# New pliomerid trilobite genus Lemureops from the Lower Ordovician (Ibexian; Tulean, Blackhillsian) of western Utah, USA 

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#### Abstract

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#### Abstract

Species of Lemureops gen. nov. (type species: L. kilbeyi sp. nov.) are common members of faunal assemblages from the Psalikilus pikum, Strigigenalis plicolabeona, Carolinites nevadensis and Presbynileus ibexensis trilobite zones in the upper Fillmore Formation of the Ibex area, western Utah. The genus is defined by several striking apomorphies, including a long, subtriangular anterior border; large subtriangular to reniform palpebro-ocular ridges; a wide, shallow, lacunate axial furrow along the glabella; an anteriorly prominent and posteriorly reduced eye socle; and a pygidium with a strongly tapered posterior outline. Lemureops is likely the sister taxon of Pseudocybele Ross, 1951a, but this hypothesis must be tested in a broader phylogenetic context once Pseudocybele is revised and related taxa presently assigned to Hintzeia Harrington, 1957, and Protopliomerella Harrington, 1957, are described and revised. New species in addition to the type are L. willsonpiperi, L. ploogi and L. koppesi; Pseudocybele lemurei Hintze, 1953, is reassigned to Lemureops. Two additional species are new, but insufficiently known for formal naming.


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THE TRILOBITE family Pliomeridae Raymond, 1913, ranges through the Ordovician and contains 42 valid genera and 163 valid formally named species (not including the taxa named herein). No new genera have been added since 1990 and only eight new species have been described in the past decade. Many genera are monotypic and others are "wastebasket" taxa containing poorly understood species. Roughly a third of pliomerid genera are composed entirely of species too poorly described to meaningfully interpret. Even many widely used genera are not obviously monophyletic, and the entire family is in need of revision using modern phylogenetic methods and greatly improved standards of description and illustration. This considerable undertaking cannot proceed without basic systematic revision of established species and description of new diversity represented by large samples of well preserved specimens. This is the aim of the present study.

This paper continues field-based revision (Adrain et al., 2001, 2003; Adrain \& Westrop 2006a, 2006b, 2007a, 2007b; McAdams \& Adrain, 2009a, b) of Lower Ordovician faunas
first reported by Hintze $(1951,1953)$ from the Pogonip Group of western Utah and by Ross (1949, 1951a, 1951b) from the Garden City Formation of southeastern Idaho and northern Utah. These mid-20th century monographs were groundbreaking works, which introduced many genera and species. They established the foundation for the Ross-Hintze lettered trilobite faunal zonation, which formed the basis for the Ibexian Series (Ross et al., 1997). However, the classic Ibexian faunas have been restudied only rarely in the last half-century, as summarised by Adrain et al. (2001).

New field collections from Hintze's (1951, 1953) Section H contain many well preserved species of pliomerids, the majority of which are new and undescribed. Although species of Lemureops gen. nov. are fairly abundant in most of our samples, they have been overlooked or misidentified in the past. Material now assigned to two of the new species was earlier assigned by Hintze (1953) and Young (1973) to Pseudocybele lemurei Hintze, 1953, and a handful of additional sclerites were misassigned to Pseudocybele


Fig. 1. A, location of the Tule Valley in Millard County, western Utah. B, road map showing location of Section H in the Ibex area of the Tule Valley. C, line of Section H (Hintze 1951, 1953, 1973), southern Confusion Range, Ibex area, Tule Valley, Millard County, western Utah, USA, depicted on portion of US Geological Survey 1: 24000 Warm Point provisional 7.5' quadrangle map (1991).
altinasuta Hintze, 1953. The goals of the present work are: 1. to revise P. lemurei Hintze, 1953; 2. to describe and name four new species of latest Tulean and Blackhillsian age, along with a further two new species described in open nomenclature; and 3. to diagnose the new genus Lemureops on the basis of synapomorphies, and to distinguish it from its putative sister taxon, Pseudocybele.

## LOCALITIES AND STRATIGRAPHY

Species of Lemureops gen. nov. occur in strata of the upper Tulean through Blackhillsian stages in the Fillmore Formation. These strata are well exposed at Hintze's $(1951,1953,1973)$ Section H , located on the eastern side of the southern Confusion Range in the Ibex area, Tule Valley, Millard County, western Utah (Fig. 1). Section H begins in informal member 3, the "light gray ledge-forming member", of the Fillmore Formation (Hintze, 1973) and continues through informal member 6, the "Calathium calcisiltite member". Hintze $(1951,1953)$ originally measured the section in feet, marking every five feet (where possible) with durable yellow highway paint and indicating the sampling
number and footage of particular prominent beds. It is hence generally straightforward to relocate the exact sampling horizons from which the material described in the 1953 monograph was collected. In 1965, Hintze remeasured the section more accurately, again in feet, and painted a second set of measurements on the rocks. These are not difficult to distinguish from the original numbers, as they are over 150 ' greater (e.g., the original sampling horizon H-24 is at $525^{\prime}$ in 1951 measurements and 699' in 1965 measurements). The 1965 measurements are the basis for Hintze's revised (1973) section description and for the species ranges reported by Ross et al. (1997). In the course of new field sampling, JMA and S.R. Westrop are remeasuring each of Hintze's and Ross's sections in metres and making new stratigraphic logs. At Ibex, sections Lava Dam North (Adrain et al., 2003), the lower part of B, the new section MME (Adrain \& Westrop, 2007a), and all of $G$ and $H$ have been remeasured and logged (see Adrain et al. [2009] for complete stratigraphic columns of sections G and H). Our new measurements in metres are used herein, but Hintze's original 1951/1953 measurements in feet

Fig. 2 (opposite). Stratigraphic occurrence of species of Lemureops in Section H. Measurements are in metres from our remeasurement of the section (see Adrain et al. 2009, for a full stratigraphic column). Hintze's original ( 1951,1953 ) sampling horizons are indicated at their equivalent metreage.

are also given. This facilitates correlation between the sets of measurements, comparison with work done prior to remeasurement, and clarification of the position of key original sampling horizons relative to new horizons. We recollected all of Hintze's original Section H sampling horizons, along with several new horizons. Bulk sample size varied, but in general was very large, on the order of tens of kilograms.

Ross (1949, 1951a) recognised two trilobite zones $(\mathrm{G}(1)=$ Hintzeia celsaora Zone of Ross et al. [1997]); $\mathrm{G}(2)=$ Protopliomerella contracta Zone) comprising what would become the Tulean Stage, and three (H = Trigonocerca typica Zone; I $=$ Presbynileus ibexensis Zone; $\mathrm{J}=$ Pseudocybele nasuta Zone) comprising what would become the Blackhillsian. This trilobite zonation was based largely on the identifications and range data presented by Hintze (1953). A revised and expanded zonation, based on new field sampling, was presented by Adrain et al. (2009) and is followed herein.

Species of Lemureops were found at fourteen sampling horizons, three of which are talus material, in the "calcarenite" and "Calathium calcisiltite" members (informal members 5 and 6 , respectively) of the Fillmore Formation. Lemureops-bearing horizons include seven of Hintze's (1951, 1953) sampling horizons: H-16, $\mathrm{H}-17, \mathrm{H}-20, \mathrm{H}-23, \mathrm{H}-24, \mathrm{H}-27$ and $\mathrm{H}-28$, and seven new horizons (Fig. 2). The sampling horizons span 103.7 m , beginning in the Tulean Psalikilus pikum Zone of Adrain et al. (2009) and ranging through the Blackhillsian Strigigenalis plicolabeona, Carolinites nevadensis and Presbynileus ibexensis zones. The genus, as far as is known, became extinct before the end of the Blackhillsian, as it is not recorded above the $P$. ibexensis Zone.

Hintze (1953, table 8) reported "Pseudocybele lemurei" from a block of talus from near the top of Yellow Hill, in the Pioche mining district of Lincoln County, eastern Nevada. He did not figure any specimens. Hintze speculated that this material was originally from an horizon near 577' (his YH-16). We resampled this horizon and found that it is much older than Hintze suspected, representing the Tulean Heckethornia bowiei Zone of Adrain et al. (2009). The horizon is near the top of Yellow Hill, and the entire line of section appears to contain Tulean strata. The origin of Hintze's talus sample, which is of Blackhillsian C. nevadensis Zone age, is unclear, as we found no samples of this age anywhere at Yellow Hill, and no material assignable to Lemureops.

## SYSTEMATIC PALAEONTOLOGY

Repository. Type and figured specimens are housed
in the Paleontology Repository, Department of Geoscience, University of Iowa, Iowa City, Iowa, USA, with specimen number prefix SUI.

Terminology. Morphological terms follow Whittington \& Kelly (1997). There is no clear distinction between the palpebral lobe and eye ridge in species of Lemureops, and the combined structure is referred to as the palpebro-ocular ridge (Whittington \& Kelly, 1997, p. 324).

## Family PLIOMERIDAE Raymond, 1913

## Lemureops gen. nov.

Type species. Lemureops kilbeyi sp. nov., from Section H 191.7 m (434'; locality H-20 of Hintze [1953]), Fillmore Formation (Blackhillsian, Strigigenalis plicolabeona Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Other species. All from Section H, Fillmore Formation, southern Confusion Range, Ibex area, Millard County, western Utah. Tulean (Psalikilus pikum Zone) species are Lemureops ploogi sp. nov., $L$. koppesi sp. nov. and $L$. sp. nov. B. Blackhillsian species are L. lemurei (Hintze, 1953) (Presbynileus ibexensis Zone), L. willsonpiperi sp. nov. (Presbynileus ibexensis Zone) and $L$. sp. nov. A (Strigigenalis plicolabeona Zone).

Diagnosis. Cranidial anterior border with doublural sector rotated up, so that most of anterior border visible in dorsal view is doublure; ventral base of anterior border furrow exposed across complete width in anterior view; large, subtriangular to reniform palpebro-ocular ridges; wide, lacunate axial furrow along glabella; strongly downturned fixigenae; strongly anterolaterally bowed posterior branch of facial suture; posterior border very long (exsag.) at genal angle; librigena with subtriangular, L-shaped field; eye socle broad and highly inflated, most strongly expressed anteriorly; thoracic segments with anterior pleural band shorter (exsag.) than posterior band; articulating facet of posterior band with notch near tip; pygidium highly vaulted, with five axial rings and a large, triangular terminal piece; posteriorly tapered from tips of first pleural ribs; W- or H-shaped indentation in terminal piece; doublure distinctly pointed at sagittal axis in anterior view.

Etymology. From the specific epithet lemurei and the Greek noun ops, eye; gender is masculine.

Remarks. The histories of species assigned herein

to Lemureops n. gen. are intertwined with those of members of Pseudocybele Ross, 1951a, and the genera are almost certainly sister taxa. Ross established Pseudocybele as a monotypic genus with the type species $P$. nasuta Ross, 1951a, from the Garden City Formation of Idaho. He considered diagnostic characteristics to include the anteriorly recurved median projection of the anterior border, narrow anterior hypostomal wings, and a pygidium with fused median pleural tips. Ross suggested that Pseudocybele was possibly derived from species then assigned to Protopliomerops Kobayashi, 1934 (now assigned to Protopliomerella Harrington, 1957, and Hintzeia Harrington, 1957), and potentially sister to Pseudomera Holliday, 1942. He also speculated that Pseudocybele may be "ancestral" to Ectenonotus Raymond, 1920, and the encrinurid Cybele Lovén, 1846. Hintze (1953) described Pseudocybele lemurei from the Fillmore Formation of western Utah. It is assigned herein to Lemureops gen. nov. Hintze differentiated $L$. lemurei from members of Pseudocybele on the basis of its large palpebro-ocular ridges, wide and shallow glabellar furrows, and wider librigenal field, but did not consider these differences to be significant at genus level.

With knowledge of the new and revised species described herein, along with new and revised species of Pseudocybele (McAdams \& Adrain 2009a, work in progress), it seems clear that two distinct clades are involved. Members of Lemureops possess a long, tall, triangular anterior border whereas the condition in species of Pseudocybele is short and rim-like, except for the (apomorphic) nasute projection. The Lemureops glabella is short, wide, and bounded by a wide, shallow axial furrow, whereas that of species of

Fig. 3. Comparison of ventral pygidial morphology of species of Lemureops and Pseudocybele. Pygidia of species of Lemureops can be distinguished from pygidia of species of Pseudocybele by their medially pointed and anteriorly tapered doublure. A, C, Lemureops kilbeyi sp. nov., SUI 110207, ventral and anterior views, x12 (H 191.7 m). B, D, Leтигеорs willsonpiperi sp. nov., SUI 110273, ventral and anterior views, x10 (H 264-267T m). E, Lemureops koppesi sp. nov., SUI 110309, anterior view, x12 (H 172.5 T m). F, G, Pseudocybele paranasuta McAdams \& Adrain, 2009a, SUI 110489, ventral and anterior views, x10 (H 285T m). H, Lemureops lemurei (Hintze, 1953), SUI 110349, anterior view, x12 (H 251.4 m). I, K, Pseudocybele altinasuta Hintze, 1953, SUI 110490, ventral and anterior views, x 12 (H 191.7 m). J, L, "Pseudocybele nasuta" Ross, 1951, SUI 110491, ventral and anterior views, x 10 (Hintze Section J $16.1 \mathrm{~m}\left[46^{\prime}\right]$; see Adrain et al. [2001] for detailed locality information).


Pseudocybele is long, narrow, and surrounded by a deep, narrow furrow. The palpebro-ocular ridges of Lemureops are large and often reniform; those of Pseudocybele are small and located far forward on the cranidium. Librigenae of Lemureops are short, broad and triangular; librigenae of Pseudocybele are elongate and narrow. Pygidia of Lemureops are broad, with a complex impression in the terminal piece; those of Pseudocybele are narrow, with a long, narrow terminal piece. Members of the two genera have significantly overlapping stratigraphic ranges in the Blackhillsian, but species of Lemureops have an older first occurrence in the Tulean and do not range into the Wah Wah Formation alongside species assigned to Pseudocybele.

Pseudocybele will be revised in detail in a forthcoming publication. However, it is important to note that $P$. nasuta must at this point be restricted to material from the type locality, which we have yet to resample. New sampling at Ibex, Garden City localities, and eastern Nevada indicates that there are at least two species of Pseudocybele present within "Zone J." Most of Ross's (1951, pl. 33, fig. 1-14; pl. 34, fig. 21-26) figured material, including the holotype cranidium, is small and likely immature. The single large cranidium from the type locality is illustrated only as a ventral view. It is at this point impossible, pending resampling of the type locality, to determine whether specimens from other localities that have been assigned to $P$. nasuta (e.g., by Hintze [1953], pl. 24, fig. $8-11$ ) are accurately assigned, or whether they belong to new species of Pseudocybele. Hence we refer to the Ibex occurrence as " $P$. nasuta" in the present work.

Hintze (1953, p. 217) observed that the pygidia of "Pseudocybele nasuta" and L. lemurei are similar dorsally, but strikingly differentiated ventrally. He emphasised differences in the width (or sagittal length) of the pygidial doublure, describing that of $L$. lemurei as even, and that of " $P$. nasuta" as "considerably wider at the midline, narrowing evenly to the antero-lateral corners" (1953, p. 217). New evidence shows that this distinction is only partially accurate. The pygidial doublure of all members of Lemureops is longest medially, coming to a distinct point at the sagittal midline, then anteriorly tapered.

These features are best visible in anterior view (Fig. 3C-E, H). In ventral view, the doublure does appear to be of equal length at the midline as at the anterior edges (Fig. 3A, B) if one includes the pleural tips. However, this observation is also true of P. altinasuta Hintze, 1953, (Fig. 3I) and Pseudocybele paranasuta McAdams \& Adrain, 2009a from Section H 285T m (Fig. 3F). The doublure of " $P$. nasuta" is extremely long medially, visibly longer than that of Lemureops and other species of Pseudocybele even in ventral view (Fig. 3J). The doublure of all three species of Pseudocybele is rounded at the midline, and tapers anteriorly. However, the doublure of " $P$. nasuta" is subtriangular in shape (in anterior view) and strongly tapered anteriorly (Fig. 3 L ), while that of $P$. altinasuta (Fig. 3K) and $P$. paranasuta (Fig. 3G) is more semicircular and gently tapered. Hintze also noted that the tips of the median pleurae are conjoined in "P. nasuta", but that they are free in $L$. lemurei. The median pleural tips of $P$. altinasuta are not fused (Fig. 3I, K ), those of P. paranasuta are nearly fused (Fig. 3F, G), and those of "P. nasuta" (Fig. 3J, L) are definitely fused.

Lemureops and Pseudocybele likely root together within the plesiomorphic and almost certainly paraphyletic Protopliomerella Harrington, 1957. Harrington established the genus for Protopliomerops contracta Ross, 1951a. The single other presently assigned species, $P$. pauca Demeter, 1973, is known from only three sclerites whose association is suspect. We have recovered several new species which would presently be assigned to Protopliomerella. Like most other Lower Ordovician pliomerid taxa, Protopliomerella is at present poorly known and in need of revision. However, several features demonstrate relationship with Pseudocybele and Lemureops. The genera share a unique, broad, shield-like "winged" cranidium, with the eye ridges completely merged with the palpebral lobes into large, anteriorly located palpebroocular ridges, and a five-segmented, spade-shaped pygidium with a triangular terminal piece. The hypostomes of the genera are also similar, and librigenae of Protopliomerella are nearly identical to those of Pseudocybele. Juvenile cranidia of species assignable to the three genera are almost indistinguishable (cf. Figs 6R, Y, 18V, AA, 23BB

Fig. 4. All specimens are from Section H 191.7 m (434'; locality H-20 of Hintze [1953]), Fillmore Formation (Blackhillsian, Strigigenalis plicolabeona Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. A-O, Lemureops kilbeyi sp. nov. A, B, D, cranidium, holotype, SUI 110162, dorsal, right lateral, and anterior views, x6. C, E, H, cranidium, SUI 110163, right lateral, dorsal, and anterior views, x6. $\mathbf{F}, \mathbf{G}, \mathbf{I}$, cranidium, SUI 110164, dorsal, left lateral, and anterior views, x6. J, K, N, cranidium, SUI 110165, left lateral, dorsal, and anterior views, x7.5. L, M, O, cranidium, SUI 110166, dorsal, right lateral, and anterior views, x7.5. P-T, Lemureops sp. nov. A, cranidium, SUI 110167, left lateral, dorsal, oblique, anterior, and ventral views, x 6 .

with Ross [1951a, pl. 33, figs 10, 30] and Ross [1951b, pl. 82, fig. 15; pl. 83, figs 1, 3]).

Species of Lemureops, though united by the synapomorphies listed above, in some cases vary considerably from one another. Lemureops koppesi and L. ploogi closely resemble each other, as do $L$. willsonpiperi and L. lemurei. However, these two pairs are strongly differentiated from each other. The stratigraphically lower pair of $L$. koppesi and L. ploogi have relatively shorter, narrower cranidia with smaller palpebro-ocular ridges and more robust occipital rings. Their anterior eye position, reminiscent of that of species of both Protopliomerella and Pseudocybele, suggests that they are plesiomorphic relative to the other species. Lemureops willsonpiperi and L. lemurei have more robust anterior borders, shorter fixigenal fields and longer posterior borders. The type species, L. kilbeyi, is stratigraphically intermediate between these pairs. Its prominently humped frontal glabellar lobe unites it with $L$. koppesi and L. ploogi, both of which have a much weaker "hump." Lemureops lemurei and L. willsonpiperi completely lack the "hump" yet their anterior border, eye position, and size of the palpebro-ocular ridge are all very similar to those of L. kilbeyi. Hence it is not clear whether their lack of the anterior glabellar structure is plesiomorphic or represents secondary loss. Phylogenetic analysis of Lemureops and related genera will be carried out once revision and description of relevant taxa is complete.

Fortey (1979, p. 106) assigned Pseudocybele (then including L. lemurei) to his new subfamily Cybelopsinae. Pseudocybele was depicted on his diagram of hypothetical relationships (Fortey, 1979, fig. 13) as having an origin within Hintzeia separate from that of the other "cybelopsines," which if true would render the subfamily polyphyletic. On the same diagram, Fortey assigned Hintzeia to a subfamily Protopliomerinae, but there is no such taxon. Hupé (1953, p. 237) erected Protopliomeropinae (though he used an incorrect stem: Protopliomeropsinae), to which Hintzeia has been referred (e.g., Edgecombe et al., 1999). Fortey's classification would hence also create (multiple) paraphyly in Protopliomeropinae. We prefer not to recognise subfamilies within Pliomeridae until they can
be supported by modern phylogenetic analysis. However, Cybelopsinae may prove to be the available name for an expanded clade including Lemureops. Cybelopsis and Strotactinus are likely part of a clade including species of Hintzeia to which the clade of Pseudocybele, Lemureops and Protopliomerella is sister, but this remains to be confirmed cladistically.

Demeter (1973, pl. 4, figs. 4, 8; pl. 5, figs. 1, $6,11)$ figured four pygidia and one fragmentary glabella as "Pseudocybele sp." Several of these sclerites may belong to species of Lemигеорs, but the available illustrations are difficult to interpret. A juvenile cranidium (Demeter, 1973, pl. 5, fig. 10) could also possibly belong to Lemureops. Most of Demeter's specimens were collected from horizons at the Mesa Section (Hintze, 1973), which we have not yet resampled. New field collections will be required to make sense of them.

Lemureops kilbeyi sp. nov. (Figs 3A, C, 4A-O, 5-9)

1973 Pseudocybele lemurei Hintze, 1953; Young, p. 110 , pl. 3, figs 8,11 (non pl. 3 , fig. $12=$ "Kanoshia (?) depressus" Young, 1973).
1973 Pseudocybele altinasuta Hintze, 1953; Young, p. 108, pl. 3, fig. 13 (only).

Diagnosis. Large hump located anteriorly on the glabellar frontal lobe; robust eye socle; hypostomal middle furrow shallow or obscure; interpleural furrows reflected by faint furrows developed on pygidial doublure.

Description. Cranidium short and broad posteriorly, with width across anterior border furrow $39.7 \%$ ( $37.1 \%-42.5 \%$ ) width across widest part of fixigenae and sagittal length $47.6 \%$ (42.7\%-51.5\%) fixigenal width; anterior border prow-like, triangular in dorsal view, longest at sagittal axis, tapered laterally, moderately inflated, with inflation highest at sagittal axis and falling exsagittally, tall medially and shorter laterally in anterior view, with slight transverse ridge along medial posterior edge, crenulated anterior of ridge, with sculpture of tiny, closely spaced granules; doublure curves over top of border and

Fig. 5. Lemureops kilbeyi sp. nov. from Section H 191.7 m (434'; locality H-20 of Hintze [1953]), Fillmore Formation (Blackhillsian, Strigigenalis plicolabeona Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. A, B, D, G, cranidium, SUI 110168, dorsal, right lateral, ventral, and anterior views, x7.5. C, E, F, cranidium, SUI 110169, dorsal, right lateral, and anterior views, x7.5. H, I, M, cranidium, SUI 110170, right lateral, dorsal, and anterior views, x7.5. J-L, cranidium, SUI 110171, dorsal, anterior, and left lateral views, x7.5. N, Q, R, cranidium, SUI 110172, dorsal, anterior, and left lateral views, x7.5. O, P, T, cranidium, SUI 110173, right lateral, dorsal, and anterior views, x7.5. S, W, AA, cranidium, SUI 110174, left lateral, dorsal, and anterior views, x10. U, V, X, cranidium, SUI 110175, anterior, left lateral, and dorsal views, x10. Y, Z, BB, cranidium, SUI 110176, anterior, left lateral, and dorsal views, x10.

faces forward, with median dorsally convex notch, only ventral rim visible in ventral view; anterior border furrow short, shorter ventrally, very deep, incised, longer and deeper at apodemal pits, then slightly shallower anterior of palpebro-ocular ridge, somewhat overhung by posterior margin of anterior border, with course subparallel to anterior margin of glabella; glabella subrectangular, with length $87.6 \%$ ( $78.0 \%-95.6 \%$ ) width at L3, with lobes independently inflated and strongly expressed, narrowest at L1, widest at L3, highly transversely arched, inflated, with increased inflation posteriorly, with sculpture of many densely packed granules concentrated medially; median lobe rectangular, dorsally inflated, with pair of slightly more inflated knobs just anterior of SO; frontal lobe trapezoidal, less inflated than median, with large, densely granulose hump protruding from anterior; L1 and L2 roughly equal in length, L3 longer, exsagittal regions of L1 anterolaterally expanded, exsagittal regions of L2 and L3 nearly merged with fixigena and palpebroocular ridge (respectively), lobes separated by moderately long, deep sulci with apodemal pits at adaxial ends (except S3); course of S2 slightly posteriorly directed, S1 and S3 anteriorly directed (S3 more strongly than S 1 ), all sulci disconnected from axial furrow; SO long, moderately shallow medially, extremely deep at lateral apodemal pits, moderately long medially, slightly longer laterally, extremely short at convergence with posterior border furrow; LO long medially, tapered laterally to apodemal pits, then slightly longer near axial furrow, strongly transversely arched and moderately dorsally inflated, with dense granulose sculpture; doublure smooth, long medially, slightly tapered toward apodemal pits, with gently curved anterior margin; axial furrows anteriorly divergent until mid-L3, then convergent toward anterior border furrow, moderately shallow, extremely wide and lacunar, widest opposite S1, narrower anteriorly and posteriorly, reduced to narrow furrow opposite anterior half of L3, separated from glabella by small, narrow ridge along lateral lobes and narrow, shallow auxiliary furrow following contours of lateral lobes of larger specimens, and separated from

LO by transverse ridge just anterior of posterior border furrow; palpebro-ocular ridge very long and wide, located far forward on cranidium, with anterior margin even with S3 and posterior margin even with L2, reniform with $\delta$ even with L3, highly laterally inclined in anterior view, with dense sculpture of small granules; palpebroocular furrow sinuous, narrow, moderately deep, shallower anteriorly, convergent with anterior border and axial furrows at apodemal pits; sutural ridge narrow, sinuous, anterolaterally curved, with anteriormost end even with L3; sutural ridge furrow narrow, extremely shallow, anteriorly convergent with palpebro-ocular furrow; median portion of fixigenal field (axial furrow to the lateralmost part of palpebral lobe) short, highly transversely arched, slightly inflated and ridgelike just abaxial from axial furrow, with dense sculpture of granules and pits; lateral portion of fixigenal field long, rounded laterally and anterolaterally, strongly laterally declined, with sculpture of dense granules and pits adaxially, and dense pits abaxially; posterior border furrow very long, deep, slightly shorter near LO, narrow and shallowing anteriorly along lateral curvature of fixigenal field, course slightly posteriorly angled, then curved anterolaterally along lateral margin of fixigenal field; posterior border gently dorsally inflated, with inflation highest posteriorly, moderately long near axis, very long laterally, wrapped around lateral portion of fixigenal field, longest at genal angle, then tapered to a point anteriorly, with small articulating ledge set off by short, deep furrow near axis; doublure long, reaching nearly to posterior border furrow, with gentle Panderian notch at genal angle; genal angle smooth, wide, slightly less than $90^{\circ}$.

Librigenal field with width at midpoint of eye $38.0 \%$ ( $32.0 \%-44.7 \%$ ) length of field along lateral border furrow; anterior branch of facial suture along field slightly shorter than or equal to length along anterior projection of lateral border, portions form nearly $90^{\circ}$ angle at border; posterior branch of facial suture with steeply sloped adaxial portion until point of inflection about halfway from $\varepsilon$ to $\omega$, then gently sloped down to lateral border furrow; eye moderately long and

[^0]
wide, moderately dorsally inflated, inclined at about $45^{\circ}$ anteroventrally, with visual surface of many small, tightly packed lenses; circumocular furrow moderately shallow, deeper anteriorly, narrow; eye socle wide, long, wrapped around eye anteriorly, inflated, with sculpture of dense, coarse granules, socle separated from librigenal field by wide, shallow furrow; librigenal field L-shaped, with upright branch of "L" wide and moderately long and lower branch of "L" long, narrow, and tapered to a point, field gently convex, slightly inflated near eye socle, uninflated along lower branch of "L", with dense granulose sculpture and concentration of pits on posterior half; branching caecal lines visible in ventral view; lateral border furrow very narrow, deep, incised, slightly posteriorly declined in course; lateral border long, wide, with width $78.6 \%(66.2 \%-87.7 \%)$ width of librigenal field at midpoint of eye, tapered to gentle point posteriorly, nearly straight in exterior view, highly arched in ventrolateral view, highly dorsally inflated, with dense granulose sculpture and diagonal (declined at about $40^{\circ}$ posteriorly) bands of shallow pits crossing at middle of anterior projection and at junction of anterior branch of facial suture and lateral border; anterior projection long, slightly wider than remainder of lateral border anteriorly; doublure broad posteriorly, tapered to less than half width of lateral border anteriorly, absent along anterior projection of lateral border, with dense sculpture of miniscule granules.

Rostral plate not recovered.
Hypostome with sagittal length $88.1 \%$ (81.2\%$92.9 \%$ ) maximum width across anterior wings and $118.3 \%$ ( $108.9 \%-121.7 \%$ ) width across shoulders, with smooth posterior lobe of middle body and doublure, and fine, dense granulose sculpture on median anterior lobe of middle body and borders; anterior border extremely short medially, defined medially by short, incised anteriorly convex furrow, flared laterally into anterior wings; anterior wings short, narrow, triangular, with large, deep wing process pits and confluent with lateral border; lateral notch long and shallow; lateral border narrow anteriorly,
wider posteriorly, slightly inflated, with upturned rim, scalloped in appearance due to small paired spines located on shoulders, midway between shoulders and posterolateral corners of lateral border, and at posterolateral corners; lateral border furrow narrow, very shallow anteriorly, deeper across from shoulders, then shallower posteriorly; posterior border moderately long, tapered posteriorly, ventrally curved, with rim like that of lateral border, with small median spine; posterior border furrow effaced; middle body moderately ventrally inflated (posterior lobe only slightly), moderately short and wide, with width $75.0 \%$ (70.7\%-82.6\%) length, strongly tapered posteriorly, not clearly divided into anterior and posterior lobes by middle furrow; middle furrow present only as slightly deeper medially directed portion of lateral border furrow slightly posterior from shoulder; doublure wide, slightly recurved dorsolaterally to form dorsal rim.

Thoracic segments fairly narrow (may be due to thoracic position), highly vaulted axially and pleurally; axis wide, $46.6 \%$ ( $42.5 \%-58.2 \%$ ) total segmental width; articulating half ring short, wide, laterally tapered, semilunate, very short and ridge-like exsagittally; articulating furrow long, shallow medially, strongly tapered laterally into deep apodemal pits; axial ring short, roughly equal in length to articulating half ring, wide, moderately to highly inflated, tall (anterior view), with dense granulose sculpture dorsally, effaced anteriorly; axial ring doublure short, slightly tapered laterally, with sculpture of anastamosing ridges; axial furrows narrow, shallow, subparallel to slightly anteriorly divergent along axial ring, then merged with pleural furrow and strongly anteriorly convergent; inner pleurae short, narrow; fulcral angle steep, about $45^{\circ}$ to subvertical; outer pleurae wide, posteriorly raked, expanded in length exsagittally, longest just before notch in posterior pleural band; anterior pleural band short, narrow, slightly inflated, with small triangular articulating projection near axial furrow set off posteriorly by short, shallow furrow, with small anteriorly directed hook at ventrolateral tip (lateral view), and with dense finely granulose

Fig. 7. Lemureops kilbeyi sp. nov. from Section H 191.7 m (434'; locality H-20 of Hintze [1953]), Fillmore Formation (Blackhillsian, Strigigenalis plicolabeona Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. A, D, left librigena, SUI 110189, external and ventrolateral views, x10. B, E, right librigena, SUI 110190, ventrolateral and external views, x10. C, right librigena (note malformed field with gap), SUI 110191, external view, x7.5. F, left librigena, SUI 110192, external view, x7.5. G, H, J, left librigena, SUI 110193, external, internal, and ventrolateral views, x6. I, left librigena, SUI 110194, external view, x10. K, right librigena, SUI 110195, external view, x12. L, left librigena, SUI 110196, external view, x15. M, right librigena, SUI 110197, external view, x10. N, right librigena, SUI 110198, external view, x10. O, right librigena, SUI 110199, external view, x7.5. P, Q, left librigena, SUI 110200, external and ventrolateral views, x10. R, S, Y, pygidium, SUI 110201, dorsal, posterior, and right lateral views, x10. T, Z, AA, pygidium, SUI 110202 , dorsal, right lateral, and posterior views, x10. U, V, BB, pygidium, SUI 110203, dorsal, left lateral, and posterior views, x10. W, X, CC, pygidium, SUI 110204, dorsal, left lateral, and posterior views, x12.


Fig. 8. Lemureops kilbeyi sp. nov. from Section H 191.7 m (434'; locality H-20 of Hintze [1953]), Fillmore Formation (Blackhillsian, Strigigenalis plicolabeona Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. A, C, O, thoracic segment, SUI 122839, dorsal, anterior, and right lateral views, x10. B, D, E, G, thoracic segment, SUI 122840, dorsal, right lateral, ventral, and anterior views, x10. F, H, I, thoracic segment, SUI 122841, dorsal, anterior, and left lateral views, x7.5. J, L, N, thoracic segment, SUI 122842, left lateral, dorsal, and anterior views, x15. K, M, P, Q, thoracic segment, SUI 122843, left lateral, dorsal, ventral, and anterior views, x10.

Fig. 9 (opposite). Lemureops kilbeyi sp. nov. from Section H 191.7 m (434'; locality H-20 of Hintze [1953]), Fillmore Formation (Blackhillsian, Strigigenalis plicolabeona Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. A, E, I, pygidium, SUI 110205, dorsal, left lateral, and posterior views, x10. B, F, J, O, pygidium, SUI 110206, dorsal, right lateral, posterior, and ventral views, x12. C, G, K, P, Q, pygidium, SUI 110207, dorsal, left lateral, posterior, ventral, and anterior views, x12. D, H, L, pygidium, SUI 110208, dorsal, right lateral, and posterior views, x12. M, N, R, pygidium, SUI 110209, dorsal, right lateral, and posterior views, x15. S, X, Y, pygidium, SUI 110210, dorsal, left lateral, and posterior views, x12. T, U, Z, pygidium (note malformed fourth and fifth pleural ribs on left side), SUI 110211, dorsal, posterior, and right lateral views, x12. V, W, AA, pygidium, SUI 110212, dorsal, left lateral, and posterior views, x12.

sculpture; pleural furrow very short and shallow near axis, slightly expanded and much deeper laterally, shorter and shallower ventrolaterally; posterior pleural band long, slightly constricted sagittally, expanded ventrolaterally, moderately inflated, with short crescentic articulating tongue on posterior margin near axis, set off by short deep furrow, furrow carries inward along lateral margins of axial ring doublure (ventral view) creating small anteriorly convergent ridges, posterior pleural band also with large notch near ventrolateral tip, dense finely granulose sculpture dorsally, and sparser, coarser granules ventrolaterally; pleural doublure not present along inner pleurae, short at fulcrum and flared posterolaterally, long near pleural tips.

Pygidium composed of five distinctly impressed segments and a terminal piece, longest sagittally, widest across tips of posterior band of first pygidial segment, with width $88.6 \%$ ( $82.5 \%-96.6 \%$ ) length excluding articulating half ring, and overall dense sculpture of fine granules; articulating half ring moderately long medially, tapered laterally, semilunate, slightly beveled laterally; articulating furrow short, deep, incised; axis long, very wide anteriorly, $63.0 \%(59.2 \%-64.7 \%)$ pygidial width, tapered to a gentle point at end of terminal piece, highly vaulted anteriorly, progressively less vaulted posteriorly, with terminal piece nearly flat; all axial rings independently dorsally inflated, nearly equal in length, and all with finely granulose sculpture; inter-ring furrows short, very deep laterally, slightly shallower medially, with anterior furrows deeper than posterior furrows; terminal axial piece large, triangular in shape with narrow posterior, bounded laterally and posteriorly by pleurae of fifth segment, slightly topographically recessed from rest of axis, ventroposteriorly sloped, with W-shaped impression; axial furrow narrow, moderately shallow, cut transversely by deeper inter-ring and interpleural furrows, barely impressed over fifth axial ring; each pleural rib independently inflated, pleurae of equal length as corresponding axial ring, with slightly bulbous tips, pleurae decrease in length posteriorly, such that the pygidium has a tapered shape, with gentle ventral curvature (lateral view) beginning at posterior third of segment and continuing through tips, with tips just barely free; first pygidial segment expresses anterior and posterior pleural bands, all others with only posterior band; anterior
pleural band tapered laterally, with anterolaterally curved margin, band curved rearward at about $45^{\circ}$ below horizontal, width spans half width of first posterior band, slightly inflated near axis, but flattened laterally, with axial furrow unimpressed, and small articulating flange near axis set off by short, deep furrow (see lateral and ventral views); pleural furrow (first pygidial segments) short, deep, incised; interpleural furrows very short, moderately deep, incised; both pleural furrow and interpleural furrows more broadly curved at anterior of pygidium, posterior furrows narrowly curved, sub-vertical (4th interpleural) to posteromedially diagonal (5th interpleural), echoing trend of pleurae; doublure triangular in anterior view, short anteriorly, longest posteromedially, with trace of interpleural furrows, with slightly inflated rim anteriorly, and tips of pleurae free.

Ontogeny. Major cranidial changes during ontogeny include broadening of the entire cranidium, lengthening and thickening of the anterior border, shortening and widening of the glabella, inflation of the glabellar lobes and deepening of the sulci, merger of the lateral glabellar lobes and the palpebro-ocular ridges or fixigenae, development of the frontal lobe bump, development of the lacunate axial furrow and ridge, lengthening and inclination of the palpebro-ocular ridges, constriction of the fixigena behind the palpebro-ocular ridges, loss of the genal spine, and steepening of the fulcral angle and lateral fixigenae (cf. Figs 4A, 6R). Changes in the hypostome of $L$. kilbeyi include slight elongation, broadening of the shoulders and anterior wings, elongation of the middle body, effacement of the posterior lobe of the middle body, and reduction of the border spines (cf. Fig. $6 \mathrm{C}, \mathrm{P}$ ). Librigenal changes are less pronounced, but include broadening of the librigenal field and inflation of the eye socle (cf. Fig. 7A, P). Thoracic changes cannot be assessed with the known specimens. Pygidial changes include broadening and inflation of the axis, relative shortening of the terminal piece, lengthening (measured parallel to interpleural furrows) of the pleurae, reduction in posterior taper, and deepening of the terminal piece impression (cf. Figs 6X, 9B).

Material. Holotype, cranidium, SUI 110162; assigned specimens SUI 110163-SUI 110166,

Fig. 10. Lemureops lemurei (Hintze, 1953) from Section H 251.4 m (611'), Fillmore Formation (Blackhillsian, Presbynileus ibexensis Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. A, $\mathbf{B}, \mathbf{C}, \mathbf{E}$, cranidium, SUI 110326, dorsal, ventral, anterior, and right lateral views, x7.5. D, F, G, cranidium, SUI 110327, dorsal, right lateral, anterior, and ventral views, x7.5. H, J, M, cranidium, SUI 110328, dorsal, anterior, and left lateral views, $\mathrm{x} 7.5 . \mathbf{K}, \mathbf{N}, \mathbf{Q}$, cranidium, SUI 110329, dorsal, anterior, and right lateral views, x 7.5 . L, $\mathbf{O}, \mathbf{P}$, cranidium, SUI 110330, dorsal, anterior, and right lateral views, x7.5.



SUI 110168-SUI 110212, and SUI 122839-SUI 122843 from Section H 191.7 m (434'; locality H-20 of Hintze [1953]), Fillmore Formation (Blackhillsian, Strigigenalis plicolabeona Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. Also occurs (not illustrated) at Section H 197.1 m (S. plicolabeona Zone), 208.2 m (Hintze's [1953] H-23; Carolinites nevadensis Zone), and 222.1 m (Hintze's H-24; C. nevadensis Zone).

## Etymology. After Steve Kilbey.

Remarks. Lemureops kilbeyi is compared with $L$. lemurei, L. willsonpiperi, L. koppesi and L. ploogi under discussion of those species below. Young (1973, pl. 3, figs 8, 11) studied material from H 191.7 m . He figured two sclerites of L. kilbeyi sp. nov. as Pseudocybele lemurei Hintze, 1953, and a juvenile cranidium (Young, 1973, pl. 3, fig. 13) as Pseudocybele altinasuta Hintze, 1953. He did not recover the tail, and misassociated that of "Kanoshia (?) depressus" Young, 1973, with the Lemureops material (Young, 1973, pl. 3 , fig. 12).

Several sclerites assigned to L. kilbeyi are malformed and possibly represent healed injuries. One cranidium (Fig. 4A, B, D) has a malformed postocular ridge protruding as a prong from the right posterior branch of the facial suture. One pygidium (Fig. 9T, U, Z) has malformed fourth and fifth left pleurae. One pygidium (Fig. 9S, $\mathrm{X}, \mathrm{Y}$ ) has a differently expressed terminal piece indentation. In some cranidia (Fig. 5C, N), there is a median projection extending posteriorly from the anterior border. One librigena (Fig. 7C) has a notch-shaped hole on the posterior portion of the librigenal field, from the suture line downward.

Lemureops lemurei (Hintze, 1953) (Figs 3H, 10-15)

1953 Pseudocybele lemurei; Hintze, p. 217, pl. 24, figs 3, 4a-c, 5-6, 7a-b.

Diagnosis. Robust, widely spaced crenulations on anterior border; ventral aspect of anterior border slightly protruding (anterior, lateral views); S3
incised; prominent pair of bumps at posterior of median glabellar lobe; palpebro-ocular ridges very large, steeply inclined; eye socle low, broad, effaced; broad, blunt protrusion at posterior tip of lateral border; long, narrow pygidium with broad, shallow depression in terminal piece.

Description. Lemureops lemurei is sufficiently similar to L. willsonpiperi that full written description is replaced by a comparison listing all differences.

Ratios are given to facilitate comparison with other species of Lemureops. The sagittal length of the cranidium is $48.2 \%$ ( $46.6 \%-49.7 \%$ ) the width across the posterior fixigenae, and the width across the anterior border is $38.2 \%$ ( $34.9 \%-41.3 \%$ ) the width across the posterior fixigenae. The glabella is $90.7 \%$ ( $80.2 \%-97.6 \%$ ) as long as it is wide. The cranidium of $L$. lemurei is distinguished from that of $L$. willsonpiperi by its narrower anterior border, with more widely spaced and robust crenulations; more visible and slightly anteriorly protruding posterior wall of the anterior border (in anterior view); narrower, more transversely arched glabella; deeper, more incised S3 (visible ventrally); deeper, slightly narrower axial furrow; more steeply inclined palpebro-ocular ridges; prominent pair of bumps on the median glabellar lobe just anterior from SO; deeper SO and posterior border furrow; and taller LO.

The hypostome is $90.4 \%(85.7 \%-98.7 \%)$ as long (sag.) as it is wide across the anterior wings and the length is $133.8 \%(128.0 \%-143.0 \%)$ the width across the shoulders. Hypostomes differ in that that of L. lemurei has broader anterior wings; granulose middle body sculpture on only the anteriormost part; a shorter, more strongly ventrally curved posterior margin; and shorter, thicker spines than that of $L$. willsonpiperi. Hypostomes of both species share a pair of striking median longitudinal lineations of shallow pits, but those of $L$. lemurei are more effaced than those of $L$. willsonpiperi.

The width of the librigenal field under the midpoint of the eye is $47.7 \%(41.1 \%-58.5 \%)$ the length of field measured along the lateral border, and the width of the lateral border is $63.5 \%$

Fig. 11. Lemureops lemurei (Hintze, 1953) from Section H 251.4 m (611'), Fillmore Formation (Blackhillsian, Presbynileus ibexensis Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. A, B, D, cranidium, SUI 110331, dorsal, left lateral, and anterior views, x10. C, E, F, cranidium, SUI 110332, dorsal, right lateral, and anterior views, x10. G, H, J, cranidium, SUI 110333, dorsal, left lateral, and anterior views, x10. I, K, L, cranidium, SUI 110334, dorsal, left lateral, and anterior views, x10. M-O, cranidium, SUI 110335, anterior, dorsal, and left lateral views, x10. P-R, hypostome, SUI 110336, ventral, posterior, and left lateral views, x10. S-U, hypostome, SUI 110337, right lateral, posterior, and ventral views, x12. V, W, BB, CC, hypostome, SUI 110338, ventral, dorsal, left lateral, and posterior views, x10. X, Y, DD, hypostome, SUI 110339, ventral, right lateral, and posterior views, x12. Z, AA, EE, hypostome, SUI 110340, ventral, right lateral, and posterior views, x 10 .

( $55.6 \%-70.7 \%$ ) the width of the field. Librigenae of L. lemurei have slightly wider, shorter, and more convex librigenal fields; less prominent (particularly anteriorly) eye socles; and slightly longer anterior projections of the lateral border than librigenae of $L$. willsonpiperi.

The axial width of segments of $L$. lemurei is $43.7 \%(40.2 \%-49.8 \%)$ of their total width. $L$. lemurei and $L$. willsonpiperi share many thoracic features, but there are some striking differences. L. lemurei has a taller, more rounded axial ring; more parallel-sided axial furrow; shorter, less prominent articulating flanges and furrows; and larger pleural tip notches.

The pygidium of $L$. lemurei is $94.4 \%$ ( $87.6 \%-$ $100.5 \%$ ) as wide across the first pleural tips as it is long (length excludes articulating half ring), and the axial width is $58.2 \%(52.4 \%-63.4 \%)$ of the total pygidial width. Pygidia of $L$. lemurei and L. willsonpiperi are fairly similar, but differ in the following respects: L. lemurei pygidia are more convex; longer and narrower, with a broader axis and terminal piece; more inflated axis; shallower terminal piece impression; and more steeply tapered posterior margin compared to those of L. willsonpiperi.

Ontogeny. Cranidia assigned to L. lemurei are probably all holaspid. However, it is possible to observe the anterior border lengthening and the crenulations strengthening, the glabella expanding anteriorly, the axial furrow widening and shallowing slightly, and the inclination of the palpebro-ocular ridges increasing (cf. Figs $10 \mathrm{D}, 11 \mathrm{~N}$ ). The hypostome becomes shorter and broader overall, but the middle body becomes more elongate (cf. Fig. 11P, X). Librigenal changes include broadening of the field, slight effacement of the eye socle, and straightening of the lateral border (cf. Fig. 14D, N). All pygidial material is fairly similar in size, but the pygidium broadens slightly, the terminal piece impression shallows, and the posterior point of the terminal axial piece narrows and extends further posteriorly (cf. Fig. 13B, D).

Material. Holotype, cranidium, BYU 26461 (Hintze 1953, pl. 24, figs 4a-c) and paratypes (hypostome, librigena, cranidium, and pygidium), BYU 26457-BYU 26460, sequentially (Hintze,

1953, pl. 24, figs 3, 5, 6, 7a-b) from Section H 545 '/ locality H-25 of Hintze (1953); equivalent to our H 229.3 m , though we could not relocate this fauna (see discussion below), Fillmore Formation (Blackhillsian, Zone I, Presbynileus ibexensis Zone), Ibex area, Millard County, western Utah. Assigned specimens SUI 110326SUI 110364 from Section H 251.4 m (611'), Fillmore Formation (Blackhillsian, P. ibexensis Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Remarks. Specimens assigned to L. lemurei display some intraspecific variation. The largest cranidium (Fig. 10A-C, E) has a shorter anterior border and slightly less sloped lateral fixigena than the other specimens. One hypostome (Fig. $11 \mathrm{Z}, \mathrm{AA}, \mathrm{EE}$ ) has a long posterior border, well impressed middle furrow, and less tapered posterior margin of the middle body.

Although L. lemurei and L. willsonpiperi are qualitatively differentiated above, some of their prominent differences can be confirmed quantitatively using reduced major axis (RMA) regression (Imbrie, 1956). Two comparisons were carried out: width of the anterior border vs. oblique height of the palpebro-ocular ridge in anterior view, and sagittal length of the pygidium from the articulating furrow vs. width of the pygidium across the first pleural tips (Fig. 15, insets). These measurements were taken in millimetres using ImageJ (NIH, 2008), and compared using bivariate plots and RMA regression in PAST (Hammer et al., 2001). Tests for significant differences in slope and y-intercepts follow the procedures outlined by Imbrie (1956) and Jones (1988).

Results of RMA regression (Fig. 15) indicate that slopes of the cranidial regression lines are significantly different $(\mathrm{z}=3.725, \mathrm{p}=<0.01)$. These results show that $L$. lemurei has tall palpebro-ocular ridges and a narrow anterior border, and $L$. willsonpiperi has comparatively short palpebro-ocular ridges and a wide anterior border. Palpebro-ocular ridge height compared to anterior border width increases at a faster rate in L. lemurei compared to L. willsonpiperi. For specimens of the same anterior border width, $L$. lemurei has significantly taller palpebro-ocular ridges. Ratios are closer in small specimens.

Fig. 12. Lemureops lemurei (Hintze, 1953) from Section H 251.4 m (611'), Fillmore Formation (Blackhillsian, Presbynileus ibexensis Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. A, E, I, pygidium, SUI 110341, dorsal, right lateral, and posterior views, x15. B, F, J, pygidium, SUI 110342, dorsal, left lateral, and posterior views, x15. C, G, K, pygidium, SUI 110343, dorsal, left lateral, and posterior views, x12. D, H, L, pygidium, SUI 110344, dorsal, left lateral, and posterior views, x15. M, O, P, R, W, thoracic segment, SUI 110345, dorsal, anterior, left lateral, posterior, and ventral views, x7.5. N, Q, S, Y, thoracic segment, SUI 110346, dorsal, ventral, anterior, and left lateral views, x10. T-V, X, thoracic segment, SUI 110347, ventral, dorsal, anterior, and left lateral views, x10.



Fig. 14. Lemureops lemurei (Hintze, 1953) from Section H 251.4 m (611'), Fillmore Formation (Blackhillsian, Presbynileus ibexensis Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. A, B, right librigena, SUI 110355, external and internal views, x7.5. C, F, right librigena, SUI 110356, external and ventrolateral views, x7.5. D, G, left librigena, SUI 110357, external and ventrolateral views, x7.5. E, H, right librigena, SUI 110358, internal and external views, x7.5. I, left librigena, SUI 110359, external view, x10. J, M, right librigena, SUI 110360, external and ventrolateral views, x7.5. K, right librigena, SUI 110361, external view, x7.5. L, O, right librigena, SUI 110362, external and ventrolateral views, x10. N, left librigena, SUI 110363, external view, x12. P, right librigena, SUI 110364, external view, x12.

Fig. 13 (opposite). Lemureops lemurei (Hintze, 1953) from Section H 251.4 m ( 611 '), Fillmore Formation (Blackhillsian, Presbynileus ibexensis Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. A, E, I, pygidium, SUI 110348, dorsal, right lateral, and posterior views, x23. B, C, F, G, J, pygidium, SUI 110349, dorsal, ventral, anterior, left lateral, and posterior views, x12. D, H, L, pygidium, SUI 110350, dorsal, right lateral, and posterior views, x15. K, O, P, pygidium, SUI 110351, dorsal, right lateral, and posterior views, $x 12 . \mathbf{M}, \mathbf{Q}, \mathbf{U}$, pygidium, SUI 110352, dorsal, right lateral, and posterior views, $\mathbf{x} 15 . \mathbf{N}$, R-T, pygidium, SUI 110353, dorsal, ventral, left lateral, and posterior views, x15. V-X, pygidium, SUI 110354, posterior, dorsal, and left lateral views, x12.


Fig. 15. Bivariate plots and reduced major axis regression lines of cranidial and pygidial measurements of Lemureops lemurei and L. willsonpiperi. Lemureops willsonpiperi from the interval H $256-261 \mathrm{~T} \mathrm{~m}$ was assigned a different symbol (plus sign) from material from the interval H 264-267T m (solid circle) to demonstrate that sclerites from the different horizons belong to the same species. A, width across anterior border compared to oblique height of palpebro-ocular ridge. Leтигеорs lemurei: $\mathrm{N}=8$, slope $=0.863$, constant $=-0.6178, \mathrm{r}=0.98$, standard error $=0.0695$. Lemureops willsonpiperi $\mathrm{N}=20$, slope $=0.581$, constant $=-0.0297, r=0.976$, standard error $=0.0297$. B, sagittal pygidial length from articulating furrow compared to pygidial width across pleural tips of first segment. Lemureops lemигеi: $\mathrm{N}=10$, slope $=1.02$, constant $=-0.174, \mathrm{r}=0.905$, standard error= 0.153 . Lemureops willsonpiperi: $\mathrm{N}=17$, slope $=1.03$, constant $=0.158, \mathrm{r}=0.947$, standard error $=0.086$.

Slopes of the pygidial regression lines are not significantly different ( $\mathrm{z}=0.956$ ), but intercepts of the lines are significantly different ( $\mathrm{z}=17.206, \mathrm{p}=$ $<0.01$ ). Therefore, although the width increases proportional to the length at nearly the same rate in both species, pygidia of $L$. willsonpiperi are considerably wider than those of $L$. lemurei at a given sagittal length.

Hintze (1953) established $L$. lemurei based on type material from his sample H-25 (545'), but this is one of the few original sampling horizons we have been unable to relocate. We collected a bulk sample from the equivalent meterage (229.3), which broke down during acid processing into large chunks of mostly dolomitised detritus and yielded very few silicified trilobite sclerites, all of which are fragmentary and unidentifiable. We also sampled potential horizons at H 229.6 and 230.3 m , but none yielded well preserved fossils. This is in marked contrast to the fairly well preserved material apparently from the same level figured by Hintze (1953, pl. 24, figs 3-7). Hintze (1953, Table 9) reported Carolinites genacinaca Ross, 1951a, Isoteloides flexus Hintze, 1953,
and Presbynileus ibexensis (Hintze, 1953) as common, and Pseudocybele lemurei as abundant, at H 545'. He therefore assigned this horizon to the Presbynileus ibexensis Zone. It is possible that Hintze's sample was from a small bed with limited outcrop which has been completely removed. Stratigraphically close fossiliferous horizons help to resolve zonal boundaries with respect to the enigmatic H-25. H 222.1 (Hintze's [1953] H-24/525') is the highest horizon Hintze (1953) assigned to the (now abandoned) Trigonocerca typica Zone. However, newly collected material from the horizon clearly represents the new, younger, Carolinites nevadensis Zone. A talus sample from H 226 T m also yields a C. nevadensis Zone fauna, and a newly sampled fossiliferous horizon at 229.0 m ( $544^{\prime}$ ) yields sparse material, but also represents the C. nevadensis Zone. The first positive evidence of the $P$. ibexensis Zone occurs at H 251.4 m (611'; same bed as Hintze's [1953] H-27/ 610'). We therefore placed the boundary directly below this horizon.

Our Lemureops lemurei material was collected at Section H 251.4 m (611'), from the same

Fig. 16. Lemureops willsonpiperi sp. nov. from Section H 264-267T m (650-660'), Fillmore Formation (Blackhillsian, Presbynileus ibexensis Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. A, C, D, F, cranidium, holotype, SUI 110213, dorsal, anterior, right lateral, and oblique views, x6. B, E, G, I, cranidium, SUI 110214, dorsal, ventral, anterior, and right lateral views, x7.5. H, L, N-P, cranidium, SUI 110215, right lateral, dorsal, ventral, oblique, and anterior views, x7.5. J, K, M, cranidium, SUI 110216, dorsal, anterior, and right lateral views, x7.5.


thick bed as Hintze's H-27 (610'). Hintze did not figure any material from this horizon, but his (1953) faunal list closely agrees with our collection and included Pseudocybele lemurei. The single fossiliferous horizon between 229.3 m and 251.4 m is our H 238.2 m (573'), which is within the same thick bed as Hintze's H-26 (572'). This material is from the beds overlying a microbial buildup, and contains unidentifiable silicified trilobite hash, as Hintze (1951) reported in his description of Section H. However, Hintze did include "Pseudocybele lemurei" in the 1953 faunal list for this horizon. Adrain et al. (2001) described Dimeropygiella mccormicki based on material collected from the matrix of the microbial buildups.

Lemureops lemurei and L. kilbeyi differ in many of the same ways as do $L$. kilbeyi and $L$. willsonpiperi. In addition, L. lemurei differs in the possession of a narrower cranidium, more rounded glabella, shorter posterior border furrow, longer LO, prominent bumps at the posterior of the median glabellar lobe, and larger and more inclined palpebro-ocular ridges. Hypostomes differ in that those of $L$. lemurei have a slightly smaller middle body and slightly more robust spines. Librigenae are generally similar in form, but those of $L$. lemurei have a shorter, broader librigenal field, lower eye socle, and more prominent caecal pitting on the lateral border. Thoracic segments are very similar, but those of $L$. lemurei display sparser, finer sculpture. Pygidia are most clearly distinguished by the nearly effaced sculpture, greater posterior taper, and lightly impressed terminal piece in $L$. lemurei. Lemureops lemurei is compared to L. koppesi and L. ploogi below.

Lemureops willsonpiperi sp. nov. (Figs 3B, D, 15-24)

Diagnosis. Cranidial axial furrow broad, very shallow; hypostome with pitted middle body; librigena with pronounced anterior portion of eye socle and effaced posterior portion; pygidium with slightly anterolaterally recurved pleural tips, and broad, moderately deep impression in terminal piece.

Description. Cranidium short and wide, wider posteriorly, with width across anterior border furrow $38.6 \%$ ( $35.1 \%-43.0 \%$ ) width across posterior fixigenae and sagittal length 46.1\% (42.4\%-50.0\%) fixigenal width; anterior border longest at sagittal axis and rapidly tapering exsagittally, prow-like, triangular in dorsal view, moderately inflated, with inflation highest at sagittal axis and falling exsagittally, tall medially and tapered laterally in anterior view, strongly crenulated, with sculpture of tiny, closely spaced granules; doublure wraps over top of border, visible mainly in anterior view, short rim in ventral view; anterior border furrow short, very deep, longer and deeper at apodemal pits, then slightly shallower anterior of palpebroocular ridge, course nearly transverse; glabella subrectangular, with length $84.3 \%$ ( $74.8 \%$ 90.3\%) width, forwardly expanding, strongly transversely arched, with individually inflated lobes; L1 smallest, short, subrectangular; L2 rectangular, slightly longer and wider than L1; L3 largest, longest, more rounded; median lobe with pair of subtle raised bumps just anterior from SO; S1 and S2 deep, slightly longer than anterior border furrow, sub-horizontal in course, with apodemal pits at proximal ends; S3 short, shallow, anterolaterally convex; all glabellar sulci deeper toward axis and very shallow just sagittal from axial furrow, glabellar sculpture of small, moderately densely packed granules medially, lobes effaced laterally; axial furrow shallow and wide for most of course, deeper and narrower along LO, L1, and anterior half of L3, anteriorly divergent until middle of L3, then anteriorly convergent; SO moderately long, slightly shorter medially, moderately deep, deepest in apodemal pits, confluent with lateral border furrow; LO long medially, slightly tapered laterally, taller posteriorly than anteriorly, with dense sculpture of fine granules and medium-sized median tubercle on most specimens; doublure long, smooth, bandlike, slightly tapered laterally; palpebro-ocular ridge very long (anterior border furrow to S2), wide, tall, reniform, steeply inclined, with dense, minutely granulose sculpture; palpebro-ocular furrow moderately narrow, sinuous, shallow, deeper posteriorly; narrow, sinuous ridge curves anterolaterally from posterior of palpebro-ocular

Fig. 17. Lemureops willsonpiperi sp. nov. from Section H $256-267 \mathrm{~T}$ m (630-660'; exact interval listed with each specimen), Fillmore Formation (Blackhillsian, Presbynileus ibexensis Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. A, B, D, H, cranidium, SUI 110217, dorsal, oblique, anterior, and left lateral views, x7.5 (H 256-261T m). C, E, I, cranidium, SUI 110218, dorsal, right lateral, and anterior views, x 10 (H 256-261T m). F, J, G, cranidium, SUI 110219, dorsal, right lateral, and anterior views, x7.5 (H 256-261T m). K, L, O, R, cranidium, SUI 110220, right lateral, oblique, dorsal, and anterior views, x6 (H 264$267 \mathrm{~T} \mathrm{~m}) . \mathbf{M}, \mathbf{N}, \mathbf{Q}$, cranidium, SUI 110221, dorsal, anterior, and left lateral views, x7.5 (H256-261T m). P, S, T, cranidium, SUI 110222, right lateral, anterior, and dorsal views, x7.5 (H 264-267T m). U-W, cranidium, SUI 110223, anterior, right lateral, and dorsal views, x10 (H264-267T m).

ridge, backed by short, shallow furrow; fixigenal field very wide, long near glabella, very short behind posterior end of palpebro-ocular ridge, then flared laterally, strongly arched, with steeply sloped lateral area, posterior margin nearly transverse, anterior margin (along posterior branch of facial suture) strongly anterolaterally bowed, with sparse granules near axis and dense sculpture of small pits throughout field; posterior border furrow long, but tapers anterolaterally to connect to the lateral border furrow of the librigena; course transverse to slightly posterolateral until even with maximum anterior curvature of posterior fixigena, then sharply curved anteriorly, deep, but shallower near axis and along anterior curvature; posterior border transverse to slightly posterolaterally curved from near axis to genal angle, then strongly anteriorly curved, moderately long near axial furrow, lengthens laterally toward genal angle, then tapers to narrow point, very wide, with widest point slightly anterolateral from genal angle, slightly inflated, with inflation highest near axis and on posteriorly curved rim, with small articulating flange set off by furrow
just lateral from LO; doublure narrow and twisted near axis, with short, diagonal articulating groove, lengthening toward genal angle, very long/wide at genal angle, with large, gently curved Panderian notch.

Rostral plate not recovered.
Hypostome with sagittal length $100.5 \%$ ( $89.4 \%-108.0 \%$ ) width across anterior wings and $135.0 \%(129.0 \%-140.0 \%)$ width across shoulders, with dense granulose sculpture except for smooth posterior lobe of middle body; hypostomal suture gently posteriorly curved; anterior border extremely short medially, flared laterally into trapezoidal anterior wings; doublure rim-like, short medially and tapered laterally; anterior border furrow extremely short, incised, strongly anteriorly convex; anterior wings short, moderately broad, sub-vertical, with large, deep wing process pits; anterior lobe of middle body very large, sub-oval, narrower posteriorly, strongly ventrally inflated, with median paired longitudinal lineations of small pits; middle furrow hardly impressed on some specimens, shallow or discontinuously pitted on others;

Fig. 18 (opposite). Lemureops willsonpiperi sp. nov. from Section H 264-267T m (650-660'), Fillmore Formation (Blackhillsian, Presbynileus ibexensis Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. A, B, E, cranidium, SUI 110224, dorsal, left lateral, and anterior views, x7.5. C, H, K, cranidium, SUI 110225, left lateral, dorsal, and anterior views, x7.5. D, L, O, cranidium, SUI 110226, right lateral, dorsal, and anterior views, x10. F, G, J, N, cranidium, SUI 110227, right lateral, dorsal, ventral, and anterior views, x10. I, Q, R, cranidium, SUI 110228, right lateral, dorsal, and anterior views, x7.5. M, S, V, cranidium, SUI 110229, left lateral, dorsal, and anterior views, x10. P, U, X, cranidium, SUI 110230, left lateral, dorsal, and anterior views, x7.5. T, W, Y, cranidium, SUI 110231, left lateral, anterior, and dorsal views, x6. Z-BB, cranidium, SUI 110232, anterior, right lateral, and dorsal views, x10.

Fig. 19 (overleaf). Lemureops willsonpiperi sp. nov. from Section H 264-267T m (650-660'), Fillmore Formation (Blackhillsian, Presbynileus ibexensis Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. A, D, E, cranidium, SUI 110233, dorsal, anterior, and left lateral views, x12. B, C, F, cranidium, SUI 110234, right lateral, dorsal, and anterior views, x15. G, H, J, cranidium, SUI 110235, dorsal, left lateral, and anterior views, x12. I, K, L, cranidium, SUI 110236, dorsal, right lateral, and anterior views, x15. M, N, $\mathbf{P}$, cranidium, SUI 110237, dorsal, right lateral, and anterior views, x12. O, Q, R, cranidium, SUI 110238, dorsal, left lateral, and anterior views, x15. S, T, X, cranidium, SUI 110239, dorsal, left lateral, and anterior views, x12. U-W, cranidium, SUI 110240, left lateral, dorsal, and anterior views, x15. Y, BB, CC, cranidium, SUI 110241, right lateral, dorsal, and anterior views, x12. Z, AA, DD, cranidium, SUI 110242, right lateral, dorsal, and anterior views, x20.

Fig. 20 (page 521). Lemureops willsonpiperi sp. nov. from Section H 256-267T m (630-660'; exact interval listed with each specimen), Fillmore Formation (Blackhillsian, Presbynileus ibexensis Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. A, C, right librigena, SUI 110243, internal and external views, x7.5 (H 264-267T m). B, left librigena, SUI 110244, external view, x20 (H 264-267T m). D, G, right librigena, SUI 110245, external and ventrolateral views, x7.5 (H 264-267T m). E, left librigena, SUI 110246, external view, x10 (H 256-261T m). F, I, L, left librigena, SUI 110247, external, ventrolateral, and internal view, x7.5 (H 264-267T m). H, K, left librigena, SUI 110248, external and ventrolateral views, x10 (H 264-267T m). J, M, right librigena, SUI 110249, external and ventrolateral views, x7.5 (H 264-267T m). N, left librigena, SUI 110250, external view, x10 (H 256-261T m). O, P, R, right librigena, SUI 110251, external, internal, and ventrolateral views, x10 (H 264-267T m). Q, T, right librigena, SUI 110252, external and ventrolateral views, x10 (H 256-261T m). S, V, W, right librigena, SUI 110253, internal, external, and ventrolateral views, x10 (H 264-267T m). U, left librigena, SUI 110254, external view, x10 (H 264-267T m). X, left librigena, SUI 110255, external view, x10 (H 264-267T m). Y, left librigena, SUI 110256, external view, x10 (H 256-261T m).



posterior lobe of middle body U-shaped, short medially, tapered laterally; lateral border furrow narrow, wider posteriorly, deep; lateral notch long and gently curved; shoulders narrow, triangular; lateral border narrow, with two pairs of conical spines (at shoulder and between shoulder and posterior border pair); posterior border short, longest medially, ventrally curved, with pair of small, conical spines flanking larger median posterior spine; doublure narrow (short medially), sub-horizontal across lateral border, then subvertical and rim-like as posterior wings, with densely granulose sculpture; posterior wings small, triangular.

Librigena with width of field taken at midpoint of eye $42.7 \%$ ( $35.5 \%-50.9 \%$ ) length of field along lateral border furrow; anterior branch of facial suture moderately long, sloped near $90^{\circ}$ to border furrow, sub-horizontal along anterior projection, slightly anteriorly bowed along eye socle; first half of posterior branch of facial suture steeply sloped slightly bowed along eye socle, then more gently sloped to lateral border, sub-horizontal along lateral border; eye elliptical, set at about $45^{\circ}$ angle, slightly inflated, with visual surface of many tiny, closely packed lenses, visual surface separated from eye socle by circumocular furrow; circumocular furrow with variable depth and width, but moderately deep and wide anteriorly, narrow and shallower posteriorly on most specimens; eye socle wide and prominently inflated anteriorly, narrower and less inflated posteriorly; librigenal field moderately wide, moderately short near eye, long at lateral border furrow, subtriangular, highly tapered posteriorly, gently convex, with sculpture of many tiny granules very dense near eye and sparser toward librigenal border, and with small pits located along posterior branch of facial suture; lateral border furrow narrow, very deep, slightly narrower and shallower posteriorly, course slopes very slightly posteriorly; lateral border wide, $64.4 \%$ (57.2\%-72.8\%) width of field, tapered to gentle point posteriorly, long, with long anterior projection, highly inflated, with dense sculpture of many small granules over most of border, but
effaced far posteriorly, also with two posteriorly sloping lines of pits, one on anterior projection and the other from right angle formed by anterior branch of facial suture, both continuing until exsagittal margin of lateral border; doublure lacking along anterior projection, wide along rest of lateral border, small triangle of inner side visible in external view far posteriorly, and with gentle arc of pits on some specimens.

Thoracic segments highly arched, (anterior segments) broad, with axial width $35.5 \%$ ( $32.7 \%$ $37.4 \%$ ) total width; articulating half ring short, slightly narrower than axial ring, semilunate; articulating furrow deep, shallower posteriorly (lateral view), long sagittally, tapered exsagittally into deep apodemal pits; axial ring slightly longer than articulating furrow, moderately tall, highly arched, slightly posteriorly pointed, with dense granulose sculpture dorsally, smooth anteriorly; axial furrow narrow, laterally bowed, moderately deep posteriorly, shallower anteriorly; pre-fulcral pleural region sub-horizontal, pleurae steeply ventrally sloped post-fulcrum and slightly anterolaterally flared; anterior pleural band much shorter than posterior, only about $3 / 4$ posterior width, with set of articulating ridges delineated by narrow, incised furrows, and anteriorly curved hooklike articulating process at ventral tips; pleural furrow short, shallow near axis, deeper and shorter laterally; posterior pleural band moderately transverse and short near axis, with articulating flange set off by incised furrow, strongly flared ventrolaterally, inflated posteriorly, with ridge and concentration of granules following anterolaterally flared section, and with sharp notch at pleural tips.

Pygidium highly vaulted, composed of five segments and a large terminal piece, longest sagittally, widest across tips of first segment, with width $108.7 \%$ ( $102.6 \%-119.6 \%$ ) length, evenly tapered from tips of first segment backward, with dense granulose sculpture (slightly coarser on pleurae); articulating half ring semilunate, longest sagittally, tapered exsagittally; articulating furrow short, shallow medially, deep laterally; axis long, very wide anteriorly, $49.6 \%$ ( $45.2 \%-54.9 \%$ )

Fig. 21. Lemureops willsonpiperi sp. nov. from Section H 264-267T m (650-660'), Fillmore Formation (Blackhillsian, Presbynileus ibexensis Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. A, F, I, hypostome, SUI 110257, ventral, left lateral, and posterior views, x10. B, G, M, hypostome, SUI 110258, ventral, right lateral, and posterior views, x10. C, H, J, hypostome, SUI 110259, ventral, left lateral, and posterior views, x10. D, E, K, L, hypostome, SUI 110260, ventral, left lateral, posterior, and dorsal views, x10. N, P, Q, hypostome, SUI 110261, posterior, ventral, and left lateral views, x12. O, R, Y, hypostome, SUI 110262, posterior, ventral, and left lateral views, x12. S-U, hypostome, SUI 110263, ventral, right lateral, and posterior views, x15 (H 264-267T m). V, W, X, H, thoracic segment, SUI 110264, anterior, ventral, dorsal, and right lateral views, x7.5. Z, BB, DD, EE, II, thoracic segment, SUI 110265, dorsal, ventral, anterior, right lateral, and posterior views, x7.5. AA, CC, GG, thoracic segment, SUI 110266, dorsal, anterior, and left lateral views, x10. FF, JJ, MM, thoracic segment, SUI 110267, right lateral, anterior, and dorsal views, x10. KK, LL, $\mathbf{N N}$, thoracic segment, SUI 110268, anterior, right lateral, and dorsal views, x7.5.

pygidial width, tapered to a rounded point at end of terminal piece, highly vaulted anteriorly, progressively lower posteriorly, with terminal piece almost flat; all axial rings individually inflated, sub-equal in length, all with finely granulose sculpture; inter-ring furrows short, very deep laterally, slightly shallower medially, anterior furrows deeper than posterior furrows; terminal axial piece long, narrow, triangular, bounded laterally by pleurae of fifth segment, posteriorly sloped, with W-shaped impression; axial furrow narrow, shallow, shallower posteriorly, crossed transversely by deeper inter-ring and interpleural furrows, hardly impressed over fifth axial ring or anterior pleural band of first segment; first pygidial segment expresses anterior and posterior pleural bands, subsequent segments express only posterior band; anterior pleural band of first segment very short, tapered laterally, narrower than posterior band, slightly inflated near axis, with small, anteriorly-directed hooklike structure at ventral tips, and small articulating processes near axis set off by short, incised furrows; pleural furrow short, deep, incised; interpleural furrows very short, deep, deeper and longer toward tips; sub-horizontal pleural area (prefulcrum) narrow, post-fulcral area wide and steeply down-sloping, pleurae as long as axial rings, individually inflated, with slightly more bulbous tips, increasingly angled posteriorly in course, with fourth pair nearly parallel to sagittal midline, and fifth angled inward toward axis, with broad notch near tips (lateral view), slightly recurved anterolaterally toward tips, and tips just barely free; doublure triangular, longer medially and tapered laterally, slightly inflated anteriorly, slightly depressed dorsomedially.

Ontogeny. During ontogeny, the cranidium of L. willsonpiperi becomes broader, with shorter and more highly arched fixigenae (cf. Figs 16B, 19AA). The anterior border lengthens, thickens, arches, and develops crenulations. The glabella becomes proportionately shorter and wider, with inflated lobes separated by deep furrows. Later in development, the lateral lobes merge with the palpebro-ocular ridges or fixigenae. The palpebro-
ocular ridges lengthen, curve increasingly outward, and become steeply inclined. The posterior border furrow lengthens, as does SO, and the axial furrow widens and shallows considerably. The posterior border lengthens, particularly at the genal angle, while the genal spine reduces and is lost. The hypostome becomes wider, with a longer posterior border and longer, more robust spines (cf. Fig. 21B, S). The librigena becomes longer and wider as the main part of the field broadens and the posteriorly tapered part narrows. The lateral border and anterior projection lengthen as the anterior border straightens, and the caecal pits become prominent. The eye socle inflates, especially anteriorly (cf. Fig. 20B, C). The pygidium narrows, while the axis inflates and becomes wider in proportion, the terminal piece lengthens, and the posterior taper increases (cf. Figs 22A, 23U).

Material. Holotype, cranidium, SUI 110213, from Section H 264-267 m (650-660'), Fillmore Formation (Blackhillsian, Presbynileus ibexensis Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. Assigned specimens SUI 110214-SUI 110292, from Section H 256-267 m (630-660'; exact interval listed with each specimen in figure captions), Fillmore Formation (Blackhillsian, P. ibexensis Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

## Etymology. After Marty Willson-Piper.

Remarks. Lemureops willsonpiperi most closely resembles $L$. lemurei, with which it was compared through differential description above. RMA regression (also above) quantitatively demonstrates cranidial and pygidial differences. Lemureops willsonpiperi is compared to $L$. koppesi under discussion of those species below.

Lemureops kilbeyi and L. willsonpiperi have similar anterior borders, palpebro-ocular ridges, glabellae and occipital lobes. However, the anterior border of L. kilbeyi is broader and more gently sloped; its palpebro-ocular ridges are less evenly reniform; its glabella is wider

Fig. 22. Lemureops willsonpiperi sp. nov. from Section H 264-267T m (650-660'), Fillmore Formation (Blackhillsian, Presbynileus ibexensis Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. A, E, J, pygidium, SUI 110269, dorsal, right lateral, and posterior views, x7.5. B, F, K, pygidium (note malformed left pleural region), SUI 110270, dorsal, right lateral, and posterior views, x7.5. C, G, H, pygidium, SUI 110271, dorsal, posterior, and left lateral views, x10. D, I, M, pygidium, SUI 110272, dorsal, left lateral, and posterior views, $\mathbf{x 1 0} \mathbf{L}, \mathbf{P}, \mathbf{Q}, \mathbf{T}, \mathbf{U}$, pygidium, SUI 110273, ventral, dorsal, right lateral, posterior, and anterior views, L, P, Q x10, T, U x7.5. N, O, R, S, pygidium, SUI 110274, dorsal, ventral, posterior, and left lateral views, x10. V, DD, EE, pygidium, SUI 110275, dorsal, right lateral, and posterior views, x10. W, X, CC, pygidium, SUI 110276, dorsal, right lateral, and posterior views, x10. Y, Z, DD, pygidium, SUI 110277, left lateral, dorsal, and posterior views, x10. AA, B, GG, pygidium, SUI 110278, right lateral, dorsal, and posterior views, x10.



Fig. 24. Lemureops willsonpiperi sp. nov. from Section H 256-261T m (630-640'), Fillmore Formation (Blackhillsian, Presbynileus ibexensis Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. All are x10. A, E, I, pygidium, SUI 110290, dorsal, right lateral, and posterior views. B, F, H, pygidium, SUI 110291, dorsal, right lateral, and posterior views. C, D, G, pygidium, SUI 110292, dorsal, left lateral, and posterior views.
with the lateral lobes separated by very deep furrows; its median tubercle is only weakly expressed on LO; its fixigenae are longer and more gently sloped; and its posterior border is much shorter at the genal angle. Hypostomes of the two species share the same general shape, but that of $L$. kilbeyi is fairly shallowly vaulted, has tiny spines or rounded angles on the lateral and posterior borders, and granulose sculpture only on the anterior lobe of the middle body while that of $L$. willsonpiperi is more deeply vaulted, has very sharply pointed spines, has denser granulose sculpture, and a linear arrangement of pits on the middle body. Librigenae are very similar, but that of L. kilbeyi has a more complete eye socle, wider lateral border, slightly smaller eye, longer posterior wedge-shaped portion of the field, and less well expressed caecal pits on the lateral border. Thoracic segments belonging to L. kilbeyi possess a wider axis, taller axial rings,
denser and more robust granulose sculpture, and a larger pleural notch than those of $L$. willsonpiperi. Pygidia are less similar: that of $L$. kilbeyi is longer, narrower, and much less posteriorly tapered, with a deep W-shaped indentation in the terminal piece compared to a shallow 'W' bordering a depressed area in L. willsonpiperi.

Compared to L. ploogi, L. willsonpiperi has a much longer and wider anterior border, with strong crenulations. The cranidium and glabella of $L$. willsonpiperi are wider, the palpebroocular ridges are much larger and arcuate, and the fixigenae are much shorter. Lemureops willsonpiperi has much wider librigenae with a prominent eye socle, and prominent caecal pits on a narrower lateral border. Pygidia of L. willsonpiperi are wider, with a narrower axis, larger pleurae, and a weak terminal piece impression.

One hypostome (Fig. 21A, F, I) has a malformed

Fig. 23 (opposite). Lemureops willsonpiperi sp. nov. from Section H 264-267T m (650-660'), Fillmore Formation (Blackhillsian, Presbynileus ibexensis Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. A, E, J, pygidium, SUI 110279, dorsal, right lateral, and posterior views, x12. B, F, K, pygidium, SUI 110280, dorsal, right lateral, and posterior views, x12. C, G, H, pygidium, SUI 110281, dorsal, right lateral, and posterior views, x12. D, I, N, pygidium, SUI 110282, dorsal, right lateral, and posterior views, x20. L, M, R, pygidium, SUI 110283, right lateral, dorsal, and posterior views, x12. O-Q, pygidium, SUI 110284, dorsal, left lateral, and posterior views, x12. S, W, BB, pygidium, SUI 110285, dorsal, left lateral, and posterior views, x12. T, W,Y, pygidium, SUI 110286, dorsal, posterior, and left lateral views, x12. U, Z, $\mathbf{E E}$, transitory pygidium, SUI 110287, dorsal, posterior, and left lateral views, x15. V, AA, FF, pygidium, SUI 110288 , dorsal, right lateral, and posterior views, x20. CC, DD, GG, pygidium, SUI 110289, dorsal, posterior, and right lateral views, x 20 .

second marginal spine pair, with the left side completely missing and only a small nub on right side. One pygidium (Fig. 22B, F, K) has a malformed right axial furrow and pleurae.

Lemureops koppesi sp. nov. (Figs 3E, 25A-N, P, R-T, V, 26-28, 29A-T)

Diagnosis. Short, triangular LO; small eye; pygidium with dense, medially concentrated granulose sculpture; pygidial doublure depressed only under axis.

Description. Lemureops koppesi is considered similar enough to L. ploogi not to warrant a full written description. All differences are set out in extended comparison. Lemureops ploogi is described in full below.

Ratios are given for comparison with other species of Lemureops. The cranidium of $L$. koppesi is $49.2 \% ~(45.3 \%-52.7 \%)$ as long sagittally as it is wide across the posterior fixigenae. The glabellar length is $97.1 \%$ ( $86.2 \%-106.2 \%$ ) the glabellar width. Lemureops koppesi differs from L. ploogi in its slightly taller and more anteriorly rounded cranidial anterior border, larger (longer and wider relative to cranidial size) glabella, longer lateral glabellar lobes, shorter (in anterior view)
palpebro-ocular ridges, narrower axial furrow, shallower fixigenal pits, medially unconstricted SO, shorter and more triangular LO, and in the possession of a small median tubercle on LO instead of a large hump.

The width of the librigenal field measured under the midpoint of the eye is $33.3 \%$ ( $30.2 \%$ $37.6 \%$ ) the length of field measured along the lateral border, and the width of the lateral border is $85.2 \%(69.9 \%-96.4 \%)$ the width of the field. Librigenae of $L$. koppesi can be distinguished from those of L. ploogi by their wider and shorter librigenal field, swollen and granulose eye socle, and narrower lateral border.

The sagittal length of the hypostome is $99.2 \%$ ( $96.4 \%-102.0 \%$ ) of the width across the anterior wings, and $134.0 \%$ ( $131.0 \%-137.0 \%$ ) the width across the shoulders. Hypostomes of L. ploogi are not available for comparison. Hypostomes of L. koppesi are compared below to those of other congeners.

Thoracic segments of L. koppesi and L. ploogi, particularly posterior segments, are similar in many respects. However, those of $L$. koppesi have only slightly raised axial rings, while those of $L$. ploogi have large, humped axial rings. Lemureops koppesi differs additionally in its small pleural notch and finer axial ring sculpture.

Fig. 25 (opposite). A-N, P, R-T, V, Lemureops koppesi sp. nov. from Section H 172.5T-173.2 m, Fillmore Formation (Tulean, Psalikilus pikum Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. Magnifications are x7.5 except where noted. A, B, D, cranidium, SUI 110301, dorsal, left lateral, and anterior views (H 172.5T m). C, F, H, cranidium, SUI 110302, dorsal, anterior, and right lateral views (H 172.5 T m ). E, G, K, N, cranidium, holotype, SUI 110303, left lateral, dorsal, ventral, and anterior views (H $172.5 \mathrm{~T} \mathrm{~m})$. I, J, L, cranidium, SUI 110304, dorsal, right lateral, and anterior views, x12 (H 172.5 T m ). M, P, S, cranidium, SUI 110305, right lateral, dorsal, and anterior views (H 172.5T m). R, T, V, cranidium, SUI 122844, left lateral, anterior, and dorsal views, x10 (H 173.2 m ). O, Q, U, Lemureops sp. nov. B, from Section H 182.6 $\mathrm{m}\left(410^{\prime}\right)$, Fillmore Formation (Tulean, Psalikilus pikum Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA, cranidium, SUI 122845, dorsal, anterior, and right lateral views, x7.5.

Fig. 26 (overleaf). Lemureops koppesi sp. nov. from Section H 163.3-176.0 m, Fillmore Formation (Tulean, Psalikilus pikum Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. A, D, F, I, cranidium, SUI 110367, dorsal, anterior, oblique, and right lateral views, x7.5 (H 163.3 m ). B, G, J, cranidium, SUI 110365, dorsal, anterior, and right lateral views, x7.5 (H 163.3 m ). C, E, H, cranidium, SUI 110366, dorsal, anterior, and right lateral views, x12 (H 163.3 m$) . \mathbf{K}, \mathbf{M}, \mathbf{O}$, cranidium, SUI 122846, right lateral, dorsal, and anterior views, x7.5 (H 176.0 m ). L, N, Q, cranidium, SUI 122847, dorsal, anterior, and right lateral views, x10 (H 173.2 m ). P, R, S, cranidium, SUI 122848, anterior, right lateral, and dorsal views, x12 (H 176.0 m ).

Fig. 27 (page 531). Lemureops koppesi sp. nov. from Section H 163.3-173.2 m, Fillmore Formation (Tulean, Psalikilus pikum Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. A, D, right librigena, SUI 122849, external and ventrolateral views, x7.5 (H 163.3 m). B, E, left librigena, SUI 122850, external and ventrolateral views, x7.5 (H 173.2 m ). C, F, right librigena, SUI 110369, external and ventrolateral views, x7.5 (H 163.3 m ). G, right librigena, SUI 122851, external view, x10 (H 163.3 m ). H, L, O, right librigena, SUI 110293, internal, external, and ventrolateral views, x10 (H 172.5T m). I, K, left librigena, SUI 110294, ventrolateral and external views, x10 (H 172.5T m). J, N, left librigena, SUI 110295, ventrolateral and external views, x7.5 (H 172.5 T m). M, P, left librigena, SUI 110296, external and ventrolateral views, x10 (H 172.5T m). Q, right librigena, SUI 110297, external view, x10 (H 172.5T m). R, S, V, Y, hypostome, SUI 110298, ventral, dorsal, posterior, and left lateral views, x15 (H 172.5T m). T, U, X, BB, hypostome, SUI 110299, ventral, dorsal, posterior, and right lateral views, $x 12$ (H 172.5 T m ). $\mathbf{W}, \mathbf{Z}, \mathbf{A A}$, cranidium, SUI 110300 , right lateral, dorsal, and anterior views, x20 (H 172.5T m).




The pygidium of $L$. koppesi is $94.2 \%$ ( $87.9 \%$ $100.6 \%$ ) as wide across the first pleural tips as it is long (length excludes articulating half ring) and the width of the axis is $57.8 \%$ ( $51.3 \%-65.4 \%$ ) the width across the pleural tips. Pygidia of $L$. ploogi are not well preserved, but comparison can nonetheless be made. Pygidia of L. koppesi are relatively longer and narrower than those of L. ploogi; with narrower axes; a shallower terminal axial piece impression; and sculpture of denser, coarser granules medially than laterally (compared to fine, dense granules all over $L$. ploogi).

Ontogeny. Cranidial development is similar to that seen in L. kilbeyi, but the cranidium remains fairly narrow as a whole, and the anterior border remains relatively short and narrow (cf. Figs 26M, 27Z). The hypostomal spines reduce to nubs, and the wings enlarge (cf. Fig. 27R, T). The pygidium lengthens and narrows, while the axis inflates and narrows. The terminal piece widens as the rest of the axis narrows, and the axial area develops coarsely granulose sculpture (cf. Fig. 29B, O).

Material. Holotype, cranidium, SUI 110303, from Section H 172.5 T m ( 380 ’ T), Fillmore Formation (Tulean, Psalikilus pikum Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. Assigned specimens SUI 110293-SUI 110313, SUI 110365-SUI 110369, SUI 112844, and SUI 112846-SUI 112856 from Section H 163.3-176.0 m (exact interval listed with each specimen in figure captions), Fillmore Formation (Tulean, P. pikum Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. Specimens of L. koppesi were sampled from a single very large block of talus (H 172.5 T m ) resting at H 172.5 m . New collections made in 2009 demonstrate that the origin of this block is horizon H $173.2 \mathrm{~m} . L$. koppesi is also found in situ at horizons H 163.3 m and H 176.0 m .

## Etymology. After Peter Koppes.

Remarks. Specimens assignable to Lemureops koppesi from H 163.3 m represent the earliest
appearance of the genus at Ibex. The material is fragmentary, often missing the outer layer of cuticle, and encrusted in silicified debris, but clearly posseses the diagnostic characteristics of a short and triangular LO, small eye, and medially concentrated granulose sculpture (somewhat effaced due to poor preservation) on the pygidia.

Several features of $L$. koppesi compare closely to those of L. kilbeyi. The anterior glabellar lobe is slightly swollen, though not to the extent of the large hump on that of $L$. kilbeyi; the axial furrow is well separated from the glabella by a ridge (on some specimens); and the fixigena is long. The hypostomes are very alike, except that the middle body in $L$. koppesi is granulose anteriorly, the lateral and posterior borders are densely granulose, and there is a trace of the middle furrow. The librigenae have similarly wide lateral borders and fields, but those of $L$. koppesi have a significantly smaller eye and very granulose, less well developed socle. The pygidia have similarly impressed terminal pieces, but that of $L$. koppesi is narrower with a narrow axis, is much more tapered, and has medially concentrated granulose sculpture.

The cranidium of $L$. koppesi is not similar to that of either $L$. willsonpiperi or $L$. lemurei. Most notably, it has a taller glabella, smaller palpebroocular ridges, long fixigenae, and the posterior border is short at the genal angle. Librigenae are similar in general shape, but those of $L$. koppesi have a narrower field, smaller eye, longer wedgeshaped portion of the field, and wider lateral border than those of either $L$. willsonpiperi or $L$. lemurei. The hypostome of $L$. koppesi is similar to that of $L$. lemurei, but has slightly smaller spines and a less curved posterior border. The hypostome of $L$. willsonpiperi has longer, sharper spines and a less densely granulose border area. The pygidia of all three species are fairly similar, but that of $L$. koppesi is narrower than that of either of the stratigraphically younger species, and has a wider and more vaulted axis than that of $L$. willsonpiperi (but narrower than that of $L$. lemurei), a distinct impression on the terminal piece, and dense, medially concentrated granulose sculpture. Pygidia of both L. lemurei and $L$.

Fig. 28. Lemureops koppesi sp. nov. from Section H 163.3-176.0 m, Fillmore Formation (Tulean, Psalikilus pikum Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. A, B, E, G, thoracic segment, SUI 110306, dorsal, ventral, left lateral, and anterior views, x7.5 (H 172.5T m). C, D, F, I, K, thoracic segment, SUI 110307, dorsal, right lateral, ventral, anterior, and posterior views, x7.5 (H 172.5T m). H, J, M, $\mathbf{O}$, thoracic segment, SUI 122852, left lateral, dorsal, anterior, and posterior views, x7.5 (H 176.0 m ). L, N, P, $\mathbf{Q}$, thoracic segment, SUI 122853, left lateral, anterior, dorsal, and posterior views, x10 (H 176.0 m ). R, V, Z, pygidium, SUI 122854, dorsal, left lateral, and posterior views, x15 (H 173.2 m ). S, W, AA, pygidium, SUI 122855, dorsal, left lateral, and posterior views, x10 (H 163.3 m$)$. T, U, Y, pygidium, SUI 122856, dorsal, left lateral, and posterior views, x12 (H 163.3 m$) . \mathbf{X}, \mathbf{B B}, \mathbf{C C}$, pygidium, SUI 110368, posterior, right lateral, and dorsal, x10 (H 163.3 m).

willsonpiperi have very finely granulose to nearly effaced sculpture, and their terminal pieces are only lightly impressed.

Several specimens of $L$. koppesi are malformed. One cranidium (Fig. 25A, B, D) has a small conical projection located slightly adaxial from the left genal angle. The left half of the occipital furrow and left L1 are malformed on one cranidium (Fig. 25E, G, K, N). One librigena (Fig. 27C, F) has an unusually robust eye socle. The fields of two librigenae (Fig. 27 B, E; G) are narrow compared to the other specimens.

Lemureops ploogi sp. nov. (Figs 29U-CC, 30)
Diagnosis. LO very tall, medially humped; librigena with wide lateral border compared to width of librigenal field; humped axial rings on thoracic segments.

Description. Cranidium short and wide with length (excluding posteriorly overhanging occipital hump) $45.5 \%$ ( $43.7 \%-47.3 \%$ ) width across posterior fixigenae, narrow anteriorly and wide posteriorly with width across anterior border $34.4 \%$ (31.2\%-37.3\%) width across widest point of posterior fixigenae; anterior border prow-like, somewhat short, longest medially and tapered laterally, slightly wider than widest point of glabella, short in anterior view, highly transversely arched, moderately inflated, particularly medially, with fine granulose sculpture; doublure wraps partway over border, visible mainly in anterior view and only as rim ventrally; anterior border furrow short medially, moderately long at apodemal pits, then short again along palpebroocular ridge, very deep, highly incised, course gently convex anteriorly in dorsal view; glabella subrectangular with width $93.7 \%$ ( $87.8 \%-97.1 \%$ ) length, forwardly expanding, highly transversely arched, increasingly arched posteriorly, with each lobe well defined by furrows and independently inflated, and with medially concentrated sculpture of many densely packed granules; L1 shortest and smallest in area, slightly anteriorly curved laterally; L2 medium sized, nearly transverse; L3 longest, largest, more rounded in outline
than other lobes, directed anteriorly, and nearly merged with palpebro-ocular ridge; frontal lobe slightly larger than L3, with steeply sloped anterior portion, and slight raised bump anteriorly; L1-L3 short and deep, with courses running anteriorly at approximately $45^{\circ}$, with apodemal pits at proximal end of each furrow, separated from axial furrow by low, narrow ridge running parallel to axial furrow; axial furrow moderately narrow along LO and posterior half of L1 and very narrow from anterior half of L3 forward, otherwise extremely wide and lacunate, moderately deep, course anteriorly divergent until midpoint of L3, then anteriorly convergent into anterior border furrow at apodemal pits, also convergent with palpebro-ocular furrow at midpoint of L3; palpebro-ocular ridges located far forward on cranidium, adjacent to anterior border, large, subtriangular in dorsal view, highly convex, inclined dorsolaterally at roughly $45^{\circ}$ angle in anterior view, with sculpture of many fine granules; palpebro-ocular furrow narrow and incised over gently sigmoidal course, slightly wider posteriorly, convergent with axial and anterior border furrows at apodemal pits; fixigenal field broad, moderately long, longest behind anterolateral curvature of margin slightly abaxial from eye, shortest and highly dorsally arched behind palpebro-ocular ridges, lateral portions of field steeply declined, posterior margin nearly transverse, lateral margin gently rounded, with dense sculpture of small pits and granules (fewer granules laterally); SO long, slightly constricted medially, deep, very deep at apodemal pits, separated from posterior border furrow by small ridge; LO very long medially, tapered laterally, very tall, inclined slightly posteriorly, with a very large rounded swelling on the sagittal axis, and with dense sculpture of very fine granules over all; doublure band-like, long medially and tapered laterally; posterior border furrow long over most of course, but strongly tapered along distal portion, course mainly transverse to slightly anterolateral, but sharply curved anteriorly along lateral portion, deep, but shallower along anterior curvature; posterior border curvature follows posterior border furrow, border short near axis,

Fig. 29. A-T, Lemureops koppesi sp. nov. from Section H 172.5T m (380'), Fillmore Formation (Tulean, Psalikilus pikum Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. Magnifications are x12 except where noted. A, E, I, M, pygidium, SUI 110308, dorsal, left lateral, posterior, and ventral views. B, F, J, N, pygidium, SUI 110309, dorsal, posterior, ventral, and anterior views. C, G, K, pygidium, SUI 110310, dorsal, left lateral, and posterior views. D, H, L, pygidium, SUI 110311, dorsal, right lateral, and posterior views, x15. O, P, R, pygidium, SUI 110312, dorsal, posterior, and left lateral views x15. Q, S, T, pygidium, SUI 110313, dorsal, left lateral, and posterior views, x15. U-CC, Lemureops ploogi sp. nov. from Section H $172.5 \mathrm{~m}(380$ '), Fillmore Formation (Tulean, Psalikilus pikum Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. U, Z, AA, pygidium, SUI 110314, dorsal, posterior, and left lateral views, x12. V, W, BB, pygidium, SUI 110315, dorsal, posterior, and right lateral views, x12. X, Y, CC, pygidium, SUI 110316, dorsal, posterior, and left lateral views, x10.

expanded laterally until maximum length at genal angle, then tapered to a point anterolaterally, wide, with widest point just anterolateral of genal angle, slightly inflated, with inflation highest posteriorly, with small articulating flange set off by furrow just lateral from LO; doublure short near axis, expanded greatly under genal angle, with gentle Panderian notch located slightly posteromedial to genal angle.

Librigena with width of field at midpoint of eye $33.3 \%(32.6 \%, 34.0 \%)$ length of field along lateral border furrow; anterior branch of facial suture along field short, slightly shorter than length along anterior projection of lateral border, nearly vertical until lateral border furrow, then nearly horizontal; posterior branch of facial suture long, with slope posteriorly from eye roughly $45^{\circ}$ for first half of length, then at about $30^{\circ}$ to lateral border furrow; eye socle fine and narrow; librigenal field gently convex, moderately narrow under eye, highly tapered posteriorly, beginning at mid-length of lateral border, with sculpture of fine granules and some small pits along posterior edge; lateral border furrow narrow, deep, slightly shallower posteriorly, incised, with slight ventrolateral dip in course across from eye socle; lateral border wide, $87.1 \%(79.3 \%-94.9 \%)$ width of field, inflated, flared and squared off anteriorly, tapered to a point posteriorly, with dense sculpture of fine tubercles; doublure absent along most of anterior projection, broad posteriorly, with smooth sculpture.

Rostral plate and hypostome not recovered.
Thoracic segments highly vaulted, degree of vaulting depending on position in thorax (cf. Fig. $26 \mathrm{U}, \mathrm{AA}$ ), with width of axis $40.3 \%$ ( $33.6 \%$ $45.8 \%$ ) total width; articulating half ring short, less than half length of segment, semilunate; articulating furrow long medially, tapered laterally into apodemal pits, moderately deep to shallow, very deep in pits; axial ring shorter medially, slightly flared laterally, slightly wider than articulating half ring, very tall and pointed, echoing shape of LO, with dense sculpture of fine granules dorsally, tiny granules laterally, and smooth on anterior slope of ring; ring doublure short, band-like, tapered toward apodemal pits, and smooth; axial furrow bowed outward, very shallow across anterior pleural band, almost unimpressed, narrow and shallow across posterior
pleural band; pleurae near horizontal near axis, with sub-horizontal area wider on more anterior segments, strongly ventrally curved from fulcrum, with curvature greater on more posterior segments; anterior pleural band very short, gently posteriorly curved and slightly recurved anteriorly at tips, tips at about $2 / 3$ total segmental width, with anteriorly directed hook-like structure, and dense sculpture of minute granules; pleural furrow short, highly incised, shallow near axis, deeper abaxially, curved anteriorly; posterior pleural band gently posteriorly curved, moderately long near axis, flared ventrolaterally, long at tips, slightly inflated, with inflation highest on posterior rim, ventrolateral portion with deep notch at tips, with fine granulose sculpture and larger granules concentrated posteriorly and at tips, also with small articulating flanges near axis set off by very short incised furrow; pleural doublure short near axis, expanding laterally, long under pleural tips, with shallow Panderian notch.

Pygidium highly vaulted, composed of five segments plus terminal piece, with width across first pleural tips $97.5 \%$ ( $95.8 \%-99.4 \%$ ) sagittal length excluding articulating half ring, and with dense, finely granulose sculpture; articulating half ring short, tapered laterally, broad, semilunate; articulating furrow short, deep, incised, slightly posterolaterally curved; axis highly vaulted anteriorly, progressively less arched posteriorly, with nearly flat terminal piece, very broad anteriorly, $58.1 \%$ ( $53.7 \%-61.3 \%$ ) width across first pleural tips, tapered to gentle point at tip of terminal piece; axial rings individually inflated, of similar lengths; inter-ring furrows short, deep, incised; axial furrow narrow, shallow, shallower posteriorly; pleurae individually inflated, strongly arched from fulcrum, with narrow pre-fulcral sub-horizontal area, length of pleurae decreases posteriorly, increasingly curved posteriorly in dorsal view, with fifth pleurae wrapped around terminal piece, with rounded, slightly flared tips, tips notched similar to thoracic segments; first segment only with anterior and posterior pleural bands; anterior pleural band short, narrower than posterior, reaches only to notch in pleural tips; interpleural furrows very short, deep, incised, follow course of pleurae; terminal piece triangular, long, narrow, uninflated, nearly sub-

Fig. 30. Lemureops ploogi sp. nov. from Section H 172.5 m (380'), Fillmore Formation (Tulean, Psalikilus pikum Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. A, D, G, K, cranidium, SUI 110317, dorsal, anterior, left lateral, and ventral views, x7.5. B, E, H, cranidium, holotype, SUI 110318, dorsal, anterior, and left lateral views, x7.5. C, F, I, J, cranidium, SUI 110319, dorsal, anterior, right lateral, and ventral views, x7.5. L-N, cranidium, SUI 110320, dorsal, anterior, and left lateral views, x12. O, P, left librigena, SUI 110321, external and internal views, x7.5. Q, T, right librigena, SUI 110322, external and internal views, x10. $\mathbf{R}, \mathbf{S}, \mathbf{U}, \mathbf{B B}$, thoracic segment, SUI 110323, dorsal, ventral, anterior, and left lateral views, x7.5. V, Y, CC, thoracic segment, SUI 110324, dorsal, anterior, and left lateral views, x6. W, X, Z, AA, thoracic segment, SUI 110325, dorsal, right lateral, ventral, and anterior views, x7.5 .
horizontal, with W-shaped impression.
Ontogeny. Little ontogenetic material is known for L. ploogi, but one small cranidium (Fig. $30 \mathrm{~L}-\mathrm{N}$ ) shows that the anterior border lengthens and thickens, the glabella shortens and widens anteriorly, the axial furrows widens and shallows, and the palpebro-ocular ridges and occipital hump enlarge. The librigenal field narrows slightly (cf. Fig. 300, Q). The known pygidia are poorly preserved, but it is evident that the pygidium overall becomes shorter and wider, the axis widens, and the posterior taper decreases (cf. Fig. 29U, X).

Material. Holotype, cranidium, SUI 110318, and assigned specimens SUI 110314-SUI 110317 and SUI 110319-SUI 110325 from Section H 172.5 m (380'/ Hintze's [1953] H-16), Fillmore Formation (Tulean, Psalikilus pikum Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. Also occurs at Section H 178.2 m (not figured).

Etymology. After Richard Ploog.
Remarks. Hintze (1953, p. 35) reported $P$. altinasuta from H 380' (172.5 m; Hintze's H-16), which was likely a misidentification of $L$. ploogi. Cranidia of L. ploogi and $L$. lemurei are not very similar. Major differences include the narrower cranidium of L. ploogi, its shorter anterior border, narrower glabella, smaller and less arcuate palpebro-ocular ridges, and longer fixigenae. Librigenae show the same general shape, but those of L. ploogi are much narrower and longer, with a wider lateral border and narrower eye socle. Pygidia are similar in outline, but those of L. ploogi are shorter and wider than those of $L$. lemurei, with a slightly gentler posterior taper, wider axis compared to pygidial width, and more strongly impressed terminal piece.

Compared to L. kilbeyi, L. ploogi has a narrower cranidium, with shorter and narrower anterior border, more bulbous glabellar lobes, smaller palpebro-ocular ridges, and slightly longer fixigenae. As with $L$. lemurei, the librigenae of $L$. ploogi are narrower than those of $L$. kilbeyi, with a wider anterior border and more effaced eye socle. However, neither L. ploogi nor L. kilbeyi have strongly expressed caecal pitting on the border, and both have similar overall granulose sculpture. The pygidium of L. ploogi is wider (compared to sagittal length), and more strongly posteriorly tapered than that of L. kilbeyi. Lemureops ploogi is highly similar to $L$. koppesi. They are compared in the differential description of $L$. koppesi above. It is also compared to $L$. willsonpiperi above.

Specimens of L. ploogi display some intraspecific variation. The holotype cranidium (Fig. 30A, D, G) has a slightly taller, more pointed LO and wider axial furrow than the other two large cranidia.

Lemureops sp. nov. A (Fig. 4P-T)
Material. Assigned specimen SUI 110167 from Section H 191.7 m (434'; locality H-20 of Hintze [1953]), Fillmore Formation (Blackhillsian, Strigigenalis plicolabeona Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Remarks. A single well preserved Lemureops cranidium from H 191.7 m differs from those of $L$. kilbeyi found at that horizon. Although this species is not well known enough to name, it is clearly distinct. Compared to L. kilbeyi, Lemureops sp. nov. A has a shorter and less robustly crenulated anterior border; lacks the diagnostic central frontal lobe tubercle; its glabella is narrower and more parallel-sided; the palpebro-ocular ridges and fixigenae are more steeply sloping; the occipital ring is very tall and pointed, and the cranidium is proportionately shorter and wider. Lemureops willsonpiperi is distinguished from L. sp. nov. A by its long, robustly crenulated anterior border; much larger palpebro-ocular ridges; a low occipital ring with median tubercle; and longer posterior border. Lemureops lemurei also has a long, highly crenulated anterior border; in addition, it differs from $L$. sp. nov. A in its shorter fixigenal field (inter-ocular, postocular, and lateral); and wider, more rounded glabella. Lemureops ploogi differs from $L$. sp. nov. A in its much smaller, subtriangular palpebroocular ridges; narrower fixigenae; much denser granulose sculpture; and it possesses a large knob on the occipital ring. Lemureops koppesi also has much denser granulose sculpture and a more rounded glabella; furthermore, its very short, nearly arcuate anterior border; shorter, more gently pointed occipital ring; and shorter posterior border doublure differentiate it from $L$. sp. nov. A. Compared to all other species of Lemureops, L. sp. nov. A has shallower axial, palpebro-ocular, posterior border and occipital furrows.

## Lemureops sp. nov. B (Fig. 25O, Q, U)

Material. Assigned specimen SUI 122845 from Section H 182.6 m (410'; Hintze's [1953] H-17), Fillmore Formation (Tulean, Psalikilus pikum Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Remarks. A single partial cranidium from Section H 182.6 m , while not well known enough to name, clearly represents a new species of Lemureops. Compared to the stratigraphically closest species, L. koppesi, L. sp. nov. B has a medially longer and laterally shorter anterior border with a slight median posterior projection; a shorter and wider glabella overall (dorsal view), although the strongly dorsally inflated median area is narrower (anterior view); shorter and wider individual lateral glabellar lobes; medially concentrated glabellar sculpture; a taller and more pronounced frontal glabellar "hump"; longer and larger palpebro-ocular ridges; a much shorter fixigena, particularly posterior from the palpebro-ocular lobe, but also distally; a taller LO (cf. Fig 25E, U); a longer posterior border furrow; and a longer posterior border (measured at the genal angle) relative to fixigenal length. Lemureops sp. nov. B more closely resembles $L$. kilbeyi in features such as the shape and inflation of the glabella, possession of a strong glabellar "hump", length of the fixigena posterior from the palpebro-ocular ridges, and length of the posterior border furrow. However, it differs in having a shorter, more laterally tapered anterior border without crenulations; a wider glabella (measured across L3); a wider, less raised glabellar "hump"; coarser and medially concentrated glabellar sculpture; a longer and much taller LO; and more strongly pitted fixigenae. Lemureops sp. nov. B possesses a similar LO to that of $L$. sp. nov. A, but the cranidium of the latter species is overall longer and wider, with a longer anterior border and narrower glabella lacking a "hump". Lemureops lemurei has a much longer, crenulated anterior border; shorter, more rounded glabella with longer, narrower lateral lobes and effaced sculpture; much longer palepbro-ocular ridges; an extremely short fixigena; longer posterior border; and a short LO. The cranidium of $L$. willsonpiperi differs in the same ways as that of $L$. lemurei, except that its glabellar sculpture is finer and not medially concentrated. In comparison to $L$. ploogi, $L$. sp. nov. B differs in the same was as from L. koppesi; additionally L. ploogi possesses an extremely tall and humped LO.

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[^0]:    Fig. 6. Lemureops kilbeyi sp. nov. from Section H 191.7 m (434'; locality H-20 of Hintze [1953]), Fillmore Formation (Blackhillsian, Strigigenalis plicolabeona Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. A, E, I, K, hypostome, SUI 110177, ventral, dorsal, posterior, and right lateral views, x12. B, F, J, hypostome, SUI 110178, ventral, right lateral, and posterior views, x12. C, G, L, hypostome, SUI 110179, ventral, left lateral, and posterior views, x6. D, H, M, hypostome, SUI 110180, ventral, right lateral, and posterior views, x12. N, hypostome, SUI 110181, ventral view, x15. O, R, V, cranidium, SUI 110182, left lateral, dorsal, and anterior views, x15. P, Q, S, T, hypostome, SUI 110183, ventral, dorsal, right lateral, and posterior views, x12. U, Y, DD, pygidium, SUI 110184, dorsal, left lateral, and posterior views, x10. $\mathbf{W}, \mathbf{A A}, \mathbf{G G}$, pygidium, SUI 110185, dorsal, posterior, and left lateral views, x12. X, BB, CC, pygidium, SUI 110186, dorsal, right lateral, and posterior views, x10. Z, EE, FF, cranidium, SUI 110187, dorsal, anterior, and right lateral views, x15. HH-JJ, pygidium, SUI 110188, dorsal, left lateral, and posterior views, x15.

