eye Length (EL/GL)	Eye Position (MOD/GL)	AGW/ MGW	AGW/ PGW	PGW/ CW	Historic Identification	Identification Source	Taxonomic Assignment Here
25	FHPR 16739	Ophir	7	?	?	?	?	?	?	?	New specimen	–	*G. producta*
26	FHPR 11285	Ophir	?	?	?	0.637	0.571	1.36	1.24	?	New specimen	–	*G. producta*
27	DMNH EPI.42919	Ophir	?	?	?	0.600	0.600	1.11	1.00	?	New specimen	–	*G. producta*
28	UU 10051.08	Spence	8	Short, typical	No	0.545	0.594	1.10	1.05	0.301	*Glossopleura campbelli*	Robison & Babcock, 2011	*G. campbelli*
29	BPM 1003	Spence	8	Short, typical	No	0.412	0.588	1.10	1.10	0.329	*Glossopleura campbelli*	Robison & Babock, 2011	*G. campbelli*
30	UU 10051.09	Spence	8	Medium, all	T2–T8	0.656	0.625	1.31	1.17	0.302	*Glossopleura yatesi*	Robison & Babcock, 2011	*G. yatesi*
31	UU 10051.10	Spence	8	Medium, all	T2–T8	0.444	0.666	1.41	1.33	0.284	*Glossopleura yatesi*	Robison & Babcock, 2011	*G. yatesi*
32	KUMIP 314054	Spence	8	Short, typical	T4?	0.421	0.579	1.37	1.13	0.266	*Glossopleura similaris(?)*	Catalog	*Glossopleura similaris*(?)
33	Robison et al., 2015 fig. 88(L)	Spence	8	Short, typical	T3–T8	0.438	0.563	1.20	1.09	0.311	*Glossopleura gigantea*	Robison et al., 2015	*Glossopleura gigantea*
34	Robison et al., 2015 fig. 88(R)	Spence	8	Short, typical	T3–T8	0.424	0.636	1.33	1.10	0.240	*Glossopleura gigantea*	Robison et al., 2015	*Glossopleura gigantea*
35	USNM 96526	Spence	?	?	?	0.476	0.524	1.20	1.09	?	*G. similaris*	Resser, 1939	*G. similaris*
36	USNM 62641	Spence	?	?	?	0.381	0.523	1.26	1.09	?	*G. utahensis*	Resser, 1939	*G. utahensis*
37	FHPR 17094	Spence	7	Short, typical	No	0.485	0.732	?	?	0.247	New specimen	–	*G. bion*
38	Robison et al., 2015 fig. 86(L)	Spence	7	Short, typical	No	0.524	0.762	1.33	1.20	0.270	*G. bion*	Robison et al., 2015	*G. bion*
39	Robison et al., 2015 fig. 86(R)	Spence	7	Short, typical	No	0.594	0.658	1.44	1.30	0.250	*G. bion*	Robison et al., 2015	*G. bion*
40	USNM 62702	Stephen	7	Short, typical	None preserved	0.389	0.600	1.19	1.06	0.269	*Glossopleura stephenensis*	Resser, 1935	*G. boccar*
41	USNM 62703	Stephen	7	Short, typical	None preserved	0.518	0.593	1.38	1.06	0.297	*Glossopleura boccar*	Walcott, 1916	*G. boccar*
42	USNM uncataloged	Gordon	8?	Medium, all	T6–T8?	0.428	0.660	1.29	1.12	0.275	*Anoria baton*	Schwimmer, 1973	*Anoria*? *bessus*
43	USNM uncataloged	Gordon	7	Short, typical	None preserved	0.418	0.567	1.23	1.11	0.293	*Anoria baton*	Schwimmer, 1973	*Glossopleura baton*
44	USNM 62696	Gordon	7	Short, typical	None preserved	0.383	0.433	1.50	1.25	0.284	*Anoria baton*	Resser, 1935	*Glossopleura baton*
45	USNM 62699	Gordon(?)	7	Medium, all	None preserved	0.298	0.483	1.23	0.94	0.354	*Anoria bessus*	Walcott, 1916; Resser, 1935	*Anoria*? *bessus*
46	SGDS 1975	Chisholm	7	Short, typical	No	0.575	0.600	1.30	1.12	?	New Specimen	–	*Glossopleura boccar*
47	SGDS 1976	Chisholm	?	?	?	0.435	0.529	1.32	1.21	?	New Specimen	–	*Glossopleura boccar*
48	SGDS 1974	Chisholm	7	Short, typical	T5(?), T7	0.543	0.435	?	?	?	New Specimen	–	*Glossopleura boccar*
49	SGDS 1973	Chisholm	7	Short, typical	None preserved	0.546	0.522	?	?	?	New Specimen	–	*Glossopleura boccar*
50	LACMIP 10782	Monola	8	Short, typical	None preserved	0.538	0.523	?	?	?	*Sonoraspis nelsoni*	Stoyanow, 1958	*Glossopleura mohavensis*

TABLE 1 (continued).

	Specimen Number	Formation	Number of Thoracic Segments	5th Thoracic Pleural Spines	Axial Spine Bases	Eye Length (EL/GL)	Eye Position (MOD/GL)	AGW/ MGW	AGW/ PGW	PGW/ CW	Historic Identification	Identification Source	Taxonomic Assignment Here
51	USNM 116348	Arrojo	8	Short, typical	None preserved	?	?	?	?	?	*Sonoraspis torresi*	Stoyanow, 1952	*Glossopleura* sp.
52	USNM 116334	Arrojo	8	Short, typical	T3–T8	0.421	0.632	1.17	1.08	?	*Sonoraspis gomezi*	Stoyanow, 1952	*Glossopleura* sp.
53	Poulsen, 1927 pl. 16, fig. 20	Cape Wood	?	?	?	0.526	0.632	1.44	1.30	?	*Glossopleura walcotti*	Poulsen, 1927	*Glossopleura walcotti*
54	Poulsen, 1927 pl. 16, fig. 21	Cape Wood	?	?	?	0.560	0.640	1.33	1.23	?	*Glossopleura walcotti*	Poulsen, 1927	*Glossopleura walcotti*
55	Poulsen, 1927 pl. 16, fig. 22	Cape Wood	?	?	?	0.611	0.611	1.20	1.09	?	*Glossopleura walcotti*	Poulsen, 1927	*Glossopleura walcotti*
56	LACMIP 2469	Pole Canyon	8	Short, typical	T1–T8	?	?	?	?	?	*Sonoraspis californica*	Susuki and Lumsden, 1962	*Glossopleura mohavensis*
57	USNM 208256	Carrara	?	?	?	0.500	0.565	1.46	1.35	?	*Glossopleura walcotti*	Palmer and Halley, 1979	*Glossopleura walcotti*
58	USNM 208258	Carrara	?	?	?	0.600	0.625	1.44	1.30	?	*Glossopleura walcotti*	Palmer and Halley, 1979	*Glossopleura walcotti*
59	USNM 208250	Carrara	?	?	?	0.421	0.579	1.38	1.22	?	*Glossopleura lodensis*	Palmer and Halley, 1979	*Glossopleura lodensis*
60	USNM 208251	Carrara	?	?	?	0.636	0.591	1.17	1.04	?	*Glossopleura lodensis*	Palmer and Halley, 1979	*Glossopleura lodensis*

ranges, and others. Kolmogorov-Smirnov tests with the data sets were by calculators on Social Science Statistics (socscistatistics.com) and binomial tests were through StatTrek (stattrek.com). Principal components analysis (PCA) of cranidium measurements was with PAST 4.03. Phylogenetic analysis of species within the three dolichometopid genera was in TNT 1.5 (Goloboff and Catalano, 2016) and Mesquite.

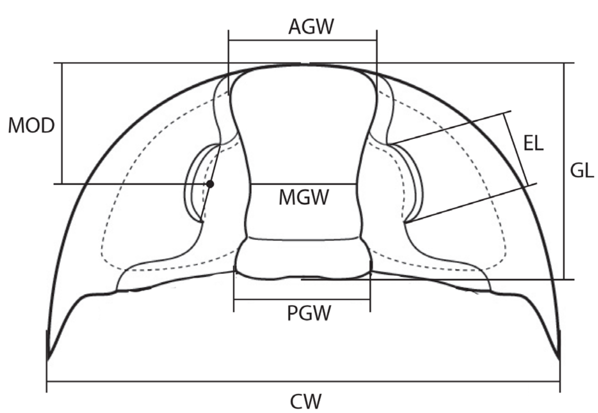

FIGURE 1. Measurements taken of dolichometopid cephala for this study. Abbreviations: AGW, anterior glabella width; CW, cephalon width; EL, eye length; GL, glabella length; MGW, mid-glabella width; MOD, mid-ocular distance; PGW, posterior glabella width.

Abbreviations—BPM, Back to the Past Museum, Cancún, Mexico; **DMNH**, Denver Museum of Nature and Science, Denver, Colorado; **FHPR**, Utah Field House of Natural History State Park Museum, Vernal, Utah; **GRCA**, Grand Canyon National Park Museum, South Rim, Arizona; **KUMIP**, University of Kansas Collection of Invertebrate Paleontology, Lawrence, Kansas; **LACMIP**, Natural History Museum of Los Angeles County, Invertebrate Paleontology, Los Angeles, California; **MWC**, Museums of Western Colorado, Fruita, Colorado; **SGDS**, Saint George Dinosaur Discovery Site, Saint George, Utah; **UCR**, University of California Riverside, Riverside, California; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; **UU**, University of Utah Department of Geology & Geophysics, Salt Lake City, Utah.

RESULTS

Characters and Continuous Variation

Eye (palpebral lobe) length and position. Historically, *Anoria* and *Sonoraspis* have been distinguished from *Glossopleura* in part based on a

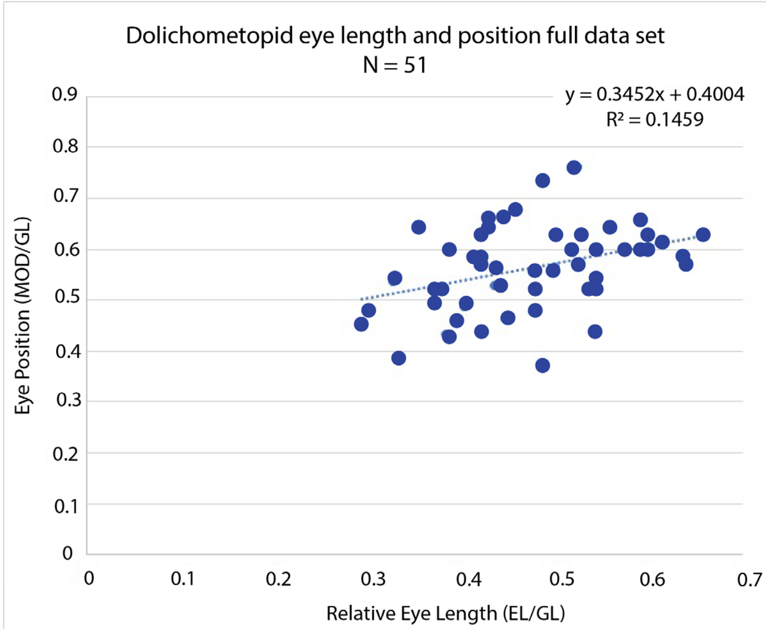

FIGURE 2. Relative eye position and length for dolichometopids measured in this study, showing low degree to which the studied specimens demonstrate large, posteriorly positioned eyes (toward upper right; historically features attributed to *Glossopleura*) or smaller, more anteriorly positioned eyes (toward lower left, normally attributed to *Anoria* and *Sonoraspis*). Data set equation shows a shallow slope and very weak correlation.

qualitative trend of smaller and more anteriorly positioned eyes, and a wider and less anteriorly expanded glabella versus the long and posteriorly positioned eyes, and narrow more anteriorly expanded glabella, of *Glossopleura* (e.g., Stoyanow and Susuki, 1955; Harrington et al., 1959). Results of relative eye length and position comparison between *Anoria, Glossopleura,* and *Sonoraspis* indicate continuous variation in all these parameters. For the entire data set, there is only a weak trend of anterior positioning with smaller eye size and larger eye size with most posterior positioning (Figure 2; slope = 0.3452) and extremely low correlation (R^2 = 0.1459). Eye position in particular varies greatly within the total sample (Figure 3) and, more importantly, within the samples assigned to each of the genera. Support for the eye position trend in these dolichometopids in general is weak (Figure 4), and its utility in distinguishing the genera at all is questionable. Figure 4 also indicates no significant change in eye length or position, at least with increasing size within the holaspid sample studied.

Similarly, eye length relative to glabella length is continuously variable, with *Anoria* and *Glossopleura* populations intermixed in the mid-ranges (Figures 3 and 4). In fact, short eyes tend to be associated more with the subset of Bright Angel Formation specimens assigned to *Anoria* (6 of 7 with shortest eyes), although specimens assigned to *G. mckeei* consistently do have longer eyes (Figure 3). The distinction breaks down in other formations, however, as *Sonoraspis* and *Anoria lodensis* (from the Cadiz Formation) both plot among traditional *Glossopleura*, with the latter Cadiz species actually longer-eyed and none from the Cadiz as small-eyed as *Anoria tontoensis* (Figure 3). If there is a distinction between *Anoria* and *Glossopleura* in relative eye length it would be at 0.380 of glabella length (*Anoria* EL/GL <0.380 and *Glossopleura* EL/GL >0.380; Figure 3). This would be an entirely arbitrary distinction, however, based on historical assignment of type and referred *Anoria* material, mostly from the Bright Angel Formation.

Comparisons of relative eye length for *Glossopleura* and *Anoria* indicate little support for a clear distinction between the genera based on this character, however. Both the total sample and the subsamples for each genus are normally distributed (Figure 5), including according to Kolmogorov-Smirnov tests for normality (D=0.11886 for *Anoria*, N =10; D=0.09329 for *Glossopleura*, N=34; D=0.09421 for combined data, N=44). Means for the relative eye lengths for *Anoria* and *Glossopleura* are distinct, but the 95% confidence ranges overlap. The mean EL/GL for *Anoria* is 0.3575, and

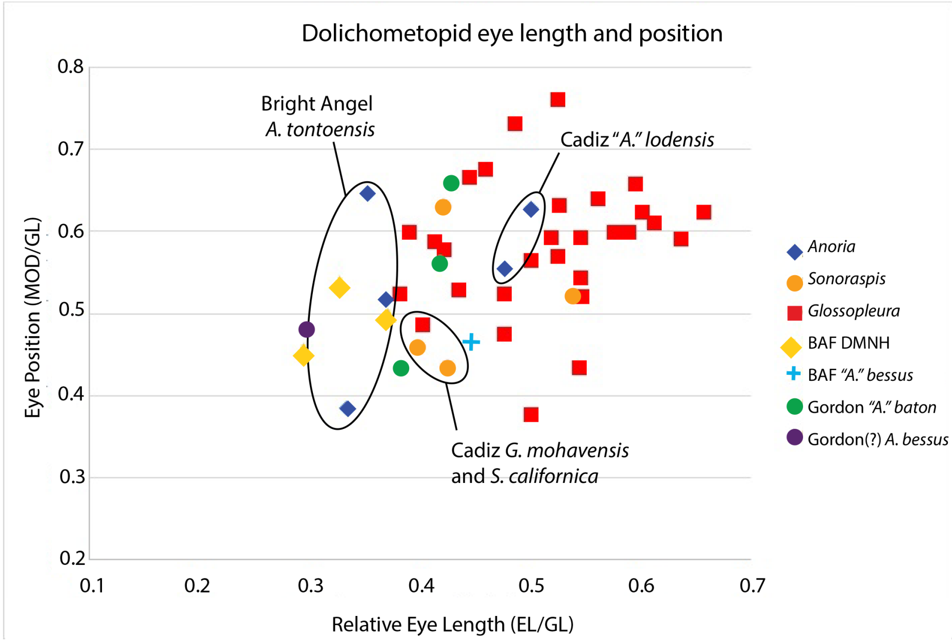

FIGURE 3. Relative eye position and length for dolichometopids in this study, by taxon and formation group (most traditional *Glossopleura* species blended). This version of the data shows the intermixing of *Glossopleura* and traditional *Anoria* and *Sonorapis*. Note that within taxa, eye position may vary greatly. Only eye length shows possible distinction between genera. *Anoria tontoensis* from the Bright Angel Formation (along with one specimen of *A. bessus* from the Gordon Shale) is smaller-eyed and separates from *Glossopleura* (including *G. mckeei*) but only at an arbitrary EL/GL of 0.380. *A. lodensis*, *G. mohavensis*, and *S. californica* all plot within *Glossopleura*.

that for *Glossopleura* is 0.4931. Based on the normal distributions, the 95% confidence ranges are 0.2662–0.4488 for *Anoria* and 0.3210–0.6652 for *Glossopleura*, an overlap of 32.0%. Thus, to retain the distinction between *Anoria* and *Glossopleura*, based on an arbitrary break in relative eye length or on continuous variation within glabella anterior expansion or relative width, would be, as noted by Schwimmer (1973) for the separation of *Anoria* and *Glossopleura*, more of a functional or practical consideration than a natural and statistically-based separation.

Specimens featuring distinctly small pygidia and moderately long pleural spines on all thoracic segments (mostly assigned to *A. baton* and *A. bessus* from the Gordon Shale of Montana, Deiss, 1939, plus two specimens from the Bright Angel) plot at a range of eye lengths from among *A. tontoensis* on the short end up to traditional long-eyed *Glossopleura*, too (Figure 3).

Glabella shape. Comparisons of the anterior expansion of the glabella relative to the mid-width and posterior width, another qualitative character used for distinction of species and genera, show this trend to have essentially continuous variation also, with *Glossopleura* and other genera intermixed. Although species of *Anoria* and *Sonoraspis* do have relatively low ratios, indicating less anterior expansion than in *Glossopleura* (Figure 6A), the trend is weak and the R^2 is moderate at just 0.6494 (Figure 6B). Similarly, the ratio of the posterior glabella width to the full cephalon width in complete specimens does show a mean glabella width broader relative to the cephalon in *Anoria* (0.305) compared to *Glossopleura* (0.281), but with 70% overlap of the two-standard deviation 95% confidence intervals. These anterior glabella expansion and relative glabella width characters are, along with relative eye positioning, additional continuously varying features that defy discrete character state assignment for individual genera and sometimes species.

PCA on quantifiable characters. PCA incorporating eye length, eye position, glabella length, and anterior, mid, and posterior glabella width indicates significant overlap between *Glossopleura* and *Sonoraspis* for all components (Figure 7). *Anoria* significantly overlaps the other two as well (Figure 7B) but to a lesser degree (e.g., Figure 7A), especially comparing components 2 and 3 (Figure 7C), in which overall size (effectively accounted for in PC1) is not a factor. Breaking the PCA down by

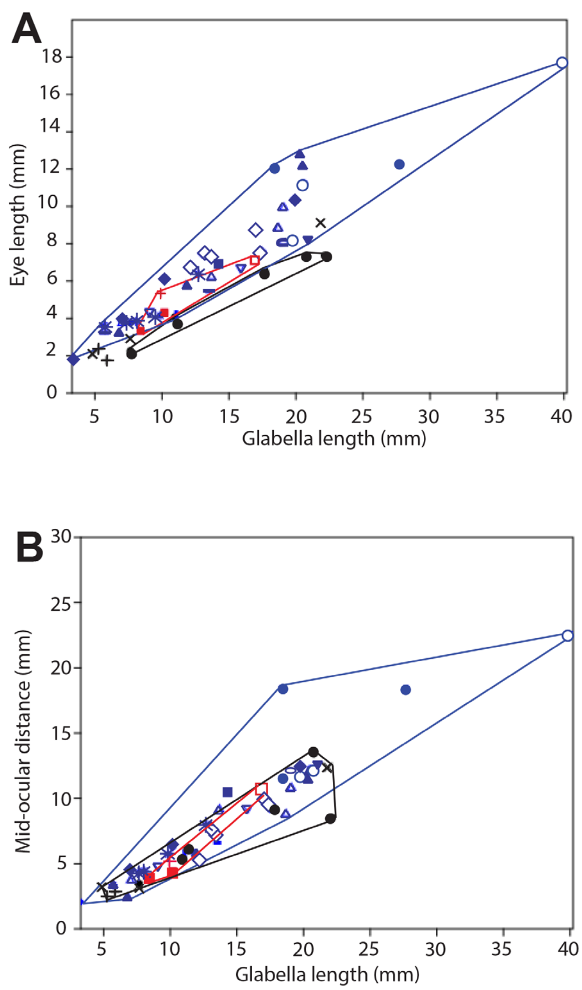

FIGURE 4. Comparison of cranial measurements (in mm) in dolichometopids assigned to *Glossopleura* (blue), *Sonoraspis* (red), and *Anoria* (black). A) Eye length relative to glabella length. B) Eye position as represented by mid-ocular distance versus glabella length. Genera coded by color as noted above. Species denoted by symbols as listed alphabetically here: *Glossopleura bion* (filled blue squares), *G. boccar* (open blue diamonds), *G. campbelli* (open blue circles), *G. gigantea* (open blue ovals), *G. lodensis* (blue stars), *G. mckeei* (open blue triangles), *G. mohavensis* (blue dashes), *G. producta* (filled blue triangles), *G. similaris* (open inverted blue triangles), *G. stephenensis* (filled inverted blue triangles), *G. utahensis* (vertical blue bars), *G. walcotti* (filled blue diamonds), *G. yatesi* (filled blue circles); *Sonoraspis californica* (filled red squares), *S. gomezi* (open red squares), *S. nelsoni* (red pluses); *Anoria baton* (black pluses), *A. bessus* (black X), and *A. tontoensis* (filled black circles),

species (see Figure 7 caption), it is clear that *A. tontoensis* is most separated from *Glossopleura*, *Sonoraspis*, and other species assigned to *Anoria*. PCA thus supports the distinction of *Anoria tontoensis* of the Bright Angel Formation from other dolichometopids and the broad overlap of *Glossopleura*, *Sonoraspis*, and other species of *Anoria*.

Axial nodes. Thoracic axial nodes (probable spine bases) are highly variable in being present in species assigned to all three genera but only in just less than half of specimens (Table 1); in the others it is taphonomically equivocal as to whether the absence of axial nodes is due to lack of preservation or to true absence. In only a few specimens (e.g., a *G. bion* from the Spence Shale) was it clear that the dorsal surface of the exoskeleton lacked axial nodes. At least one sample from the Bright Angel Formation of the Grand Canyon has two clearly different forms represented by thoracic segments with smooth axial rings and others with defined nodes. These nodes occur also on pygidia, as they do in some *Glossopleura* (Sundberg, 2005), but there are several untubercled pygidia in the sample as well.

Elongate pleural spines. The length of pleural spines on the thoracic segments has been used to distinguish some genera and species, particularly the elongate spine on the fifth thoracic (almost rivalling the T3 on olenellids) for *Anoria* (*Anoria tontoensis* and *A. lodensis*) and moderately long spines on most of the thoracic segments in *A. bessus* and *A. baton*. However, the elongate T5 spines are only present in three specimens of the total sample studied here (Table 1).

Thoracic segments number. Most specimens of the included genera have seven thoracic segments, but there appear to be rare exceptions in which individuals have eight (Table 1). However, it appears that specimens from the Cadiz Formation, which historically have been assigned to all three genera, consistently have eight thoracic segments (again with one or two possible exceptions), and Spence Shale specimens of *Glossopleura* mostly have eight thoracic segments (Table 1). Having eight thoracic segments appears to be characteristic more of populations in some formations, and thus geographic regions, than it is consistent for genera, as the character seems to cut across taxa assigned based on eye length and position and other characters.

Phylogenetic Analysis

Phylogenetic analysis of 12 dolichometopid taxa for which there are relatively complete specimens, and utilizing 17 characters of the cephalon (1–6), thorax (7–10), and pygidium (11–17) (Appendix; Appendix Table 2; Figure 8), returned 40 most parsimonious trees (MPTs) of 41 steps, a

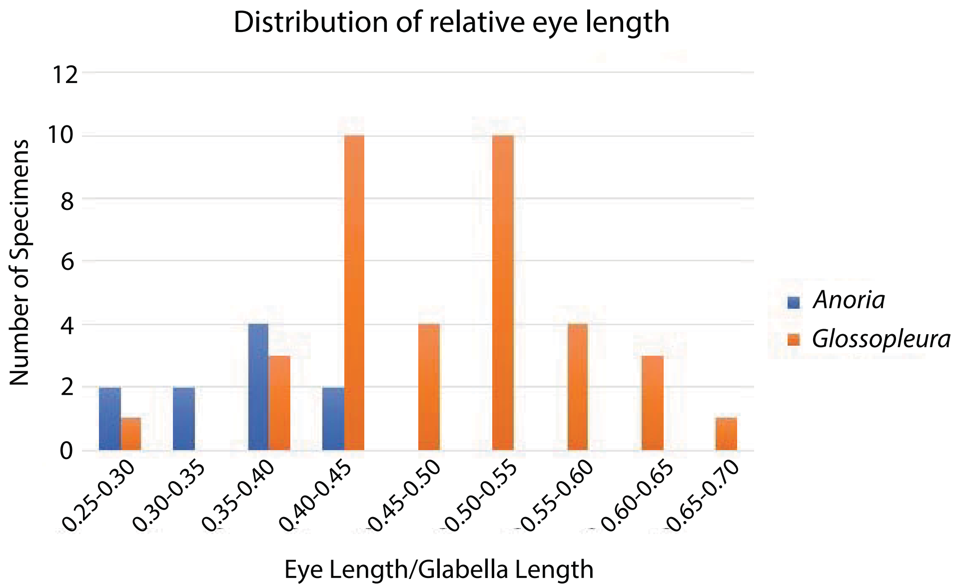

FIGURE 5. Distributions of EL/GL ratios for *Glossopleura* and *Anoria* specimens measured for this study. Individual generic and total-sample distributions are normal by Kolmogorov-Smirnov tests.

strict consensus of which was a polytomy (Figure 9A). However, in many of the trees there were consistent sister taxa pairs: *G. boccar*+*G. producta*; *G. gigantea*+*G. yatesi*; and *G. mohavensis*+*Sonoraspis californica*, the latter pairing reflecting findings presented above. *Anoria tontoensis* was most frequently basal or at least separate from other taxa, but *A. lodensis* and *A. bessus* moved around among species of *Glossopleura*. Removal of the less well-represented taxon *G. bion* resulted in an analysis returning four MPTs with 38 steps, the strict consensus of which gave slightly more resolution (Figure 9B). All four MPTs again paired *G. gigantea*+*G. yatesi* and also *G. boccar*+*G. producta*, both pairings being reflected in the strict consensus tree as well (Figure 9B). The strict consensus also suggested a clade of Spence Shale *Glossopleura* species and the Cadiz Formation's *G. mohavensis* and *S. californica*, if the latter species is separate. Another possible clade includes *Anoria bessus, G. boccar, G. producta,* and *A. lodensis*. Relationships of these clades to the Bright Angel taxa *Anoria tontoensis* and *G. mckeei* are unresolved. If we assume a few of the synonymies suggested above, and in some cases elsewhere, too *(G. mckeei = G. boccar; S. californica = G. mohavensis;* and *G. producta = G. boccar)* and rerun the analysis, we end up with two MPTs of 35 steps and another clade of Spence *Glossopleura* and a clade of *Anoria bessus*+(*G. boccar*+*G. lodensis*), both in an unresolved polytomy with *G. mohavensis* and *A. tontoensis* (Figure 9C).

DISCUSSION

Phylogenetic Analysis

Phylogenetic results suggest: 1) that *Sonoraspis californica* may be a junior synonym of *Glossopleura mohavensis;* 2) confirmation that *"Anoria" lodensis* is a species of *Glossopleura (G. lodensis);* and 3) that *Anoria tontoensis* may be distinct. Additionally, and more broadly, the results may indicate: 4) possible synonymy of *G. producta* with *G. boccar*; 5) *Anoria baton* and *A. bessus* may belong within *Glossopleura*; and 6) *Glossopleura* species from the Spence Shale may form a distinct clade, although this latter conclusion may be in part an artifact of positive preservation bias (better specimens) allowing clearer scoring of specimens.

Characters Relative to Populations and Paleobiogeography

The number of thoracic segments in the studied dolichometopids is variable between seven and eight within species but more frequently between formations, with the Cadiz, Spence, and Arrojo formations consistently yielding numerous specimens with eight thoracic segments and sometimes from more than one species. Similarly, the Cadiz, Bright Angel, and Arrojo formations produce species with moderate to short eyes *("S. californica", Anoria ton-*

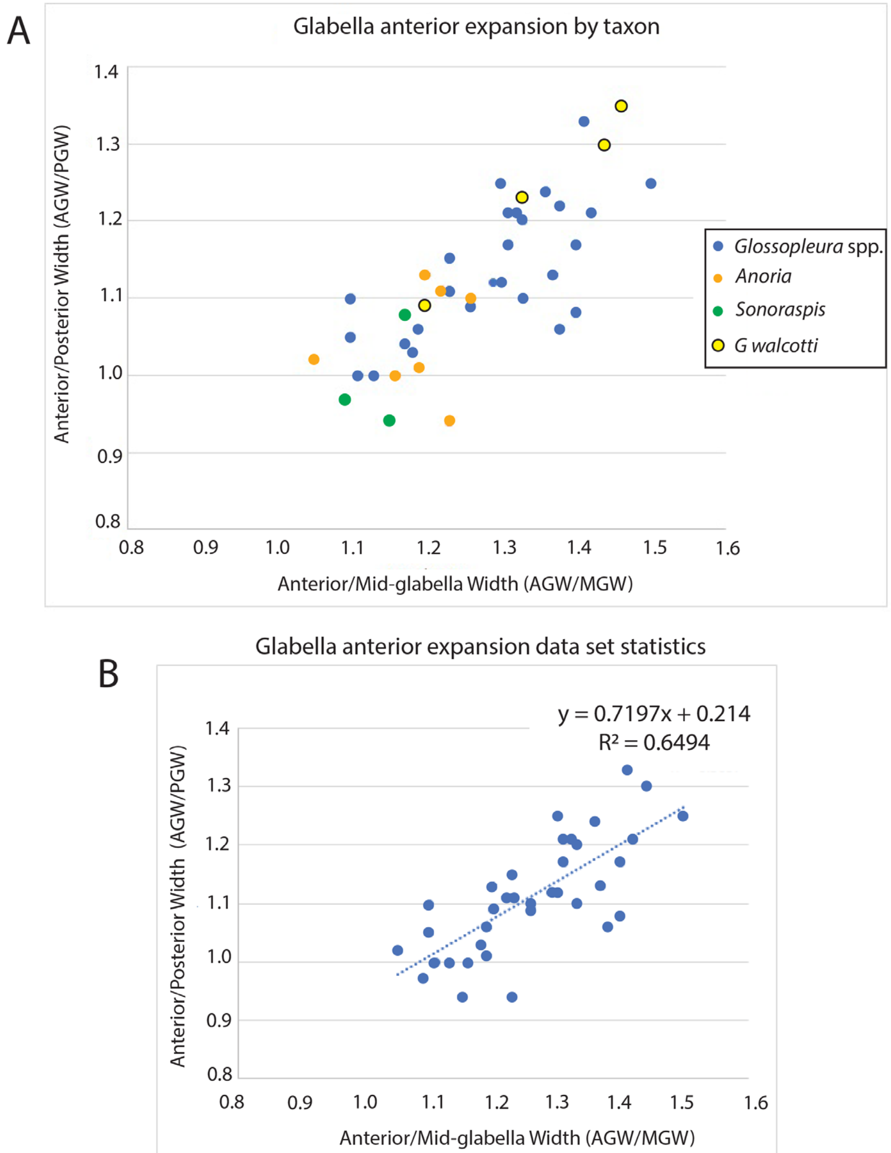

FIGURE 6. Anterior expansion of glabella in dolichometopids. A) Comparing AGW/MGW and AGW/PGW, showing *Anoria* and *Sonoraspis* less expanded but well mixed with *Glossopleura* specimens. B) Full data set statistics.

toensis, and *"S. gomezi",* respectively). Formations such as the Chisholm, Spence, Stephen, and Ophir appear to yield mainly long- to moderate-eyed forms. The range of eye size within *A.*? *bessus* from the Gordon Shale and Bright Angel Formation is anomalous. That the smaller-eyed forms on the *Glossopleura-Anoria* spectrum (Figures 3 and 4) are mostly from more southern formations (and in the case of the *Anoria tontoensis*, from more proximal settings on the shelf) may be coincidental, but this may be a pattern worth further investigation.

Cadiz Formation Dolichometopidae

Specimens collected from UCR 7359 for this project include numerous dolichometopid cranidia and pygidia plus two partial, articulated specimens of *G. mohavensis*. Type material of dolichometopids such as *Glossopleura boccar* and *G. stephenensis*, plus those of geographically closer-sourced taxa such as *G. mckeei* and *Anoria tontoensis* from the Bright Angel Formation and *G. bion* and others from the Spence Shale helped put the Cadiz Formation species in context (Table 1). The articulated specimens from the Cadiz Formation illustrated by Resser (1928), one assigned to

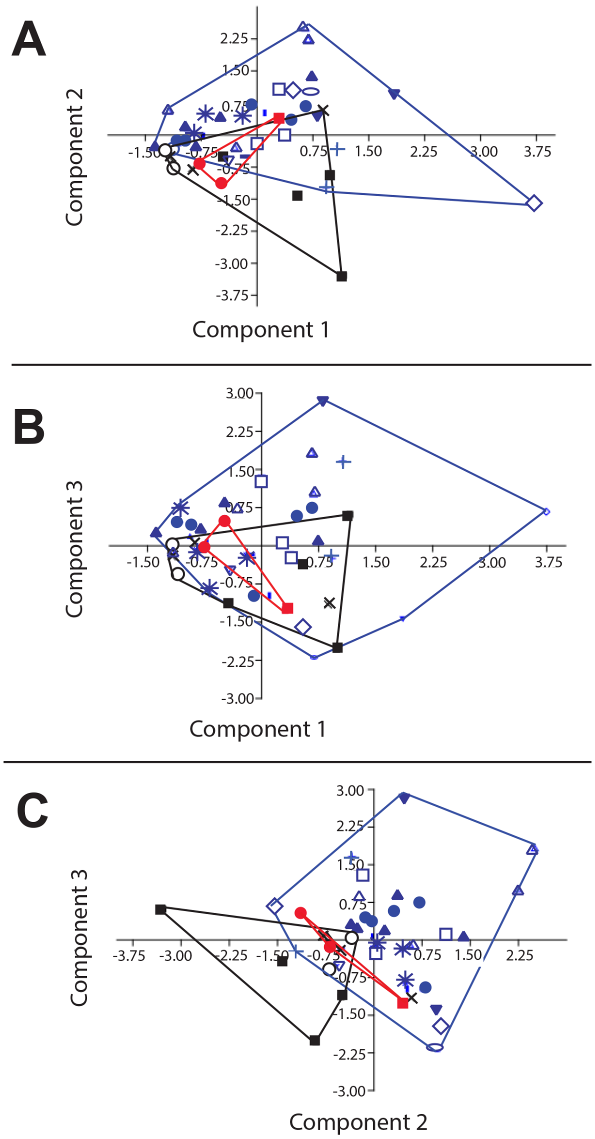

FIGURE 7. Principal components analysis of dolichometopid cranial measurements at genus level. *Glossopleura* = blue polygons. *Sonoraspis* = red polygons. *Anoria* = black polygons. A) PC1 vs PC2. B) PC1 vs PC3. C) PC2 vs PC3. Genera coded by color as noted above. Species denoted by symbols as listed alphabetically here: *Glossopleura boccar* (open blue squares), *G. campbelli* (open blue diamonds), *G. lodensis* (blue stars), *G. mckeei* (solid blue dots), *G. mohavensis* (blue dashes), *G. producta* (open blue triangles), *G. similaris* (vertical blue bars), *G. stephenensis* (open blue ovals), *G. utahensis* (inverted open blue triangles), *G. walcotti* (filled blue triangles), *G. yatesi* (filled inverted triangles); *Sonoraspis californica* (filled red circles), *S. gomezi* (filled red squares); *Anoria baton* (black X), *A. bessus* (open black circles), *A. tontoensis* (filled black squares).

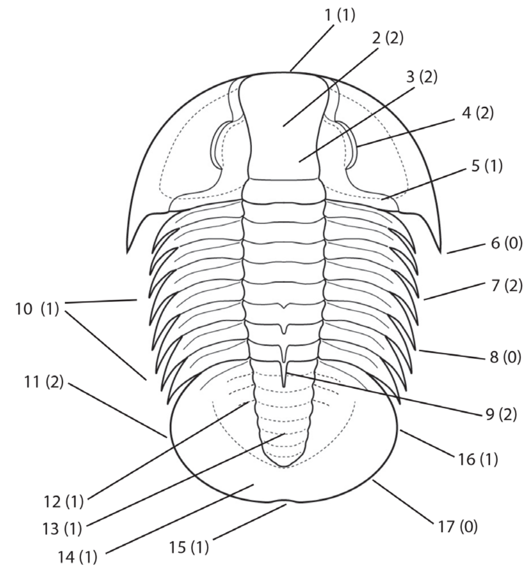

FIGURE 8. Matrix characters for phylogenetic analysis shown on an unspecified species of dolichometopid trilobite (*Glossopleura* sp.). First number is character number (see Appendix for descriptions and matrix); number in parentheses is character state demonstrated by illustrated form. (Drawing courtesy of Sam Gon III.)

G. mohavensis and the other to *G. lodensis* (Resser, 1935), appear to show medium- and long-eyed forms, one with and one without enlarged fifth thoracic pleural spines; the nature of the axial rings of these specimens cannot be determined.

Glossopleura lodensis. "Long-eyed" forms from the Cadiz Formation (as shown above) have twice previously been assigned to *Anoria lodensis* (Mason, 1935; Hazzard and Mason, 1936). Palmer and Halley (1979) note relatively short eyes in the description of *Glossopleura lodensis,* based on Resser's (1928, 1935) material, but as confirmed in Figure 3 here, the eyes of *G. lodensis* are actually long and very typical of *Glossopleura*.

Glossopleura mohavensis. Recent collecting since 2011, at locality UCR 7359 (Fuller, 1980) in the Marble Mountains near Section B of Foster (1994), recovered additional *Glossopleura mohavensis* specimens. Among medium-eyed dolichometopid forms without deep S1 or occipital furrows, as preserved, *Glossopleura mohavensis* admittedly cannot be distinguished from the type *Glossopleura boccar* except by the shorter eyes and consistent occurrence of eight thoracic segments in specimens from the Cadiz Formation. Unfortunately, Resser (1935) designated *G. mohavensis* with no diagnosis. Considering the medium-length eyes and eight thoracic segments consis-

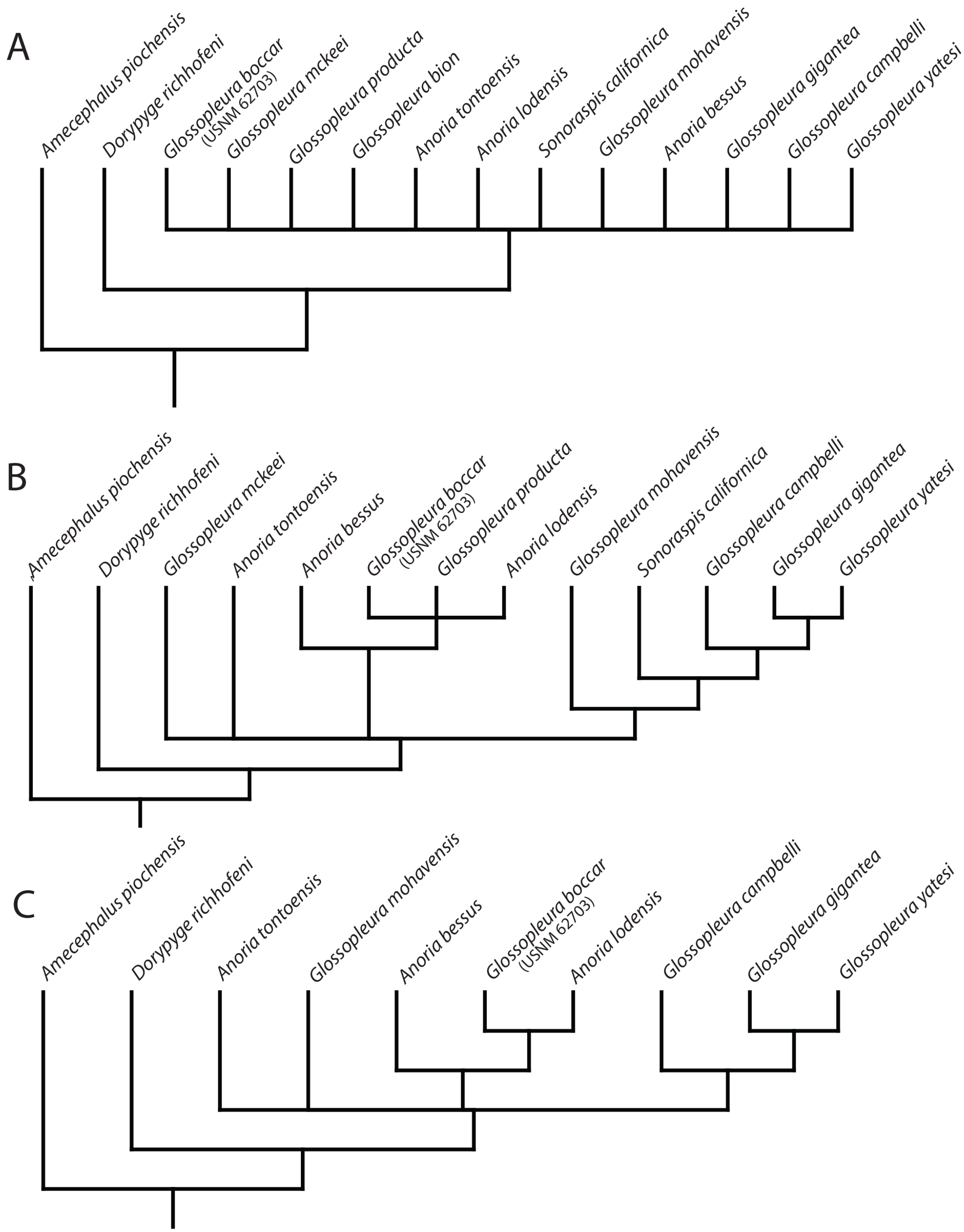

FIGURE 9. Phylogenetic analysis of 12 dolichometopid taxa for which there are relatively complete specimens, plus two outgroup taxa. A) Strict consensus of 40 MPTs of 41 steps. B) Strict consensus of 4 MPTs of 38 steps, after removal of the less well represented taxon *G. bion*. C) Strict consensus of 2 MPTs of 35 steps with just 8 dolichometopid taxa, after assuming the following synonymies: *G. mckeei* = *G. boccar; S. californica* = *G. mohavensis;* and *G. producta* = *G. boccar*. See text.

tently found in *G. mohavensis*, it is retained as separate from *G. boccar*.

In the Cadiz Formation, and in addition to *Glossopleura* and *Anoria,* Stoyanow and Susuki (1955) described *"Sonoraspis californica"* based on two specimens from another site in the Cadiz Formation, near Marble Mountains Section A of Foster (1994). Susuki and Lumsden (1962) described another specimen they attributed to *"S. californica"* from the Pole Canyon Formation of Nye County, Nevada. The genus *Sonoraspis* was designated by Stoyanow (1952, in Cooper et al., 1952) from the Arrojo Formation of Sonora, Mexico, with two species designated, *"S. torresi"* and *"S. gomezi".*

"Sonoraspis" is generally similar to *Anoria tontoensis* except in the lack of elongate fifth thoracic pleural spines and in having larger eyes, and the former has been regarded as a junior subjective synonym of *Glossopleura* (Lochman in Cooper et al., 1952; Palmer, 1954; Jell and Adrain, 2002). *"Sonoraspis californica"* from the Cadiz Formation was erected based on eight thoracic segments and "mixed characteristics of" *Glossopleura* and *Anoria* (Stoyanow and Susuki, 1955, p. 467). They specified "tubercules" (axial nodes) on the anterior thoracic segments and the "course of the facial sutures" (related to eye length and position) as similar to *Anoria* and the lack of an elongate fifth thoracic pleural spine as similar to *Glossopleura*. The lengths of the eyes in the *"S. californica"* type and paratype specimens are, however, somewhat intermediate between the long eyes of most *Glossopleura* specimens and the short eyes of the type specimen of *Anoria tontoensis* (USNM 62685); the eyes of the type *"S. californica"* material are most similar to *G. mohavensis* (Figure 3).

Glossopleura walcotti was first identified in the Cadiz Formation by Fuller (1980), but the specimen he illustrated was rather a moderate-eye-length form that would graph close to *Sonoraspis* and *G. mohavensis* in Figure 3 (EL/GL of 0.384). Considering this and the variability in occipital and S1 furrow depth among a range of specimens in the formation, Fuller's (1980) *G. walcotti* is here regarded as *G. mohavensis*.

Broader Implications for Dolichometopidae

Anoria. *Anoria tontoensis* from the Bright Angel Formation of the Grand Canyon was defined by Walcott (1924) based on the lack of a frontal border, a feature shared with *Dolichometopus boccar* (type species of the not-yet-named *Glossopleura* Poulsen 1927). Walcott (1925) later described other important aspects of *Anoria:* 1) elongate fifth thoracic pleural spines, a feature not found in all Bright Angel material referred to *Anoria* (in fact, it is only present in the type specimen USNM 62685), and present in only two other dolichometopid specimens (of *"A." lodensis* from the Cadiz Formation; Table 1); 2) "axial nodes" (likely poorly preserved spine bases) on the thoracic segments, a feature variable within samples of *Glossopleura* and *Anoria* (Table 1); and 3) seven thoracic segments, also shared by most *Glossopleura* (Table 1). The enlarged fifth thoracic, number of thoracic segments, and presence or absence of axial nodes or spines appear to be too variable as characters to be of much value distinguishing *Glossopleura* and *Anoria*, although, as noted above, eye length may differentiate the two.

Distinguishing *Anoria* and *Glossopleura* except by nearly complete specimens or very well preserved cranidia, therefore, is difficult and unreliable. This results also from the fact that axial nodes extend on to the pygidium in some specimens of *Anoria* (but also in some of *Glossopleura*), but do not in all specimens, even from the same quarry. This makes pygidia of *Glossopleura* and *Anoria* very similar and difficult to distinguish.

At this time, the only species previously assigned to *Anoria* that can be confidently separated from *Glossopleura*, and thus kept in the former genus, is *A. tontoensis* from the Bright Angel Formation (Walcott, 1916a; Foster, 2011b).

Glossopleura. Poulsen (1927) designated *Dolichometopus boccar* as the type species of *Glossopleura* and then named the new species *G. walcotti* and described its features, some of which are marginally distinctive, but he did not directly address its differentiation from *G. boccar.* Overall, the two are quite similar in the cranidia and pygidia, although *G. walcotti* is believed to have more pronounced S1 glabellar and occipital furrows (Poulsen, 1927; Sundberg, 2005). Morphological differences between (and within) populations of *Glossopleura* are subtle but variable (Sundberg, 2005) and may account for much of what has been attributed to species delineations.

The distinction of longer and more posteriorly positioned eyes in *Glossopleura* than *Anoria* (Poulsen, 1927; Harrington et al., 1959; Schwimmer, 1973) seems to be one of the few distinguishing characters potentially useful to separate the two genera, although eye length is only a marginal differentiation and eye position is of little value at all.

Palmer (1954) suggested the synonymy of *"Sonoraspis"* with *Glossopleura* due to variability in the number of thoracic segments in samples of many dolichometopid genera, a fact demonstrated in the sample studied here (Table 1) and supplemented by the other analyses above.

Characters. In the years since the original establishments of *Anoria, Glossopleura,* and *"Sonoraspis",* additional characteristics have been used to separate them also, but few of these appear to be clearly distinguishing. As outlined above, the anterior expansion of the glabella and the relative glabella width vary continuously and do not exhibit discrete character states among the genera studied here. Poulsen's (1927) type material of *G. walcotti* demonstrates a range of anterior expansion of the glabella relative to the mid-glabella width, but this is within the range of *Glossopleura* species from other formations as well (Figure 6A; e.g., Cadiz and Spence). Palmer and Halley's (1979) referred *G. walcotti* from the Carrara Formation demonstrate significant anterior expansion of the glabella, but the AGW:MGW ratios of these two specimens are not the highest recorded in this study and are comparable to specimens of other *Glossopleura* species in formations such as the Spence, Bright Angel, and Gordon (Table 1).

An additional apparent difference between *Glossopleura boccar* and *G. walcotti* is that the latter has a slight and very shallow mid-line indentation or flat section in the pygidial outline in dorsal view. This indentation or flat section in the otherwise rounded pygidial rim is only identifiable in two specimens from the current sample. Otherwise, the pygidia all strongly resemble *G. boccar* in pygidial outline, in the width of the pygidial border, and in the length and structure of the pygidial axis. In fact, the pygidial indentation is variably present even among the type material of *G. walcotti* (Poulsen, 1927). The slight indentation occurs in some specimens of other species of *Glossopleura*, too (Campbell, 1974; Robison et al., 2015). In addition, the slight flattening of the posterior border of the pygidium seen in *G. walcotti* also occurs to some degree in the pygidium of the lectotype of *Anoria tontoensis* (USNM 62685), suggesting again that even generic assignment of the isolated pygidia may be difficult.

These characters are all highly variable, and glabella width, anterior glabella expansion, and eye position in particular appear to be continuously variable features among the *Glossopleura-Anoria-"Sonoraspis"* plexus. Relative eye length is continuously variable also but an arbitrary distinction between *Anoria* and *Glossopleura* at least can be made for use in the above preliminary phylogenetic analysis and other analyses.

With eye length used as an almost sole distinction between *Anoria* and *Glossopleura* (*Anoria* EL/GL <0.380 and *Glossopleura* EL/GL >0.380), and in the absence of other reliable characters (as outlined above), some consequences are: 1) *"Sonoraspis"* from the Cadiz Formation is confirmed as a junior synonym of *Glossopleura* (eye length among medium-eyed *Glossopleura*); 2) the historic *"Anoria" lodensis* from the Cadiz is confirmed as within *Glossopleura* and is a longer-eyed form than *"Sonoraspis";* 3) *Glossopleura mohavensis* and the synonymous *"S. californica"* form a distinct species of medium-eyed *Glossopleura* in the Cadiz Formation (*G. mohavensis*); and 4) dolichometopids with small pygidia and medium-length pleural spines on all thoracic segments, historically assigned to *"Anoria" baton* and *A. bessus* (and mostly from the Gordon Shale but with at least two specimens in the Bright Angel), appear to range from small-eyed (*Anoria* range) to medium-large eyed (*Glossopleura* range).

SYSTEMATIC PALEONTOLOGY

Order Corynexochida Kobayashi, 1935
Family Dolichometopidae Walcott, 1916
Genus *Glossopleura* Poulsen, 1927

Type species. *Dolichometopus boccar* Walcott, 1916a, from the Stephen Formation, British Columbia.

Glossopleura lodensis (Clark, 1921)
Figure 10A

Bathyuriscus howelli var. *lodensis* Clark, 1921, p. 6

Dolichometopus? *lodensis* Resser, 1928, p. 10, pl. 3, fig. 9.

Dolichometopus lodensis Hazzard and Crickmay, 1933, p. 73.

Anoria lodensis Mason, 1935, p. 109–110, pl. 15, figs. 11, 12.

Glossopleura lodensis Resser, 1935, p. 34

Anoria lodensis Hazzard and Mason, 1936, p. 233.

Glossopleura lodensis Stoyanow, 1956, p. 680, figs. 1, 2.

Glossopleura lodensis Palmer and Halley, 1979, p. 78–79, pl. 16, figs. 1–5, 9, 10.

Glossopleura lodensis Fuller, 1980, p. 68.

Type specimens. Holotype USNM 78400a, complete specimen.

Occurrence. Cadiz Formation, Marble Mountains, California; Carrara Formation, Eagle Mountain,

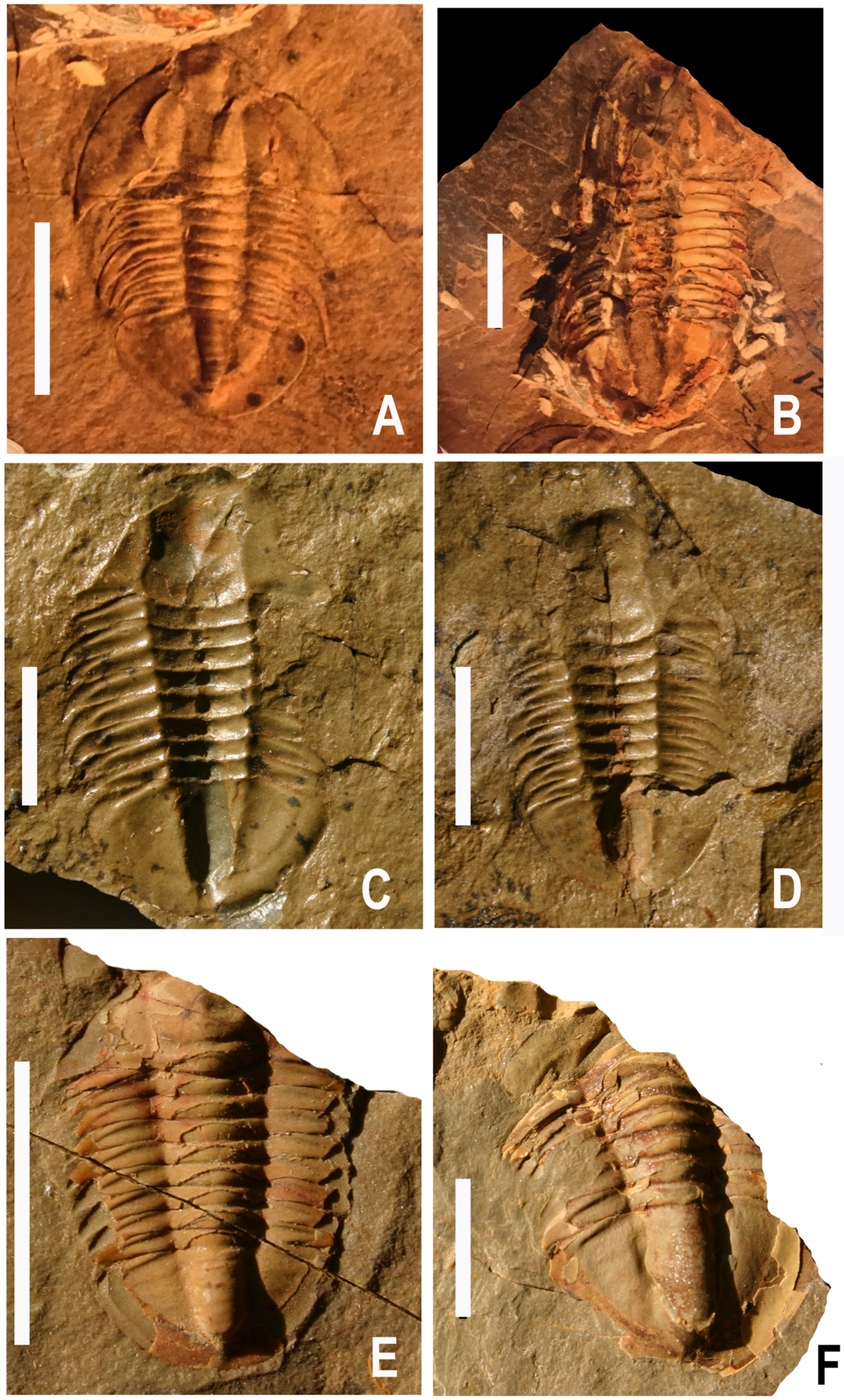

FIGURE 10. Dolichometopid trilobite specimens from the Cadiz Formation, California. A) *Glossopleura lodensis* (USNM 78400a), note eight thoracic segments, elongate T5 pleural spines, anteriorly expanded glabella, and long eyes (impression, lighting from left). B) *Glossopleura mohavensis* (USNM 78400b), note eight thoracic segments (dorsal exoskeleton, lighting from left). C) *Glossopleura mohavensis* (LACM 10785; *"Sonoraspis californica"),* note wide glabella, eight thoracic segments, and axial spine bases (impression, lighting from left). D) *Glossopleura mohavensis* (LACM 10786; *"Sonoraspis californica"),* note wide glabella, eight thoracic segments, and axial spine bases (impression, lighting from left). E) *Glossopleura mohavensis* (MWC 7769), note eight thoracic segments (dorsal exoskeleton, lighting from left). F) *Glossopleura mohavensis* (MWC 7779), (dorsal exoskeleton, lighting from left). A and B from the Bristol Mountains; C and D from near Section A of Foster (1994) (type section; north of Route 66), Marble Mountains; E and F from UCR 7359, near Section B of Foster (1994) (south of Route 66), Marble Mountains. All scale bars = 1 cm.

California, and Striped Hills, Nevada; all *Glossopleura* Assemblage Biozone, Interval Biozone undesignated (Morgan, 2021) (Wuliuan, Miaolingian).
Material examined. USNM 78400a, USNM 208250, USNM 208251, LACMIP 2471-11.
Remarks. Species features long eyes, a long pleural spine on the fifth thoracic segment, and eight thoracic segments in two complete specimens (USNM 78400a, LACMIP 2471-11).

Glossopleura mohavensis Resser, 1935
Figures 10B–F, 11G and 11H

Dolichometopus productus Resser, 1928, p. 10, pl. 3, fig. 9.

Dolichometopus productus Hazzard and Crickmay, 1933, p. 73.

Dolichometopus productus Mason, 1935, p. 113–114.

Glossopleura mohavensis Resser, 1935, p. 34

Glossopleura mohavensis Hazzard and Mason, 1936, p. 233.

Sonoraspis californica Stoyanow and Susuki, 1955, p. 468–469, pl. 1, figs. 1, 2.

Sonoraspis mohavensis Stoyanow, 1956, p. 680–681, fig. 1.

Sonoraspis nelsoni Stoyanow, 1958, p. 348–349, pl. 1, fig. 3.

Sonoraspis californica Susuki and Lumsden, 1962, p. 234–237, fig. 2.

Glossopleura californica Fuller, 1980, p. 68.

Type specimens. Holotype USNM 78400b, nearly complete specimen.
Occurrence. Cadiz Formation, Marble Mountains, California; Monola Formation, Inyo Mountains, California; Pole Canyon Formation, Currant Gap, Nevada. *Glossopleura* Assemblage Biozone, Interval Biozone (Morgan, 2021) undesignated, (Wuliuan, Miaolingian).
Material examined. USNM 78400b, LACMIP 2469, LACMIP 10785, LACMIP 10786, LACMIP 10782, MWC 7779, MWC 7769.
Remarks. Species features moderately long eyes, short pleural spines on all thoracic segments, and eight thoracic segments in seven complete specimens (USNM 78400b, LACMIP 2469, LACMIP 10782, LACMIP 10785, LACMIP 10786, MWC 7779, MWC 7769).

Glossopleura boccar (Walcott, 1916a)
Figure 11A–B and 11D–E

Dolichometopus boccar Walcott, 1916a, p. 363–365, pl. 52, figs. 1a–1f.

Dolichometopus productus (Hall and Whitfield, 1877) (part) Walcott, 1916a, p. 369–372, pl. 53, figs. 4, 4a.

Glossopleura boccar (Walcott) Poulsen, 1927, p. 268.

Glossopleura mckeei Resser, 1935, p. 33.

Glossopleura bosworthensis Resser, 1935, p. 31.

Glossopleura nitida Resser, 1935, p. 31.

Glossopleura? *stephenensis* Resser, 1935, p. 31.

Glossopleura boccar (Walcott) Rasetti, 1951, p. 164, pl. 24, figs. 1–6.

Glossopleura mckeei (Resser) Rasetti, 1951, p. 165, pl. 24, figs. 9–12, 18.

Glossopleura boccar (Walcott) Sundberg, 2005, p. 65–66, fig. 6.10–6.14.

Glossopleura boccar (Walcott) Foster, 2011b, p. 105–106, fig. 4.1, 4.2, 4.3.

Glossopleura boccar (Walcott) Morgan, 2021, p. 94–97, figs. 3.5.1, 3.5.2, 3.5.4–3.5.11

Type specimens. USNM 62703, USNM 62705, and USNM 62707, cotypes.
Occurrence. Stephen Formation, Mount Bosworth and Mount Stephen, British Columbia; Mount Cap Formation, Northwest Territories; Chisholm Formation, Half Moon Mine, Pioche, Nevada; Bright Angel Formation, Grand Canyon, Arizona; all *Glossopleura* Assemblage Biozone, *Glossopleura boccar* Interval Biozone (Morgan, 2021), (Wuliuan, Miaolingian).
Material examined. USNM 62703, USNM 62702, USNM 62705, USNM 62707, USNM 62713, USNM 62714, USNM 108592a, USNM 108592b, USNM 108592c, SGDS 1973–1976.
Remarks. This is the type species of the genus *Glossopleura*, and although it has not been identified in the Cadiz Formation, it is close in form to *G. mohavensis* except for having longer eyes and only seven thoracic segments.

Morgan (2021) proposed restricting *Glossopleura boccar* to USNM 62703 as a lectotype and USNM 62705 as a syntype/paratype, with USNM 62707 as a hypotype of *G. walcotti*.

Glossopleura walcotti Poulsen, 1927

Glossopleura walcotti Poulsen, 1927, p. 268, pl. 16, figs. 20–30.

Glossopleura expansa Poulsen, 1927, p. 269, pl. 16, figs. 31, 32.

Glossopleura sulcata Poulsen, 1927, p. 272, pl. 16, fig. 39.

Glossopleura longifrons Poulsen, 1927, p. 272, pl. 17, fig. 10 [not figs. 8, 9].

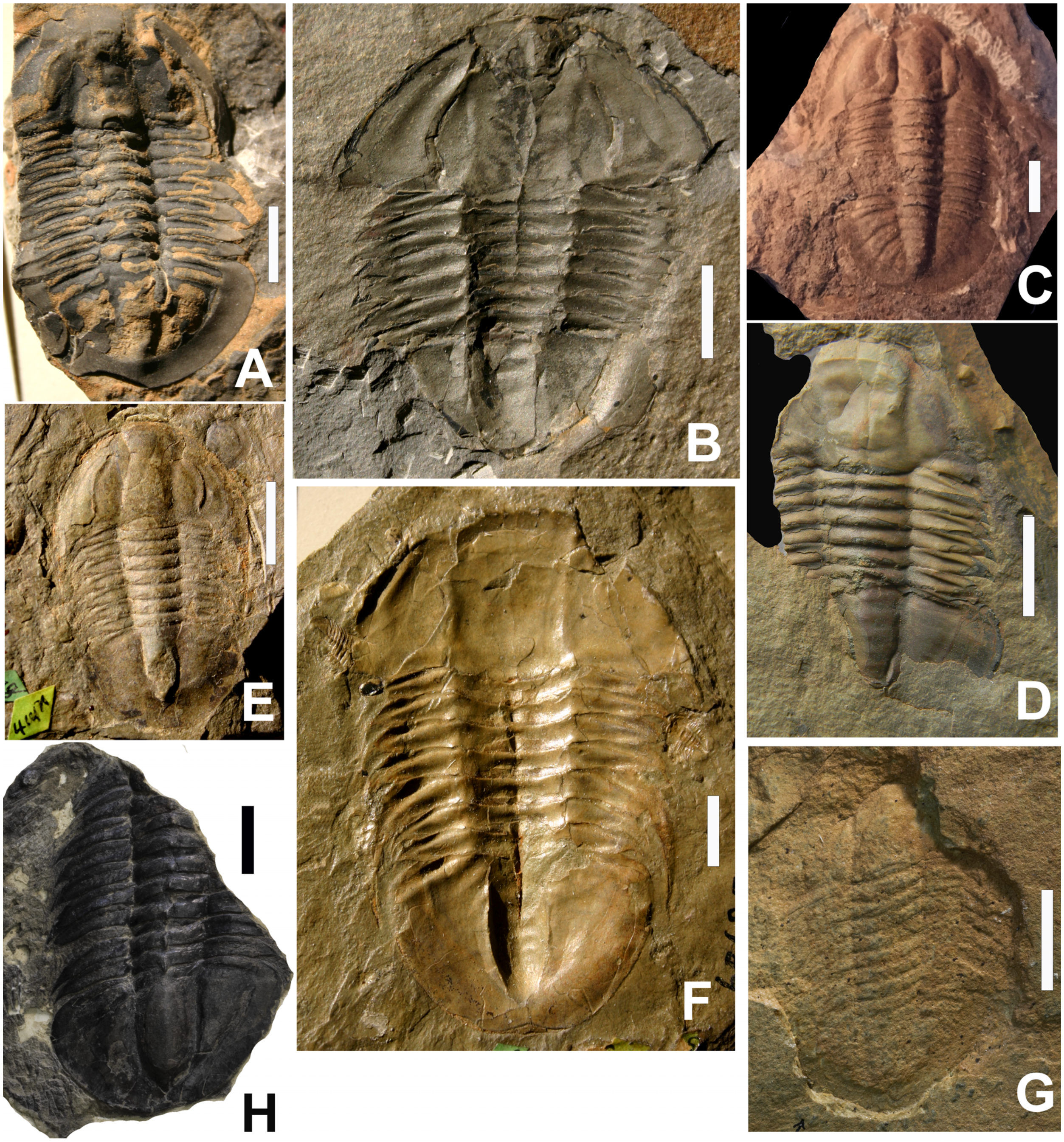

FIGURE 11. Some representative dolichometopids from other formations included in this study. A–B and D–E) *Glossopleura boccar.* C) *Glossopleura similaris*(?) F) *Anoria tontoensis.* G–H) *Glossopleura mohavensis.* A) USNM 62703, type of *Glossopleura boccar*, from the Stephen Formation. B) USNM 62702, specimen originally assigned to *G. stephenensis*, from the Stephen Formation. C) KUMIP 314054, *G. similaris*(?), from the Spence Shale (Langston Formation). D) SGDS 1975, *G. boccar*, from the Chisholm Formation. E) USNM 62714, specimen originally assigned to *G. mckeei*, from the Bright Angel Formation. F) USNM 62685, *Anoria tontoensis*, from the Bright Angel Formation. G) LACMIP 10782, specimen originally assigned to *"Sonoraspis nelsoni",* from the Monola Formation. H) LACMIP 2469/24444.1, specimen originally assigned to *"Sonoraspis californica",* from the Pole Canyon Formation. (Image in D courtesy of Andrew R.C. Milner. G and H courtesy LACM: Hendy, A., Walker, L., Mertz, W. [2020]. LACM Invertebrate Paleontology. Version 1.9. Natural History Museum of Los Angeles County. Occurrence dataset https://doi.org/10.15468/6nxzen accessed via GBIF.org on 2021-03-23.) All scale bars equal 1 cm.

Glossopleura walcotti Poulsen, 1964, p. 25–29, pl. 1, figs. 2–4.

Glossopleura walcotti Palmer and Halley, 1979, p. 79, pl. 16, figs. 6–8, 11–19.

Glossopleura walcotti Babcock, 1994, p. 94, fig. 12.

Glossopleura aff. *leona* Lochman Bordonaro and Banchig, 1995, pl. 2, figs. 14, 15.

Glossopleura walcotti Benedetto et al., 2009, fig. 2g.

Glossopleura walcotti Foglia and Vaccari, 2010, p. 434, figs. 4.10–4.23.

Glossopleura walcotti? Foster, 2011b, p. 106, figs. 4.4, 4.5.

Glossopleura walcotti Sundberg, 2018, p. 19–20, fig. 13.

Glossopleura walcotti Morgan, 2021, p. 96, fig. 3.5.3.

Type specimens. Poulsen (1927) unnumbered, cranidia; USNM 62707, hypotype (Morgan, 2021), thoracics and pygidium.

Occurrence. Cape Wood Formation and Henson Gletscher Formation, Greenland; Stephen Formation, British Columbia; Carrara Formation, California and Nevada; Emigrant Formation, Split Mountain, Nevada; La Laja Formation, San Juan, Argentina; possibly Bright Angel Formation, Grand Canyon, Arizona; all *Glossopleura* Assemblage Biozone, *Glossopleura walcotti* Interval Biozone (Morgan, 2021), (Wuliuan, Miaolingian).

Material examined. USNM 62707 (see Morgan, 2021); USNM 208256, USNM 208258; unnumbered specimens in Poulsen, 1927, pl. 16.

Remarks. *Glossopleura walcotti* is identified mainly by deep S1 glabellar and occipital furrows, although these can of course vary due to taphonomic factors quite independently from actual morphology. The presence of *G. walcotti* in the Cadiz Formation was proposed by Fuller (1980), but this could not be confirmed by the present study and most specimens are likely *G. mohavensis.*

Glossopleura producta (Hall and Whitfield, 1877)

Ogyia producta Hall and Whitfield, 1877, p. 244, pl. 2, figs. 31–34.

Bathyuriscus productus Walcott, 1886, p. 217, pl. 30, fig. 1f.

Dolichometopus productus (part) Walcott, 1916a, p. 369–372, pl. 53, figs. 2, 2a–e, 3, 3a-b.

Dolichometopus productus Resser, 1928, p. 10, pl. 3, fig. 9.

Glossopleura producta Resser, 1935, p. 31–32.

Glossopleura producta Palmer, 1954, pl. 13, figs. 7, 9–13.

Type specimens. USNM 15456, USNM 15459, cotypes.

Occurrence. Ophir Formation, Oquirrh Mountains, Utah; *Glossopleura* Assemblage Biozone, Interval Biozone (Morgan, 2021) undesignated, (Wuliuan, Miaolingian).

Material examined. USNM 15459, USNM 123356, FHPR 16738, FHPR 16739, FHPR 11285, DMNH EPI.42919.

Remarks. Much previous material from the Cadiz Formation, once identified as *Dolichometopus productus*, would at later stages have been considered *Glossopleura producta*; however, Palmer (1954) and Sundberg (2005) restricted *G. producta* to the type material from the Ophir Formation of Utah only. Most Cadiz specimens previously assigned to *Dolichometopus* (*G.*) *producta* are more likely *G. mohavensis*.

Glossopleura baton (Walcott, 1916a)

Dolichometopus baton Walcott, 1916a, p. 362, pl. 51, figs. 2, 2a–b.

Anoria baton Resser, 1935, p. 10.

Anoria baton (part) Schwimmer, 1973, pl. 6, figs. 4, 5.

Type specimens. USNM 62696–62698, partial to nearly complete specimens.

Occurrence. Gordon Shale, Montana; *Glossopleura* Assemblage Biozone, Interval Biozone (Morgan, 2021) undesignated, (Wuliuan, Miaolingian).

Material examined. USNM 62696–62698; USNM uncataloged in Schwimmer (1973).

Remarks. Most characters of these specimens are typical of various species of *Glossopleura*; most importantly, however, the eye length of the studied specimens falls within the range of *Glossopleura*, and the specimens cannot clearly be placed within *Anoria* even by this possibly more reliable character.

Glossopleura sp.

Sonoraspis torresi Stoyanow, 1952 (in Cooper et al., 1952), p. 53–54, pl. 14, figs. 1–4.

Sonoraspis gomezi Stoyanow, 1952 (in Cooper et al., 1952), p. 54–55, pl. 14, figs. 5, 6.

Glossopleura sp. Lochman, 1952 (in Cooper et al., 1952), p. 137, pl. 31, figs. 8–14.

Glossopleura leona (part) Cuen-Romero et al., 2018, p. 230.

Occurrence. Arrojo Formation, Sonora; *Glossopleura* Assemblage Biozone, Interval Biozone

(Morgan, 2021) undesignated, (Wuliuan, Miaolingian).

Material examined. USNM 116333, USNM 116349, USNM 116348, USNM 116350 (all originally *S. torresi* by Stoyanow, 1952); USNM 116335, USNM 116334, both originally *S. gomezi* by Stoyanow, 1952), all nearly complete specimens.

Remarks. These specimens compare well with those of *"S. californica"* (and thus *Glossopleura mohavensis*), especially in the number of thoracic segments, length of pleural spines, and medium length eyes in those preserving the structures. The preservation, features, and axial nodes of USNM 116334 especially are similar to *"S. californica"*. These specimens are then rather similar to *G. mohavensis* from the Cadiz Formation, although they are not formally assigned to that species here. Comparison with *Glossopleura leona* is more difficult given the preservation of nearly complete specimens in shale for the present specimens versus cranidia and pygidia only in limestone for *G. leona* (Lochman in Cooper et al., 1952).

Genus *Anoria* Walcott, 1924

Type species. *Dolichometopus tontoensis* Walcott, 1916a, from the Bright Angel Formation, Grand Canyon, Arizona.

Anoria tontoensis Walcott, 1924
Figure 11F

Dolichometopus tontoensis Walcott, 1916a, p. 373, pl. 51, figs. 1, 1a–1h.

Anoria tontoensis (Walcott, 1916a) Walcott, 1924, p. 54, p. 54, pl. 9, fig. 2.

"Anoria" tontoensis Foster, 2011b, p. 107–110. figs. 5, 6.

Type specimens. USNM 62685, lectotype, part and counterpart of a complete specimen; USNM 62686, paralectotype, nearly complete specimen.

Occurrence. Bright Angel Formation, Grand Canyon, Arizona; *Glossopleura* Assemblage Biozone, possibly *Glossopleura walcotti* Interval Biozone (Morgan, 2021) if identification of *G. walcotti* in same beds (Foster, 2011b) is correct, (Wuliuan, Miaolingian).

Material examined. USNM 62685, USNM 62686, GRCA 2797, GRCA 11520, GRCA 123303, GRCA 123304, DMNH EPI.42917.

Remarks. This is the type and only clearly valid species of *Anoria* studied in this report; previously reported specimens of other *Anoria* species from the Cadiz Formation are confirmed as belonging within *Glossopleura*.

Anoria? *bessus* (Walcott, 1916a)

Dolichometopus ? *bessus* Walcott, 1916a, p. 362–363, pl. 51, figs. 3, 3a–c.

Anoria bessus (Walcott) Resser, 1935, p. 10, p. 54, pl. 9, fig. 2.

Anoria baton (part) Schwimmer, 1973, pl. 6, fig. 3.

Type specimens. USNM 62699, nearly complete specimen; USNM 62700, pygidium; USNM 62701, cephalon with hypostome.

Occurrence. Gordon Shale, Montana; Bright Angel Formation, Grand Canyon (Grand Wash Cliffs), Arizona; *Glossopleura* Assemblage Biozone, Interval Biozone (Morgan, 2021) undesignated, (Wuliuan, Miaolingian).

Material examined. USNM 62699, USNM 62700, USNM 62701, DMNH EPI.42915, DMNH EPI.42916, USNM uncataloged (in Schwimmer, 1973).

Remarks. Species characterized by short to long eyes, reduced oval pygidium smaller than cephalon, and moderately elongate pleural spines on all thoracic segments. This latter character contrasts with the short pleural spines of most species of *Glossopleura* and the elongate fifth thoracic pleural spines of *G. lodensis* and the type material of *Anoria tontoensis*. These features are pronounced in USNM 62699 and the uncataloged specimen illustrated by Schwimmer (1973). Despite qualitatively moderately short eyes in the Gordon Shale specimens, most specimens have moderate to long eyes except USNM 62699 (EL/GL of 0.298 versus 0.428 in Schwimmer's, 1973, USNM uncataloged and 0.446 in DMNH EPI.42915). Thus, all but one specimen featuring moderately elongate pleural spines and a small, oval pygidium from the Gordon and Bright Angel formations, typical of *Anoria bessus,* actually have elongate eyes that fit within the range of *Glossopleura*. Because the single anomalous, short-eyed specimen (USNM 62699) is the most complete of the cotypes, all the studied material here is designated *Anoria*? *bessus*. The question of whether the species is better placed in *Glossopleura* (despite the short-eyed USNM 62699 and considering the results of this study regarding eye length) is left for a separate investigation.

CONCLUSIONS

Based on the material studied here (Table 1), in the Cadiz Formation: 1) the type of *Glossopleura mohavensis* (USNM 78400b) is retained as a valid species, distinguished from other species by the consistent occurrence of eight thoracic segments (in Cadiz, Pole Canyon, and Monola formations), moderate eye length (EL/GL just >0.380), and a lack of elongate T5 pleural spines; other than the number of thoracic segments, however, this species is similar to *G. boccar;* 2) the type and paratype of *"Sonoraspis californica"* (LACM 10785 and 10786) are confirmed as being included within *G. mohavensis*: there are no previously featured differences between the two taxa that are consistent, and their eye lengths and positions all match well and are among the *Glossopleura* range, and they share eight thoracic segments each; this, by qualitative and PC analysis, lends quantitative support to the idea that at the genus level *"Sonoraspis"* is a junior synonym of *Glossopleura* (Lochman in Cooper et al., 1952; Palmer, 1954); and 3) *"Anoria" lodensis* of Mason (1935; USNM 78400a) and Stoyanow (1956) is confirmed as a species of *Glossopleura (G. lodensis)* as listed by Resser (1935), characterized by elongate T5 pleural spines and frequently eight thoracic segments; USNM 78400a and LACM 2471-11 demonstrate that *G. lodensis* has the long eyes typical of many members of that genus. Thus, there appear to be just two species of *Glossopleura* in the Cadiz Formation: *G. mohavensis* and *G. lodensis*. As demonstrated here and in Mason (1935) and based on cranidial and complete material, both species occur at UCR 7359.

Additionally, study of non-Cadiz material in this report suggests: 4) *Anoria* may be a distinct genus but should be restricted to *A. tontoensis* (currently known only from the Bright Angel Formation), as the most consistently small-eyed (EL/GL <0.380) and PCA-separated dolichometopid; 5) in Montana, the species *"A." baton* should be *Glossopleura baton* based on the type material; and 6) *A.*? *bessus* specimens from the Gordon Shale and Bright Angel Formation, united by reduced, oval pygidia and moderately long pleural spines on all thoracic segments, demonstrate a wide range of relative eye lengths, from short (graphing among *Anoria* specimens in USNM 62699) up to approximately average for *Glossopleura* (in DMNH EPI.42915 from the Bright Angel Formation). This latter, broad range of relative eye lengths, in a species (*A.*? *bessus*) otherwise distinguished from all others by more clear differences in the pygidium and thorax, is a conundrum best left to future projects involving more specimens, but it may undermine the utility of even quantitative measurements of relative eye length for genus assignment in dolichometopids. Measurement of many of the previously qualitative characters used historically to separate *Anoria, Glossopleura,* and *"Sonoraspis"* vary too much along continuous spectra for the characters to be reliable for generic separation.

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APPENDIX

Character list for phylogenetic analysis.

Cephalon

1. Preglabellar field large (0) or greatly reduced or absent (1)

2. Glabella narrows anteriorly (0), inflated medially (1) or parallel sided to hourglass-shaped and expanding anteriorly (2)

3. Glabellar S1 furrows distinct (0) or shallow (1) or absent (2)

4. Ratio of eye length:cranidium length less than 0.21 (0), 0.21–0.38 (1), or > 0.38 (2)

5. Posterior limbs taper (narrow anteroposteriorly) strongly laterally (0) or only slightly and are thus relatively narrow along full length (1)

6. Genal spines extend posteriorly to thoracic segment 2 or 3 (0), 4 or 5 (1) or to 6 or 7 (2)

Thorax

7. Thoracic segments ≥ 12 (0), 7 (1), 8 (2), or variable 7 or 8 in number (3)

8. 5th thoracic pleural spines short or medium (0) or much more elongate relative to those of other segments (1)

9. Axial spines or spine bases: absent (0), not preserved or present in different specimens (1), or present (2)

10. Pleural spines of thoracic segments T3–T4 and T6–T7 short (0) or moderately elongate (1)

Pygidium

11. Pygidium very reduced (0) or somewhat smaller and narrower than cephalon such that thorax tapers slightly posteriorly (1) or very nearly equal in size to cephalon (2)

12. Furrows on pygidial pleural lobes well defined (0), shallow (1), or absent (2)

13. Furrows on pygidial axis well defined (0), shallow (1), or absent (2)

14. Pygidial border narrow (0), moderately broad (1), or very broad with antero-posteriorly short axis (2)

15. Pygidial posterior border with medial concavity in dorsal view absent (0) or present (1)

16. Pygidium antero-lateral border relatively straight (0) or rounded and curved posteriorly so that whole pygidium is nearly oval (1)

17. Pygidium border without (0) or with (1) marginal spines

APPENDIX TABLE 1. Raw data cranial measurements used for this study (in millimeters) (available for download at https://palaeo-electronica.org/content/2022/3617-cadiz-dolichometopids).

APPENDIX TABLE 2. Character matrix for taxa included in phylogenetic analysis

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Amecephalus piochensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dorypyge richhofeni	1	1	2	2	0	?	?	?	?	0	2	0	0	0	0	0	1
Glossopleura boccar USNM 62703	1	2	1	2	1	0	1	0	1	0	2	1	1	1	0	0	0
Glossopleura mckeei	1	2	2	2	1	2	1	0	1	0	2	2	2	1	0	0	0
Glossopleura producta	1	2	1	2	1	?	1	0	1	0	2	1	1	1	0	0	0
Glossopleura bion	1	2	1	2	1	0	1	0	0	0	2	2	2	2	0	1	0
Anoria tontoensis USNM 62685	1	2	2	1	0	0	1	1	1	0	2	2	1	1	1	0	0
Anoria lodensis USNM 78400	1	2	?	2	1	0	1	1	?	0	2	1	?	1	0	0	0
Sonoraspis californica LACM 10785	1	2	1	2	0	?	2	0	2	0	2	2	2	1	0	0	0
Glossopleura mohavensis	1	2	1	2	0	0	2	0	1	0	2	2	2	1	0	0	0
Anoria bessus	1	2	1	1	0	0	1	0	?	1	1	1	1	1	0	1	0
Glossopleura gigantea	1	2	1	2	1	0	3	0	2	0	2	2	1	1	1	1	0
Glossopleura campbelli	1	2	1	2	1	0	2	0	0	0	2	2	2	1	0	0	0
Glossopleura yatesi	1	2	1	2	1	1	2	0	2	1	1	2	2	2	1	1	0