UNIVERSITY OF CALIFORNIA
RIVERSIDE

A Bridge Too Many? Phylogeny and Biogeography of the Upper Cambrian Saukiid Trilobites

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

Doctor of Philosophy

in

Geological Sciences

by

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August 2014

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ABSTRACT OF THE DISSERTATION

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The family Saukiidae Ulrich and Resser, 1933 was one of the largest groups of late Cambrian trilobites, with representatives occurring on all major paleogeographic plates. However, inconsistent systematic practices that have been historically applied to this group have resulted in a muddled concept of the Saukiidae and an exaggerated species count. This has led to erroneous placement of many taxa due to a lack of distinct characters with which to diagnose some saukiid genera and species. To mitigate past systematic digressions and to re-elevate Saukiidae to a useful concept, a series of cladistic analyses were performed that incorporated all global occurrences of the Saukiidae for which there is a good fossil record. As a further test of the familial relationships of the Saukiidae, members of the Ptychaspididae and Pterocephaliidae were included to test what effect, if any, different outgroups would have on character polarity and the branching point with the Saukiidae. Results vary with outgroup choice, but suggest that some of the characters uniting Ptychaspididae and Saukiidae may be convergent. Because the 'upside-down' stratigraphic placement of taxa recovered with this outgroup is inconsistent with stratigraphic evidence, the Pterocephaliidae outgroup is preferred. The preferred phylogeny indicates that the Saukiidae is monophyletic, and is composed of two distinct groups of subfamilial rank: the Saukiinae, n. subfam., defined by the absence of a preglabellar field (*Calvinella*, *Danzhaisaukia*, *Eosaukia*, *Linguisaukia*, *Lophosaukia*, *Mictosaukia*, *Saukia*, *Sinosaukia*, and *Tellerina*); and the Prosaukiinae n. subfam., defined by possession of a preglabellar field (*Anderssonella*, *Hoytaspis*, *Lichengia*, *Pacootasaukia*, *Prosaukia*, and *Saukiella*). The ancestral geographic area(s) for each node on the preferred cladogram was then computed using Fitch optimization. The Fitch analysis revealed that toward the base of the tree, descendants that had originated from ancestors living in Laurentia likely moved westward towards Australia and North China, most likely as larvae. Further up the tree, a single dispersal event appears to have moved eastward toward South China; all taxa in a more derived position to this dispersal occur in Gondwana indicating a radiation across Gondwana from this event, and a likely Laurentian origin of the family Saukiidae.

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INTRODUCTION

Late Cambrian saukiid trilobites were a moderately diverse group with over thirty genera and more than 200 named species occurring in deposits from Afghanistan, Antarctica, Australia, north and south China, Iran, Kazakhstan, Korea, Myanmar, New Zealand North America, Oman, Thailand, and Vietnam (e.g. Mansuy 1915; Sun 1924; Ulrich and Resser 1933; Kobayashi, 1957, 1987; Shergold, 1971; Schreiber et al., 1972; Wright et al., 1984; Fortey, 1994; Choi et al., 2003). They are consistently found in shallow water facies, and thus were most common in inshore settings. Given this environmental preference, their widespread distribution is perplexing, especially considering that Laurentia was an isolated continent, separated from Gondwana by the Iapetus Ocean (McKerrow et al.,1992; Cocks and Torsvik, 2002; Scotese, 2004). Thus, if these trilobites shared recent common ancestry, either: 1, saukiids evidently managed both to bridge deep ocean basins that lay between Laurentia and other continents and to disperse widely along coastal Gondwana; or 2, prevailing paleogeographic reconstructions are wrong.

Morphologically saukiid trilobites belong to a larger clade that is characterized by a distinctive form of the glabella, and in particular by the continuous S1 furrow that crosses the axis, a transverse S2 furrows, and a well-defined lateral librigenal border (see Figure 1 for generalized saukiid morphology and definition of morphological terms). Saukiids are distinctive within this clade because they possess a reduced or absent preglabellar field, an SO (occipital furrow that is mildly w-shaped, and an anterior border that is not upsloping. Due to their distinctive morphology, the common occurrence of members of the Saukiidae in both Laurentia and Gondwanaland has long been noticed (see Walcott 1906; Walcott, 1913; Mansuy, 1915). This is intriguing, as paleogeographic reconstructions and other geological evidence such as detrital zircon spectra consistently suggest that Laurentia was geographically isolated at this time (Stewart et al., 2001). However, strong similarities in particular features led early workers to assign taxa from both paleogeographic provinces to the same genera. For example, the Laurentian saukiid genera *Tellerina* and *Prosaukia* were suggested by Kobayashi (1933) to be represented in North China by *T. paichiaensis* and *P. ulrichi* respectively. Such an attribution, if correct, implies at least two episodes of transoceanic migration because these genera are both commonly found in Laurentia, but have only been tentatively identified from Gondwana. More recently, *Mictosaukia globosa*, a saukiid species found in both Laurentia and Gondwana (Mexico: Robinson and Pantoja-Alor, 1968; Korea: *M. cf. globosa*, Lee and Choi, 2011) suggests that commonality across ocean basins can exist even at or near the species level. However, although the probability of species normally resident on the shallow shelf successfully crossing an open ocean is relatively low (and is expected to have occurred very rarely), it only has to happen once to permit confamilial occurrence on distant continents. In general a more conservative approach has been applied that questions the idea of multiple migrations in saukiids, and many subsequent authors have rejected the idea that congeneric or conspecific “saukiid” taxa occurred on Laurentia and Gondwana. Indeed, skepticism about transoceanic migration has even led to taxonomic decisions being made entirely on the basis of geography rather than morphology. For example, Shergold (1991, p. 28) explicitly rejected the assignment of Australian saukiid specimens to the Laurentian genus *Prosaukia*, and placed them instead within the less morphologically similar genus *Thailandium* despite acknowledging the fact that this material is morphologically indistinguishable from the Laurentian genus.

The systematic approach taken herein is based solely on morphological criteria, and thus episodes of migration are hypotheses that emerge from the phylogenetic analyses, rather than as *a priori* assumptions. The presence of saukiid trilobites on these two isolated landmasses must, at some taxonomic level, imply common ancestry or migration; and as all authors have agreed that the trilobites in question belong to the same family, it is necessary to invoke either: 1, transoceanic migration; 2, a saukiid ghost lineage extending back to the when Laurentia and Gondwana were last contiguous during the late Neoproterozoic some 580 million years ago (e.g. Lieberman, 2002); or 3, that prevailing reconstruction of global paleogeography during the late Cambrian is incorrect. However, global paleogeographic reconstructions are based on an ever increasing number of information sources including paleontological, paleomagnetic, mineralogical, sedimentological, and geophysical evidence. Thus, the placement of the major terranes is not likely at issue; the smaller outbound Gondwanan blocks do represent points of contention, however. Moreover, as the taxonomic history discussed above shows, the recognition of multiple congeners in both Laurentia and Gondwana must either imply either multiple transoceanic migration or prevalent convergent evolution.

It has long been evident that certain morphological features have evolved independently among trilobite clades, and the extent to which such convergence can dominate overall morphology is striking (e.g. Zhu et al., 2007, 2010). In some cases adaptive explanations for such convergence have been mooted (e.g. Fortey and Owens, 1990), but in many cases the adaptive significance remains unclear. Thus, convergence is an issue that confounds the satisfactory resolution of trilobite phylogeny, and our understanding of it must be improved if more satisfactory phylogenies are to be obtained. Documentation of convergence in the evolution of related but apparently distinct clades will permit assessment of the relationship between the acquisition of convergent characters and particular paleoenvironmental conditions.

Reasonably well-resolved phylogenies have been recovered for many groups of trilobites (e.g. Chatterton et al., 1998; Adrain and Chatterton, 1990; Westrop et al., 2010; Hopkins, 2011), but phylogenetic relationships within Trilobita are far from being fully resolved. Although saukiid and dikelocephalid trilobites were assigned to the Order Asaphida by Fortey and Chatterton (1988) on the basis of the dikelocephaliid’s possession of a median suture, and asaphoid protaspis, various authors (Zhu et al., 2010; Adrain, 2011) have recently challenged the monophyly of Asaphida and the ordinal affinities of these trilobites are presently unclear.

The family-level and lower systematic relationships of saukiids are somewhat better resolved. Since the early 1980’s there has been widespread agreement that saukiids and dikelocephalids are closely related (Ludvigsen and Westrop, 1983, Fortey and Chatterton, 1988, Adrain, 2011), and many authors (Lochman, 1956, Longacre, 1970, Ludvigsen and Westrop, 1983) have also considered the geographically widespread family Ptychasdididae to be closely related to saukiids, although relationships among the three groups have not been fully explored (see Figure 2).

Although there is debate on the monophyly of the group containing saukiid and dikelocephalid trilobites (Ludvigsen et al., 1989; Edgecombe, 1992; Adrain, 2011), saukiid relationships are, in fact, better resolved than those of many other families. There is little doubt that derived members form at least two monophyletic clades – Dikelocephaliidae and a true Saukiidae, perhaps with less-derived members of the Saukiidae falling outside of this monophyletic group. Support for a grouping comprising Saukiidae + Ptychaspididae + Dikelocephaliidae includes uninterrupted S1 glabellar furrow, a narrow (sag.) and transverse S2 furrow, a reduced and anteriorly-directed S3 furrow, and by the expansion of the posterior, rather than lateral librigenal border furrow onto the genal spine). Characters shared by Saukiidae and Dikelocephaliidae include narrow fixigenae, relatively large eyes, firmly incised arcuate palpebral furrow, a narrow palpebral field, and a pygidium generally lacking a furrow-bounded pygidial border. All saukiid taxa bear a distinct cranidial border marked by a sharply defined border furrow.

It has been suggested that the saukiids and dikelocephalids shared a common ancestor that lived no earlier than Furongian Stage 9 (early Sunwaptan) (Ludvigsen and Westrop, 1983). One candidate for a member of a combined dikelocephalid-“saukiid” stem group is the saukiid genus *Prosaukia*. For example, *Prosaukia hartii* possesses the characters of the saukiids, but can only be distinguished from *Briscoia sinclairensis* (a dikelocephalid) by the possession of a marginally more inflated cephalic border (Ludvigsen and Westrop, 1983). Thus, *Prosaukia hartii* may most closely represent the ancestral character state of the “Saukiidae” and a potential branching node for the Dikelocephaliidae. Nevertheless, although the relationships within and between these two families remain unsatisfactorily resolved, they are better understood than those of other late Cambrian trilobite groups, and offer a means to test the specific phylogenetic hypotheses outlined above.

Additionally, the presence or absence of a preglabellar field within members of the family Saukiidae offers a taxabase of potential higher taxonomic significance. The progressive shortening of the frontal area in some saukiid genera leads to the eventual closure of the preglabellar field; all saukiids either possess a preglabellar field or have secondarily lost this feature. Thus presence or absence of a preglebellar field might define two subfamilial-level taxonomic entities.

The purpose of this study is to generate the first species- and genus-level phylogenetic analysis of the family Saukiidae, in conjunction with a systematic revision of this group that will allow a much more stable taxonomic entity. Because this cladistic analysis incorporates species from all paleocontinents on which saukiids occurred, questions raised above regarding the distribution of saukiid species, their potential dispersal pathways and what these may indicate about Cambrian ocean surface currents, the distribution of outbound Gondwanan terranes, and convergence can all be addressed.

Episodes of transoceanic migration have particular significance for several reasons. Firstly, as endemism, or faunal provinciality, was prevalent among late Cambrian faunas (Shergold, 1988), such episodes were evidently uncommon. When they occurred they are highly valuable for establishing temporal and spatial correlations among endemic regions. Secondly, the shared occurrence of monophyletic clades among different regions also provides an opportunity to assess parallels in clade morphological evolution in relation to occurrence and life habits, including exploring similar variations in mature size, the relationship of morphological variance to area of taxic occurrence and whether repeated facies preferences may have resulted in convergent morphological trends that occurred on different continents (Palmer, 1972). Thirdly, phylogeny itself provides information of geographical significance and in this respect this study is of general importance to paleobiogeographic analysis of Paleozoic marine faunas. This is because Brooks Parsimony Analysis (Brooks *et al.*, 1981; Brooks, 1985) relates changes in geographic range directly to the movement of continents or other physical causes such as sea level fluctuation. While this method is employed with evident success to the distribution of terrestrial organisms, its application in trilobites (e.g. Lieberman 2002) has yielded the surprising implication that the geographic distribution of certain early Cambrian trilobites requires the clade to have first evolved during the late Neoproterozoic, some 580 million years ago (Lieberman 2002). This inference reasons that common ancestry implies an original shared contiguous distribution (i.e. origin on a single landmass that later fragmented). The particular distribution of saukiid trilobites provides an interesting test of whether this assumption holds true for polymerid trilobites. This is because the possibility that shared saukiid occurrence on different continents represents shared origin of the “Saukiidae” on a contiguous landmass is remote. To be correct this explanation would require saukiids to have been cryptic not only throughout the late Neoproterozoic, but also to have remained undiscovered throughout the great majority of the Cambrian rock record, before finally becoming manifest almost synchronously on continents separated by a substantial open ocean basin. The simpler explanation is that at least one episode of exceptional range expansion (in this case transoceanic migration) occurred, and that this was responsible for saukiid dispersal from the continent of origin to other continents. If saukiid phylogeny reveals that such migrations occurred multiple times, the value of BPA analysis for interpreting trilobite distributions may deserve reconsideration. As a working hypothesis in this proposal, the number of such migrations is assumed to be minimal, and thus we posit that:

1. Given their shelfal habitat preference, "saukiid" transoceanic migration is expected to have been the result of few, as opposed to many, episodes of migration. This will be tested via cladistic analysis which, if this hypothesis is correct, can be expected to reveal distinct clades of Laurentian and Gondwanan "saukiids" that diversified from an early common ancestor.

2. Evident similarities of form between Laurentian and Gondwanan derived "saukiids" have evolved convergently on these different paleocontinents.

3. Characters that evolved convergently may be expected to show strong and iterated association with local environmental conditions.

4. Did any instances of trilobite migration both within and between continents occur in ordered steps and, if so, what can these inform about Cambrian oceanography?

5. If multiple migrations did occur, what common morphological characteristics, if any, did closest sister taxa share when occurring on different continents?

MATERIALS AND METHODS

Species were selected for inclusion in this study based on completeness of material and availability for study. In some cases, well-preserved and well-photographed taxa were coded from literature (see Table 1).

Cladistic Analyses.

All analyses were performed using TNT v1.1 [Tree analysis using New Technology (Goloboff et al.,2008)]. TNT was chosen over PAUP* for cladistic analyses of our data set because: 1) its algorithms are capable of finding the globally optimum tree(s) in large datasets, 2) it has built in tools to explore tree space, and 3) because it generally performs analyses in a fraction of the time required by PAUP* (Giribet, 2005). Separate analyses for: 1) qualitative characters alone, 2) qualitative and morphometric characters, and 3) qualitative and gap-weighted characters were run separately in order to assess the effects of using different coding methods. Additionally, three runs were completed for each of the three analyses listed above: the first containing dikelocephaliid + pterocephaliid + ptychaspidid species, the second limiting the outgroup to only dikelocephaliid + pterocephaliid taxa, and the third with a limited outgroup comprising only dikelocephaliid and ptychaspidid taxa. Multiple runs were done in this way in order to assess the character polarity and recovered relationships between these groups with each of the three different character coding schemes.

In all analyses all characters were treated as unordered to make the fewest *a priori* assumptions about character polarity. The XINACT command was invoked to deactivate all characters that were not phylogenetically informative for some analyses. The resulting matrices were subjected to a traditional heuristic search with 100 random replicates using the TBR (Tree Bisection-Reconnection) algorithm in TNT v1.1, and holding 10 trees in memory per replicate. Nine different analyses were completed on nine separate data matrices in order to test whether different outgroup selection (*Pterocephaliidae*, *Ptychaspididae*), different character coding schemes (qualitative only, qualitative and morphometric, or qualitative and gap-weighted), would lead to more robust support or to a better fit to stratigraphic record. This approach was used to test previous hypotheses on the evolutionary lineage most closely related to the *Saukiidae* (higher level relationships), to identify synapomorphies that define possible monophyletic groups, and to examine how various character coding schemes effect topology in morphological data sets that are inherently homoplasious. These analyses and their support values are given in Table 2.

In a recent cladistic analysis of pterocephaliid trilobites, Hopkins (2011) used three methods of treating continuous character data: finite mixture coding (FMC), gap-weighting (GW), and treating continuous characters as such in TNT (as a range incorporating the minimum and maximum values of each character). All three of these methods resulted in a decrease in the number of most parsimonious trees recovered over qualitative data alone. In Hopkins (2011) analyses, FMC and GW resulted in an increase in the statistical measures of tree support (C.I., R.I.), treating continuous data 'as such' in TNT did not. Because our dataset is similar to that of Hopkins (2011) in the type of data included (mostly qualitative characters with few morphometric characters) we chose to run separate analyses for qualitative and gap-weighted, as well as binned morphometric, but omitted FMC and 'as such' analyses in TNT due to their substandard performances (Hopkins, 2011). We also chose to include binned morphometric data in which the bins were established by natural breaks in the data (see section on morphometric selection and coding, above).

Outgroup Selection.

Representative taxa from the closely related family Dikelocephaliidae, as well as groups with putative close relationships – Ptychaspididae, and Pterocephaliidae were included to test previous hypotheses on the relationships between these groups and to polarize the characters. Two Ptychaspididae were chosen for inclusion based on completeness of the exoskeletal material, these are *Asioptychaspis subglobosa* from North China (see Park and Choi, 2010), and *Ptychaspis miniscaensis* (see Bell et al., 1952; Stitt and Straatman, 1997; Westrop 1986). Members of the Ptychaspididae were included within our analyses as both ingroups and outgroups to test previous authors' hypotheses as to whether the Ptychaspididae are a sister group to the saukiids with these groups falling outside of the Dikelocephaliidae (*sensu* Lochman, 1956; Longacre, 1970), whether the Ptychaspididae is a sister group to both the Saukiidae and the Dikelocephaliidae within a superfamily-level entity (*sensu* Ludvigsen and Westrop, 1983), or whether the Ptychaspididae is a sister group to a unified Dikelocephaliidae that contains both saukiid and dikelocephaliid subfamilies (*sensu* Adrain, 2011).

Alternatively, some authors have posited a sister group relationship between the Pterocephaliidae and a united superfamily-level Dikelocephalacea (Dikelocephaliidae +

Saukiidae) with ties to the Remopleuridacea (*sensu* Fortey and Chatterton, 1988; Edgecombe, 1992). To test these authors hypotheses, two Pterocephaliidae were included in our analyses and these were selected based on exoskeletal completeness - *Pterocephaliidae norfordi* (see Chatterton and Ludvigsen, 1998), and *Sigmocheilus notha* (see Resser, 1942).

Specific Problems in Character Coding.

Taphonomy, and the extent to which it removes morphological information, represents a significant problem in morphological datasets of fossil remains. Often, specific structures will be effaced, flattened, distorted, telescoped, or some combination of these. In many saukiid taxa, the glabellar anterior presents a coding problem as it may often appear flattened in individual specimens. In well-represented taxa, individual specimens suspected of information loss due to taphonomy might not represent a problem if there are significant numbers of additional specimens available for comparison. However, specimens suspected of such distortions do become problematic in species described from very few sclerites, because the existing specimens could misrepresent the true state of a particular character.

For example, in *Eosaukia walcotti* (Mansuy), a few very well-preserved fully articulated specimens from north China have a subquadrate glabellar anterior with a nearly linear anterior and acutely rounded anterolateral corners. However, in more numerous well-preserved, but disarticulated material attributed to this species that occurs near Alice Springs, Northern Territory, Australia, the anterior of the glabella is distinctly rounded. This flattening of the glabellar anterior in the Chinese material may be due to compaction of a sclerite that was not laying completely flat when originally deposited. Downward forces applied during compaction may lead to a telescoping of sclerites, or flattening of the exoskeleton. Such differences in glabellar morphology are rather common among trilobite remains, and in specimens with very few preserved cranidia presents real problems in coding. Such flattening of the glabellar anterior may also be the case with *Eosaukia latilimbata*, a species known from fully-articulated material from southern Guizhou and Yunnan, China. Morphologically, this trilobite shares many characters with *Eosaukia walcotti*, with the notable exceptions of ornamentation and glabellar anterior shape; *E. walcotti* has a subrounded glabellar anterior, while that of *E. latilimbata* is flat, or even slightly concave. We suspect, that as more material of *E. latilimbata* is recovered, it will be found that the glabellar anterior is subround as well. Thus, this species, as currently coded based on evidence at hand, adds a suspected source of homoplasy to the analysis and may be cofounding the proper placement of this species.

Qualitative Character Selection and Coding.

Qualitative characters in cladistic analyses are characters that describe in words the presence or absence of a structure, or that further describe the complexities or nuances of that structure (e.g. shape, size, or other parameters) (Wiens, 2001). For our analyses, a set of 53 qualitative morphological characters that describe exoskeletal features was coded for all included taxa for which there is reasonably complete information available for all or nearly all sclerites. Characters were selected based upon published diagnoses and descriptions of included genera and species, on re-examinations of type and figured material, on examinations of un-figured specimens, and also based on characters developed and used in previous authors' cladistic work that included saukiid and other presumed closely related taxa (e.g. the genal structure and pre-occipital expansion at S1 of Fortey and Chatterton, 1988). In all matrices analyzed in this study, nineteen qualitative characters describe the glabella, eleven characters describe the extraglabellar morphology of the cranidium, ten characters describe the morphology of the librigena and genal spine, two characters describe the morphology of the palpebral area, one character codes the number of thoracic segments (if known), and a further nine characters detail the morphology of the pygidium. In cases where coded structures were morphologically variable within a single species (due to preservation or deemed intraspecific variation), all available material in which that specific sclerite or structure is preserved was examined; the character state for characters that vary in this way was determined by the majority of individual specimens possessing the dominant state of the character. For example, in *Saukiella junia*, the shape of the glabellar anterior varies from obtusely rounded to relatively flat; however the majority of cranidia have glabella that are obtusely rounded, so character 0 (anterior glabella shape) was coded with state 0, evenly or obtusely rounded. For qualitative characters describing the shape of a sclerite or structure, and in which there is continuous variation between end members or shape 'bins', the reconstructed structures were analyzed using outline shape analysis in order to limit potentially non-repeatable or subjective judgments from the character coding process (see section on shape analyses below). Some characters require specific notes on how they were coded, and these are outlined below in the order in which they appear in the character matrix. Note that TNT handles character numbering starting with zero; for the sake of continuity, this numbering convention is followed throughout this paper.

0. Anterior Glabella Shape. Members of the genus *Prosaukia* often have a glabellar anterior that is flattened across the front, while *Saukia, Saukiella, Mictosaukia*, and *Tellerina* generally have rounded glabellar anteriors. However, this character is often quite variable, even among members attributed to the same genera. Very fine-scale gradations between and among species led to the necessity for this character to be quantitatively 'binned' using principal component and subsequent cluster analyses of reconstructed glabellae outline shape in order to facilitate both consistency in shape 'bins', and also for repeatability of our matrix codings.

3. Pre-occipital glabellar expansion. This character refers to the anterior expansion of L1 suggested by Fortey and Chatterton (1988) as a symplesiomorphy. These authors suggested that this character is primitive and was shared by the common ancestor of both a superfamily-level Dikelocephalacea and Remopleuridacea. The state (0) for this character (present) is considered to represent the primitive condition, and (1) the derived condition.

13. Distinct row of tubercles adjacent to the glabellar furrow(s). This character refers to a distinctly differing style of tuberculation from the field ornamentation of the glabella itself (e.g. - distinctly larger tubercles), and a clear alignment of tubercles along the margins of the glabellar furrows. This character is only coded as (1)

present, if there is a clear size and/or alignment difference between the tubercles adjacent to the glabellar furrows and those of the glabellar prosopon in general.

16. Axial occipital spine (at any stage in ontogeny). Saukiid and other taxa included in our analysis often possess an axial occipital spine, especially in early ontogenetic stages (e.g. Park and Tae, 2010; Lee and Choi, 2011). During ontogeny, this spine may be reduced gradually in subsequent instars, and in the holaspid the genal spine may be expressed only as a vestigial node. This is not problematic in taxa where the holaspid stage clearly possess an occipital spine, but can be confusing because of the presence in some taxa of a different structure, the occipital node. However, taxa in which the occipital spine reduces through ontogeny to a vestigial node could easily be coded as polymorphic (possessing both an occipital spine and an occipital node). To mitigate this possibility herein, this character is coded as present only in taxa that clearly posses an occipital spine in holaspid specimens, or in which there is a clear occipital spine in the protaspid or meraspid stages. In this case, such as in *Prosaukia hartti* and *Sinosaukia distincta*, the residual occipital node is not coded as present for character 17 (axial occipital node) because of a demonstrated ontogenetic linkage between a gradually reduction of an occipital spine and a vestigial node. In rare cases (as in *Calvinella prethoparia*), where both an axial occipital spine and distinct, separate, occipital node occur, both are coded as present.

18. Course of anterior branches of facial suture anterior to palpebral lobe. This character describes the shape of the pre-ocular part of the fixigenae; the shape of this character is derived by tracing the facial suture (from the point where the palpebral lobe and the facial suture meet) forward to the midpoint of the anterior border furrow, and then drawing a straight line segment between these two points. If the line segment between these points is markedly divergent (0) with respect to the sagittal axis, the pre-ocular fixigenae is coded as expanding forward (as in *Prosaukia*, for example); if this character is coded as (1) gently bowed or parallel, there is neither expansion nor contraction (as in many *Eosaukia*); if this character is coded as (2) convergent, there is a marked contraction of the pre-ocular fixigenae (as in some *Ptychaspis* species, for example).

22. Axiomedial swelling of anterior cranidial border. This character refers to a slight posterior widening or expansion of the anterior border in some species (e.g. *Anderssonella beauchampi*).

23. Definition of anterior cranidial border. State (0) of this character refers to a cranidial border that is defined by a distinct, continuous anterior border furrow (as in *Prosaukia misa*, for example). State (1) refers to taxa that have an anterior border that is defined by a distinct break or change in slope, but not a well-defined border furrow (as in the dikelocephaliids, for example). Character (2) refers to an interrupted condition of the anterior border furrow caused by the reduction of the

preglabellar field, resulting in an anterior border furrow that is impinged upon by the glabellar anterior and its preglabellar furrow.

26. Pre-glabellar field. The preglabellar field is defined herein as the area anterior to the glabella, lying between the preglabellar furrow and the anterior border furrow. State (0) refers to the expression of this character as a distinct space lying between the anterior border furrow and the preglabellar furrow. State (1) is expressed as a confluence of the anterior border and preglabellar furrows sagittally, and immediately anterior to the glabella. State (2) refers to absence of a preglabellar field. This is defined by a preglabellar furrow, or a combined preglabellar and anterior border furrow that are less than the sagittal length of both furrows individually, or by the interruption of the anterior border furrow by the anterior of the glabella (see notes on the coding of character 23, above).

38. Expression of genal spine furrow. Fortey and Chatterton (1988) discussed their 'genal structure' (the continuation of the posterior, as opposed to the lateral librigenal border furrow into the base of the genal spine) as a possible synapomorphy for a grouping of Saukiidae + Dikelocephaliidae + Ptychaspididae. State (0) refers to the absence of the genal spine furrow (e.g. *Mictosaukia*). State (1) for this character refers to a genal spine furrow that is a continuation of the lateral librigenal border furrow. State (2) represents a genal spine furrow that is a continuation of the posterior librigenal border furrow (this state represents the 'genal structure' of Fortey and Chatterton, 1988). This state can be difficult to

diagnose in some taxa that have a confluence of the lateral and posterior border furrows. However, if the lateral border of the genal spine narrows more appreciably at, or shortly posterior to, the confluence of the librigenal border furrows, then the posterior border furrow is exerting more influence over this confluence, and this state is interpreted for this character. State (3) represents a genal spine furrow that is a distinct continuation of both border furrows (as in *Lichengia simplex*). This character could be treated as ordered because the genal structures typical of saukiids and other taxa are considered to be the apomorphic (derived) condition, while absence of these characters represent the plesiomorphic (ancestral) condition (Fortey and Chatterton, 1988).

39. Vincular structures of the ventral librigenal doublure. Vincular structures are notches in the underside of the lateral librigenal doublure that accept the ventral tips of the thoracic pleurae, forming a dovetail-like locking mechanism thought to help trilobites maintain enrollment or rigidity under adverse conditions (such as attempted predation). However, it is possible that these structures could be formed by post-molt enrollment when the exoskeleton is still pliable. Thus, while the presence of these structures currently unites some species, this character may actually represent an exoskeletal character that is shaped by a behavioral character (post-ecdysis enrollment in order to help avoid being predated), and, thus, may not represent true phylogenetic signal (see discussion in systematics section under *Eosaukia).*

44. Shape of the pygidium. The states of this character were defined semi-quantitatively by using shape analysis on reconstructed pygidial outlines, followed by subsequent principal component analysis (PCA), and finally divided into shape bins with the aid of cluster analysis. This procedure was followed in order to more accurately describe pygidial outline shape. State (0) of this character refers to pygidia that are subrectangular. State (1) describes pygidia that are transversely subovate, while state (2) describes pygidia that are subtriangular.

45. Emargination of posterior pygidial margin. This character refers to a distinct invagination, inbend, or emargination of the sagittal posterior pygidial margin. This structure is rather common in some *Prosaukia* and dikelocephaliid species.

46. Number of well-defined pygidial axial rings in holaspid (not including the terminal piece). This character refers only to well-defined, complete, furrow-bounded axial rings. In cases where a short, vague, or partial axial ring is suggested, this is not coded as present and the number of axial rings will reflect only the number that are well-defined.

52. Division of lateral pygidial pleurae. The states of this character refer to whether the propleurae and opisthopleurae of the pygidia are of approximately equal area, not whether they are exactly equally divided parallel to the pleural or interpleural furrows. This means of dividing the states of this character was chosen because not all saukiid taxa have interpleural furrows that parallel the pleural furrows, but

some in some of these taxa (for example, *Eosaukia*), the pleurae are rather evenly divided in terms of area by a diagonally-oriented interpleural furrow.

Morphometric Character Selection and Coding.

In addition to the fifty-three qualitative characters used in our analyses, seven characters were identified that further describe the morphometric ratios of various sclerites or structures in relation to other structures present on the same sclerite. All length measurements were made with either a pair of General brand digital calipers, or from photographs containing scale information that were opened and subsequently measured using the measurement tool in Adobe Acrobat. All length measurements for each species were entered into a spreadsheet, and the mean value for each sclerite or structure computed to three decimal places. Ratios of various measurements were then calculated and plotted on bar charts and sorted in order of decreasing value, allowing natural breaks in the data (abrupt changes in the ratio values) to define morphometric ratio-bins. Each taxon was then coded according to this scheme for each of the characters.

Gap-weighted Morphometric Character Selection and Coding.

There are various ways to code continuous quantitative (morphometric) data for inclusion in morphological cladistic analyses (see Hopkins, 2011 for a review of these and the application of gap-weighting and finite mixture coding to a trilobite dataset). Gap-weighting is a coding method that arranges the mean values of continuous morphometric character states from least to greatest, with the gaps between the character states receiving differential weighting based on their position relative to other characters along a numerical vector or number line (or 'attribute axis', generally from 0 to 32) (Thiel, 1993). The gaps are thus weighted by the numerical value of the length of the line segment that separates adjacent coded states of the character (Thiel, 1993). The formula for each coded state (X_s) is given by Thiel (1993) as: $X_s = \frac{x - min}{\max\ - min} \times n$, where x is the mean value of the morphometric character, *min* is the minimum value for that character, *max* is the maximum value, and *n* is the maximum number of ordered states allowed by the algorithm used in the cladistic search software (Thiel, 1993). Because the greater the distance between the values of adjacent characters is, the greater the penalty will be (in terms of length added to the trees) for transformations between distant characters. Conversely, character states that are close in value to each other will add less length to the trees. The resulting matrix that is produced contains character states with positive numbers from 0 to 30. These character states must be rounded to the nearest integer so that the maximum number of character states allowable by the algorithm of the tree search software is not violated. These character states are then downweighted to values between zero and one to three decimal places (a gap-weighted score of 0 equals a downweighted score of 0; a gap-weighted score of 30 equals a downweighted score of 1; a gap-weighted score of 13 equals a downweighted score of 0.433. If downweighting were not done in this way, parity between qualitative character transitions (which are all equal to one step) would be violated (by the maximum of 30 steps between qualitative and morphometric characters). Such highly unequal weighting would favor transitions in the morphometric data at the expense of marginalizing the information contained within the qualitative data.

Discussion.—One problem often grappled with during character development and coding in cladistic treatments of groupings that include taxa from multiple family-level subgroups is characters that are not applicable to all members included in the analysis. Inapplicable characters are those characters that further describe other characters that are not present in all member taxa in a cladistic analysis. Often, complex structures must be assigned more than one character to fully describe them in morphological terms. This is because describing complex characters as one very large, multi-state character (composite coding) can allow inapplicable data to become informative in taxon placement, resulting in recovery of spurious evolutionary histories (Strong and Lipscombe 1999).

For example, character 26 codes the presence or absence of a preglabellar field (the area between the preglabellar furrow and the anterior border furrow). Characters 27 and 53 further describe the pre-glabellar field in terms of its relative length compared with the anterior border, and as a morphometric character describing the length of the preglabellar field as a ratio of the total cranidial length, respectively. However, both characters 27 and 53 are inapplicable if the taxa under consideration does not have a preglabellar field, as there is no ratio describing these characters. If characters 27 and 53 were simply coded as (0) absent, they would always reflect the same character state as that of character 26 [also (0) absent], resulting in weighting, or redundancy, of this complex character (Strong and Lipscombe, 1999).

Ideally, character states for those characters coding, or modifying, other complex characters that are absent from certain taxa should have no bearing on the phylogenetic placement of taxa that lack the complex character; however, taxa lacking such characters may provide valuable phylogenetic information for other characters and help resolve other parts of the tree. Of the various schemes proposed for dealing with this problem in character state coding (composite coding, reductive coding, and non-additive binary coding; see Strong and Lipscombe, 1999 for a discussion of these various techniques), most authors favor reductive coding (e.g. Strong and Lipscombe, 1999; Hill, 2005). Reductive coding treats inapplicable data as query (?), or missing data. Alternatively, to keep track of which characters are missing from an analysis due to being unpreserved in a taxon, and which characters represent inapplicable states, many authors have adopted a scheme in which a question mark (?) represent the former, while a minus sign (-) represents the latter. This bookkeeping notation, while valuable for keeping track of missing versus inapplicable data, has no impact on the analysis - the phylogenetic programs used herein treat inapplicable character states as query (? = missing data).

TNT treats both unavailable observations and inapplicable states in the same way - it adds no steps to the tree for either data type irrespective of the position of the taxon that bears it (Goloboff, 2008). However, the problem in treating inapplicable characters in this way (reductive coding), is that TNT treat inapplicable characters coded as '-' as missing data ('?') - that is as representing one of the existing character states (Strong and Lipscombe, 1999). One way to mitigate the effects of inapplicable data being treated as missing is to collapse zero-length branches, the default option in TNT (Coddington and Scharff, 1994; Strong and Lipscomb, 1999; Goloboff, 2008).

For our analyses, as many character states as possible were coded so as to eliminate inapplicable states. This was possible in most cases, but not for morphometric characters that further describe other structures, or complex structures like the glabella or glabellar furrows.

Geometric Morphometric Landmark Analysis (GMLA).

For all specimens judged to be complete enough for inclusion within GML analyses (at least one landmark per landmark pair), 28 landmarks were measured (see Figure 4). Landmarks were chosen so that as many points as possible could be used to describe morphological aspects of cranidia of saukiid, dikelocephiid, and other outgroup taxa. Landmarks were placed at the convergence of at least three morphological surfaces whenever possible so that analogous points in different species could be easily located. In some cases (landmarks 11, 12, 17, 18, and 20; see Figure 4) this was not possible, and these points were defined by inflections along surfaces, such as the beginning of curvature of the glabella anterior, the widest point of the palpebral lobe, and the widest point of the palpebral furrow respectively - points which are relatively straightforward to accurately locate in most specimens. Photos of each specimen were taken, or photos of specimens were scanned from publications, or copied from electronic publications. Photos were opened in Adobe Illustrator (version CS6) and measured across several sets of bilateral landmarks in order to ascertain the longitudinal center line of each cranidium.

This was done by drawing a line segment (1 point thickness) through the averaged midpoint of at least two pairs of landmarks (e.g., between landmarks 9 and 10, or 19 and 20); this line ensured that landmarks 1 - 6 were centered longitudinally on each cranidium measured. The original photo was then saved as an RGB JPEG image file with the line segment. Images were then opened with ImageJ (version 1.47v) for landmark measurement. All options except centroid were deselected from the set measurements menu, and the 28 landmarks were measured using the point selection tool and measure command. Landmark data were then transferred into a spreadsheet, and formatted for input to the IMP714 (Integrated Morphometrics Package version 714) suite of morphometric programs (see Sheets, 2003), and saved as a tab-delimited text document. This tab-delimited file was then opened using the IMP714 program Bigfix_714. BigFix7_14 preprocesses data by reflecting and averaging landmarks across a baseline for the purpose of synthesizing missing landmark data by reflecting the opposite member of the pair across a given axis defined by the user. The output from BigFix7_14 was then read by the IMP714 program CoordGen7_14, which generates and saves the dataset in Partial Procreates Superimpositioning (as well as Bookstein coordinates and other formats) (see Sheets, 2003). Procreates superimposition realigns the landmark points to minimize the effects of variation in translation, rotation, and scale (Rohlf, 1999). This data is then read by a third IMP714 program, PCAGen7_14, which performs Principal Component Analysis (PCA) on the dataset. PCA is a statistical method that seeks to explain the greatest variance within variables in a dataset; thus principal component 1 in any PCA analysis will denote the greatest variance in the dataset, PC2 will denote the next largest variance in the data, and so on. PCA scores were saved and imported into MS Excel for graphical output.

Shape Analyses.

One problem encountered during character coding was that outline shapes do not always naturally cluster into discrete character sates. Boundaries between shape categories become subjective judgments. For example, some saukiid taxa, such as *Prosaukia misa*, possess a posterior pygidial margin that is subquadrate, while others such as *Tellerina crassimarginata* have a more evenly rounded shape. In cases where natural gaps exist in the continuum of shape variance, these gaps can be used to define natural shape-bins. However, where no natural gaps exist, defining groupings of the outline shapes of morphological features becomes difficult. To mitigate subjective judgments of structural outline shapes as much as possible, Fourier shape analyses were performed for two complex structures – the outlines of the glabella and pygidium. Analyses were performed using the computer program Shape 1.3 (Iwata and Ukai, 2002).

A photograph including a scale bar is taken and opened with the Shape 1.3 program ChainCoder. ChainCoder converts color 24-bit bitmap images to black and white, traces the outline of objects, and describes the information as chaincode, a method for describing geometric information as numbers from 0 to 7. The output from ChainCoder is then opened with Chc2Nef, a separate program that calculates the normalized Elliptical Fourier Descriptors (EFD), a series of connected trigonometric curves that accurately describe a closed shape EFDs from the chain code information

(Iwata and Ukai, 2002). The resulting EFDs are then analyzed using PrinComp, a third Shape 1.3 program that performs Principal Component Analysis (PCA), allowing variation within the set of shapes analyzed to be ranked and visualized (see Figure 5 for an example graph of pygidium shape). For trilobite shape analyses, reconstructions of the species' glabellae and pygidia were used. All reconstructions in this contribution were produced directly from the specimen or group of specimens judged to be the most complete, best preserved, and undistorted material available. The two principal components describing the largest proportion of variation were then plotted in Microsoft Excel. The name of each species represented on the resulting plot, and a graphical representation of the analyzed shape were added to the graphs in Adobe Illustrator to facilitate comparisons. Shape category bins were then established based on where taxa with well-defined shapes plotted on the PCA graph. Coding for the characters was then done based upon the bins revealed in the PCA morphospace (see Figure 5 for an example).

Stratigraphic Consistency.

A composite section that incorporates the stratigraphic ranges of as many as possible of the late Cambrian saukiid and closely related taxa included in our cladistic analyses was built using the constrained optimization software (CONOP9, CONMAN) of Sadler, et al. (2003). CONOP implements constrained optimization of biochronological (first and last occurrences of taxa) or other datable events (ash falls, isotopic excursions, geochronologically-dated beds, etc.) by minimally adjusting a sequence of local first-, last-, and co-occurrence datums so that all local sections present the same order as a hypothetical global composite sequence. These biochronological events and the composite section can then be used to correlate individual sections together (Sadler et al., 2003), or to evaluate cladistic analyses for stratigraphic consistency (e.g. - Hopkins, 2011).

CONOP9 is implemented through a ‘data-mining’ approach in which previously published range charts, stratigraphic columns incorporating fossil finds, or various fossil zonal schemes are coded for constrained optimization of the order of their appearances, co-occurrences, and disappearances (e.g. Sadler et al., 2009). Two broad categories of paleontological studies exist that can be most readily translated into first and last occurrence data that can then be used in CONOP analyses. The first and most useful of these studies contain range charts that summarize the stratigraphic occurrence of each taxon within the studied section(s). Of the studies in this category, the most useful type incorporates range charts that give a measured stratigraphic section that includes the ranges of each taxon along with the number of finds of individuals and the stratigraphic level of each find. A second category of study that contain measured sections and/or biostratigraphic zonal schemes that incorporate stratigraphic information on the taxa contained, but in which total number of individual finds per taxon are not given is also useful (e.g. Sohn and Choi 2007; Lee and Choi 2008, 2011).

Other studies that did not include stratigraphic data or measured sections can also contribute data that can be utilized by CONOP9. For example, studies which ‘bin’ trilobite occurrences into zones, subzones, biozones, or assemblages (and thus contain little or no stratigraphic information) are useful if they in some way relate ranges for individual taxa, and not all of these ranges overlap (e.g. Nelson, 1951; Bell et al., 1952). For this kind of data, each zone or assemblage is assigned a sequential number, beginning with the oldest zone; this number is then used as if it represented a stratigraphic thickness, allowing first and last occurrences for taxa listed in this way to be translated into a format useful in CONOP9.

For this study, a literature search was performed in order to identify as many published range charts that incorporate saukiid and outgroup trilobites from upper Cambrian rocks globally. This literature search was broadened to include all published range charts incorporating trilobites and genera of conodonts with a global distribution from Cambrian Series 3 through the Furongian and into the Lower Ordovician. Other sections incorporating dated events were also added to the database, including isotopic excursions (TOCE, or the Top of the Cambrian isotopic Excursion event), and geochronological datums (zircon radioisotopic dates). These data were entered into CONMAN (CONstrained optimization data MANager; Sadler et al., 2003) in three steps. First, the sections present in each publication were identified and section files created in CONMAN. secondly, all of the taxa present in each published section, along with their original author (a means of keeping track of synonymy) were entered into CONMAN populating a taxon dictionary of all globally-included taxa. Third, the stratigraphic levels of the first and last occurrence of each taxon, and/or any other events that may be present within the sections (isotopic excursions, geochronological datums) were entered into the event dictionary via CONMAN. After data entry was complete, output files were generated by CONMAN for CONOP input. CONOP analyses were run with the following settings: all sections in the section dictionary were included; all taxa in the taxon dictionary present in at least two sections globally were included; all unpaired events in the events dictionary were included (isotopic excursions, geochronological datums); all locally observed events carried the default weight (1.00); and the CONOP input and configuration files were auto-generated by CONMAN with the default fully automatic setting and fixed cooling schedule. The CONOP input file starts the program and automatically begins an analysis. Following the analysis in CONOP, various graphical and numerical outputs were generated, including the global composite range charts given in Figures 12 and 13.

Modified Brooks Parsimony Analyses (mBPA).

For mBPA analyses (see Figs. 16 and 17), seven paleogeographic regions (plus ancestor) were identified and included in biogeographic analysis; these are listed in Table 3. Boundaries of selected paleobiogeographic areas were defined based on the presence of large-scale geological features suggested by previous paleogeographic reconstructions (ocean basins, continental positions, land masses), and by the presence of regionally-endemic taxa. Separate vicariance and geo-dispersal matrices were coded using cladograms in Figures 4.2 and 6.2 that had had the paleogeographic areas occupied by each node optimized according to Fitch optimization criteria; each of these trees was then translated into two matrices, a vicariance matrix and a geo-dispersal matrix (using vicariance and geodispersal algorithms explicitly detailed by Wiley and Lieberman, 2011). The vicariance matrix more strongly weights range contractions in the tree topology; such range contractions are interpreted to represent splitting of taxon ranges by emplacement of barriers to gene flow, and subsequent speciation of a descendant taxon that has a smaller range than the ancestral stock (Lieberman and Eldredge, 1996). The geo-dispersal matrix more strongly weights range expansions present in the tree topology; such expansions are interpreted as indicating that barriers to gene flow have recently been removed, allowing species to expand their geographic ranges (Lieberman and Eldredge). Each of the resulting matrices was subjected to an exhaustive parsimony search (implicit enumeration) using TNT v1.1 (Goloboff et al., 2008), with all characters treated as ordered. The results are presented in Figures 16 and 17.

RESULTS

Results of Cladistic Analyses.

All recovered trees have similar consistency indices (0.282 - 0.338), and retention indices (0.627 - 0.679), but vary substantially in tree length, and number of most parsimonious trees recovered (see Table 2). These indices are remarkably similar to other trilobite cladistic analyses (see Cotton, 2003; table 2, Hopkins, 2011). The consistency index is given by: $C.I. = \frac{minimum\ \ \#\, of\ \ steps\ \ expected\ \ from\ \ dataset}{actual\ \ \#\, of\ \ steps\ \ on\ \ tree} \times 100$, and is thus a measure of how many steps longer a given tree is than the shortest tree possible, given the dataset used. The C.I. is used widely as a general metric for the amount of homoplasy contained in a dataset.

Analyses of matrices that included qualitative characters only resulted in low resolution consensus trees when all fifty taxa (dikelocephaliid, pterocephaliid, and ptychaspidid outgroups + saukiid taxa) were included (see Figures 6, 8, and 10). The greatest resolution achieved utilizing qualitative data alone was Analysis 4 (consensus tree in Figure 8) ; this analysis included dikelocephaliid + pterocephaliid outgroups but did not include members of Ptychaspididae. Analysis 4 recovered fewer most parsimonious trees (MPTs) than Analysis 1 (qualitative data only, all 50 taxa), the recovered trees had better C.I. and R.I. values, and the strict consensus tree had the best resolution of any analysis of qualitative data only. Analysis 7 [qualitative data only, dikelocephaliid and ptychaspidid (but no pterocephaliids) outgroups + saukiid ingroup taxa] resulted in a further decrease in the number of MPT's recovered, but support values and tree resolution both deteriorated compared with Analysis 4.

Analyses of matrices that included the same qualitative data matrix as in the analyses above, but to which an additional seven binned morphometric characters were added resulted in a general increase in resolution across the individual consensus trees, but resulted in the lowest C.I. and R.I. scores of the three analysis groups. When all fifty taxa (qualitative + binned morphometric data, dikelocephaliid, pterocephaliid, and ptychaspidid outgroups + saukiid taxa) were included in Analysis 2 (see Figure 7.1), resolution increased dramatically over all MPT's recovered from Analyses 1, 4, and 7; this analysis achieved the greatest resolution utilizing qualitative and binned morphometric data. Analysis 5 (qualitative and binned morphometric data) included dikelocephaliid + pterocephaliid outgroups but did not include members of Ptychaspididae (see Figure 9.1); it recovered more MPTs than Analysis 2, but the recovered trees had the highest C.I. and R.I. values of all analyses run with qualitative and binned morphometric data. Analysis 8 included dikelocephaliid + ptychaspidid outgroups, but did not include members of Pterocephaliidae (see Figure 11.1). This analysis resulted in a dramatic increase in the number of MPT's and a decrease in C.I. and R.I. support values and dramatic decline in tree resolution compared with Analyses 4 and 5.

Analyses of GROUP 3 matrices that included the same qualitative data matrix as used in all previous analyses, but to which an additional seven gap-weighted morphometric characters were added, resulted in fully resolved trees across all analyses.

There was a marked improvement in C.I. and R.I. scores over GROUP 2 analyses (Analyses 2, 5, and 8) and a dramatic decrease in the number of MPT's across all three analyses (a single MPT was recovered in all three analyses). Of GROUP 3 analyses (Analyses 3, 6, and 9), the highest support values (C.I. and R.I.) and the shortest tree length were achieved in Analysis 6; this analysis included dikelocephaliid + pterocephaliid outgroups but did not include members of Ptychaspididae (see Figure 11.2).

Discussion.—The reduction in the number of most parsimonious trees when continuous (gap-weighted) data are added to the analyses is striking. In general, resolution of consensus trees increase as the number of MPT's decrease. This is because of two parameters: 1, the number of MPT's; and 2, the degree of difference between them (i.e. many trivially different trees versus a few dramatically different ones). As the number of MPT's decline, there is a reduction and eventual loss of conflicting branches, resulting in a decrease in conflicting branches, and an increase in resolution. Regardless of the coding method used, there are some consistencies across all trees. The Dikelocephaliidae occurs in all nine consensus trees generated from all nine analyses, as do the following monophyletic clades: *Calvinella* (in all but Analysis 5, Figure 9.1), *Lophosaukia*, *Mictosaukia*, *Tellerina*, and a clade comprising *Eosaukia bella* + *E. micropora*.

GROUP 1 Analyses.—GROUP 1consists of Analyses 1, 4, and 7 - all 50 taxa, including representatives of the Saukiidae, Dikelocephaliidae, Pterocephaliidae, and

Ptychaspididae. For GROUP 1 analyses, the full group of 50 taxa was analyzed with qualitative characters only (Analysis 1, see Figure 6), qualitative and binned morphometric characters (Analysis 4, see Figure 7.1), and qualitative and continuous gap-weighted characters (Analysis 7, see Figure 7.2). In GROUP 1 analyses, the number of MPT's decreased dramatically as morphometric data were added to analyses [qualitative data only (Analysis 1) - 160 MPT's; qualitative + binned morphometric data (Analysis 4) - 10 MPT's; qualitative + gap-weighted data (Analysis 7) - 1 MPT]. Support values for GROUP 1 analyses have relatively low consistency indices (C.I. = 0.32 - 0.338) and moderately high retention indices (R.I. = 0.672 - 0.679). In all of our analyses, the C.I. is low; it is highest in GROUP 1 analyses, decreases markedly with the inclusion of binned morphometric data, and then increases back to nearly the same level with the inclusion of gap-weighted morphometric data. Thus, relative homoplasy is high in the qualitative dataset (Analysis 1), slightly higher in the qualitative + binned morphometric data (Analysis 4), and then drops back to nearly the level of Analysis 1 in the qualitative + gap-weighted dataset (Analysis 7) (see Table 2). The retention indices (R.I.) for GROUP 1 analyses are moderately high R.I. = 0.672 - 0.679 , but follows this same trend, decreasing from Analysis 1 to Analysis 4, and then increases again in Analysis 7.

The numerical value of these indices are remarkably similar to recent cladistic analyses of trilobite families Conocoryphidae and Pterocephaliidae, and suggest relatively high levels of homoplasy (see Cotton, 2003; and table 2, of Hopkins, 2011, respectively). Cotton (2003) suggested that both a lack of resolution in the strict consensus tree, and relatively low support indices could be a result of uncertainty about the correct position of a small number of terminal taxa (Cotton, 2003). This appears to be the case in our analysis when ptychaspidids are removed; support indices increase marginally and tree topology stabilizes (number of MPTs decreases). However, the support indices remain low (C.I. = 0.327, R.I. = 0.659). When some of the terminal taxa whose position varies in MPTs are removed (*P. misa*, *D. miserabilis*), support values increase marginally due to a reduction in homoplasy (C.I. = 0.344, R.I. = 0.666). However, these values do not significantly increase, and homoplasy remains significant.

In GROUP 1 analyses (all 50 taxa: members of Saukiidae, Dikelocephaliidae, Pterocephaliidae, and Ptychaspididae), the highest support values are those achieved in Analysis 1 (qualitative character data only, all 50 taxa). However, this analysis resulted in 160 MPT's, severely limiting the resolving power of this analysis due to consensusing of trees (see Figure 6). However, phylogenetically informative branching patterns still resolve some of the more well-supported clades. Pterocephaliidae is resolved basally, the Dikelocephaliidae are sister group to the Pterocephaliidae, with a large polytomy containing saukiid and ptychaspidid genera dominates the remainder of the cladogram, indicating a paraphyletic "Saukiidae". However, some saukiid genera consistently cluster together, including *Tellerina*, *Calvinella*, *Mictosaukia*, and *Lophosaukia*.

Analysis 4 (qualitative + binned morphometric data, all 50 taxa) achieved significantly lower C.I. and R.I. values, but resulted in a consensus tree with a significant increase in resolution over the consensus tree of Analysis 1. In this tree (see Figure 7.1), the Pterocephaliidae and Dikelocephaliidae are in the same positions as in Analysis 1, and most Laurentian genera are now fully resolved, and in a derived position relative to the dikelocephaliids and Australian taxa *Lichengia* and *Pacootasaukia*. However, the genus *Saukia*, and the relationships between Gondwanan saukiid genera are still unresolved below the generic level (see Figure 7.1). Additionally, included members of the Ptychaspididae now plot within a 'clade' that contains both Laurentian and Gondwanan saukiid taxa, and both with and without a preglabellar field. This topology again suggests that the saukiids are paraphyletic.

Analysis 7 (qualitative + gap-weighted morphometric data) has support values similar to those of Analysis 1. A single MPT was recovered and is presented in Figure 7.2. This tree resolves the Pterocephaliidae and Dikelocephaliidae as sister taxa, both plotting basally to a polyphyletic "Saukiidae" that is split into a less-derived clade comprising the predominantly Laurentian genera, a more-derived clade comprising Gondwanan genera, a clade comprising *Hoytaspis* + *Anderssonella* + Ptychaspididae, and a derived clade comprised predominantly by Gondwanan species of *"Eosaukia"*. While many authors have noted a probable sister group relationship between the Dikelocephaliidae and the Saukiidae based on similar morphological attributes (see Figure 2), or a sister group relationship between the Ptychaspididae and a group consisting of Saukiidae and Dikelocephaliidae, no previous authors have suggested that the Ptychaspididae plot as a group within the Saukiidae. In Analysis 7, characters uniting ptychaspidids with *Anderssonella beachampi* include character 23 (definition of anterior cranidial border): (0) defined by distinct, continuous anterior border furrow; character 25 [expression of interrupted (abaxial) portion of cranidial border furrow]: (0) absent (abaxial part of border furrow even continuation of medial part of furrow - e.g.

Prosaukia); character 26 [pre-glabellar field (PG field is the area between the preglabellar furrow and the anterior border]: (0) expressed as distinct space lying between the anterior border furrow and the preglabellar furrow; character 46 [number of well-defined pygidial axial rings (minus terminal piece) in holaspid] from three to four axial rings; and an increase in continuous character 55, width of the lateral librigenal border. Characters serving as synapomorphies to define Ptychaspididae in this location on this tree include: character 1 (shape of glabellar anterior in lateral profile): (1) anterior of glabella lies significantly below rest of glabella; character 2 (preoccipital glabella narrows distinctly): (0) absent (sides ~parallel); character 4 (ornament of glabella): (3) distinct, subconcentric ridges; character 9 (S3 furrow): (0) absent or reduced; character 19 (shape of posterior fixigenal field): (0) distinctly triangular; character 50 (terminal piece extends all the way to posterior border): (1) present; character 55 (continuous, length of the preglabellar field): decreases; and character 58 [continuous, spacing of the palpebral lobe from the glabella (ocular platform width]: increases. Of these, all characters except character 4 are parallelisms; character 4 is a true synapomorphy, occurring on this tree only in the ptychaspidids.

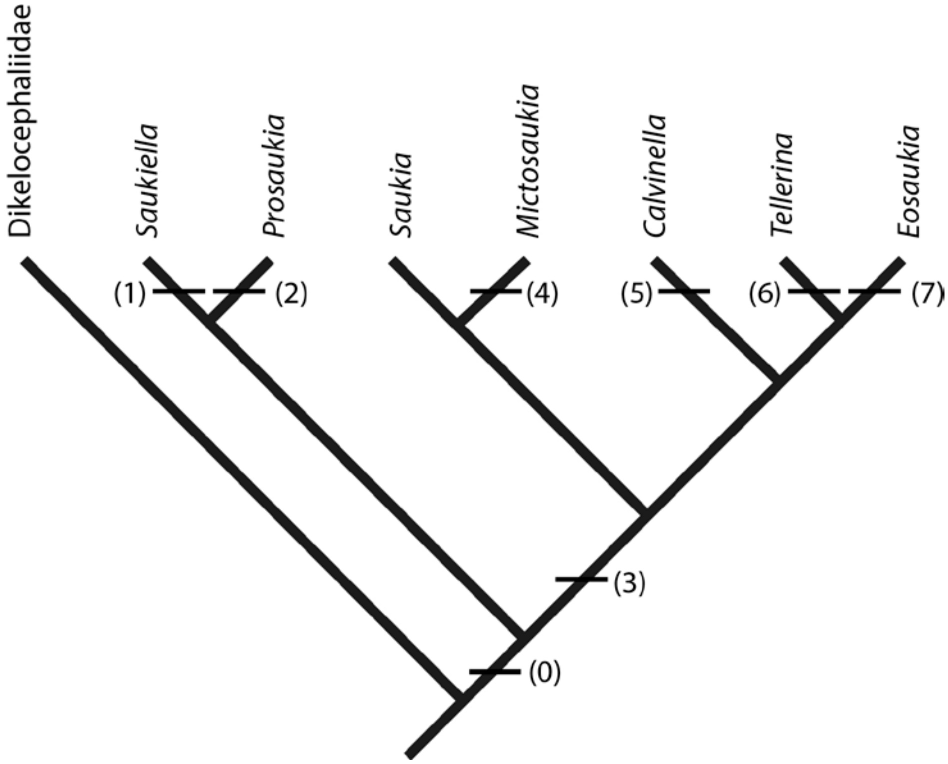
In the case of Analysis 7, it appears that the polarity of character states between Pterocephaliidae and Ptychaspididae families is leading to a spurious placement of the Ptychaspididae within a paraphyletic "Saukiidae". Such a placement is not consistent with stratigraphic evidence, or previous author's published cladistic work (e.g. - Hegna, 2006). Inclusion of members of the Ptychaspididae in our analysis results in ptychaspidids grouping with apparently more derived saukiids; thus, this is not our preferred hypothesis.

GROUP 2 Analyses.—To further test the results of GROUP 1 analyses in which Ptychaspididae plotted within a polyphyletic 'Saukiidae', GROUP 2 analyses were designed to assess clade stability with the removal of ptychaspidid taxa from the analyses as well as differences in qualitative and morphometric character codings. GROUP 2 consists of Analyses 2, 5, and 8 - 48 taxa, including representatives of the Saukiidae, Dikelocephaliidae, and Pterocephaliidae (members of Ptychaspididae were removed to observe character polarity and topological changes in trees without these taxa included). For GROUP 2 analyses, the group of 48 taxa was analyzed with qualitative characters only (Analysis 2), with qualitative and binned morphometric characters (Analysis 5), and with qualitative and continuous gap-weighted characters (Analysis 8), respectively, as was done for taxa in GROUP 1 analyses.

Analysis 2 (qualitative data only, see Figure 8) yielded a slight increase in support values over Analysis 1 with the removal of ptychaspidids from the dataset, and there was a decrease in the number of MPT's recovered. The large number of MPT's (n = 85), and slight changes in tree topology among these trees yield a consensus tree that has only marginally improved resolution over the consensus tree of Analysis 1 in which ptychaspidids were included. Marginally better resolution defines an unresolved clade that includes primarily Laurentian genera as a sister group to the Australian genera *Lichengia* and *Pacootasaukia,* with a further unresolved clade consisting of Laurentian and Gondwanan genera in a more derived position to this (see Figure 8). Thus, there is a marginal improvement in recovered trees in the qualitative data matrix when ptychaspidids are removed from the data matrix.

Analysis 5 (qualitative + binned morphometric data, no ptychaspidids, see Figure 9.1) yielded a significant drop in support values and increase in tree length over Analysis 2, indicating that binned morphometric data performed more poorly (i.e. contained more homoplasy) than did qualitative data alone when members of Ptychaspididae were removed. Analysis 5 yielded a slight increase in support values and decrease in tree length when compared with Analysis 4, indicating that in datasets that contain both qualitative and binned morphometric data, the removal of ptychaspidid taxa increased support values.

Analysis 8 (qualitative + gap-weighted data, no ptychaspidids, see Figure 9.2) yielded the highest support values and shortest tree length for all GROUP 2 analyses in which morphometric information was included, and resulted in a single, fully resolved MPT; this tree is the favored hypothesis of saukiid clade herein. This tree resolves a monophyletic Saukiidae with a close sister group relationship to the Dikelocephaliidae. The least derived members of the Saukiidae are the Gondwanan genera *Lichengia* and *Pacootasaukia*, with the Laurentian genera *Saukiella* and *Prosaukia* forming a clade with a sister group relationship to *Pacootasaukia*. *Saukia* and *Mictosaukia* form a clade lying in a derived position relative to *Saukiella* and *Prosaukia* reflecting loss of the preglabellar field, with *Calvinella* and *Tellerina*, respectively, occupying a derived position relative to these. All taxa lying in a derived position relative to *Tellerina* are Gondwanan, and reflect an increase in the complexity of the morphology of the cranidium, and a general decrease in pygidial length and number of pygidial axial segments. The slight increase in support values over those in Analysis 7, as well as the decrease in tree length, and dramatic increase in resolution all indicate that the removal of ptychaspidids from Analysis 8 produced a tree that better fits the data.



Text-figure 1. Synapomorphies that define well-supported groupings revealed by cladistic analyses (numbered 0 to 7, transitions explained below). 0) changes: (5): 1→ 2, (occipital furrow) gently curved to w-shaped; (6): 1 → 0, (S1 furrow) interrupted to entire (parallelism); (15): 1 → 0 (axial occipital tubercle) present to absent; (28): 2 → 0 (orientation of anterior border) upsloping to not strongly downsloping; (44): 0 → 1 (pygidium shape) subrectangular to subovate; (45): 1 → 0 (emargination of pygidial posterior margin) present to absent; (46): 4 → 3 (number of pygidial axial rings) >6 to 5 (reversal, parallelism); (47): 0 → 1 (pygidial postaxial ridge) absent to present. 1) changes: (26): 0 → 1, (PGF) from space between ABF and PG furrow to combined wide flat bottom furrow. 2) changes: (42): 1 → 0, (position of palpebral lobe midlength relative to glabella) posterior to anterior. 3) changes: (23): 0 → 2, (anterior border furrow) continuous to interrupted; (26): 0 → 2, (preglabellar field), present to absent. 4) changes: (15): 0 → 1, (axial occipital tubercles) absent to present (reversal); (34): 0 → 1, (posterior part of lateral librigenal furrow c-shaped) absent to present; (38): 2 → 0, (furrow of genal spine) present to absent; (57): 0.233 - 0.267 → 0.300, (l:w ratio of glabella increases). 5) changes: (16): 0 → 1, (axial occipital spine) absent to present; (45): 0 → 1, (emargination of pygidial posterior margin) absent to present (parallelism). 6) changes: (4): 1 → 2, (ornament of glabella) pustules to ridges; (9): 1 → 0, (S3 furrow) present to reduced/absent (reversal in some taxa); (54): 0.267 - 0.300 → 0.467, (length of frontal area) increases; (56): 0.267 - 0.367 → 0.200, (l:w ratio of pygidium) decreases; (57): 0.300 - 0.367 → 0.400, (l:w ratio of glabella) increases. 7) changes: (37): 1 → 0, (confluence of lateral and posterior librigenal border furrows) confluent to non-confluent (reverses in some taxa); (43): 2 → 1, (number of thoracic segments in holaspid) 2 → 1, 12 to 11; (55): 0.533-0.567 → 0.367-0.400, (width of lateral librigenal border) decreases; (56): 0.267-0.367 → 0.400, (pygidium length to width ratio) increases (reversal).

GROUP 3 Analyses.—To further test the results of GROUP 1 and 2 analyses and the stability of taxonomic groupings when various outgroups are included, GROUP 3 analyses were designed to assess clade stability with the removal of pterocephaliid taxa from the datasets. GROUP 3 consists of Analyses 3, 6, and 9 - 48 taxa, including representatives of the Saukiidae, Dikelocephaliidae, and Ptychaspididae (members of Pterocephaliidae were removed to observe character polarity and topological changes in trees without these taxa included). GROUP 3 analyses were done with qualitative characters only (Analysis 3, Figure 10), qualitative and binned morphometric characters (Analysis 6, Figure 11.1), and qualitative and gap-weighted characters (Analysis 9, Figure 11.2), respectively, as was done previously for taxa in GROUP 1 and 2 analyses.

All three GROUP 3 analyses resulted in a decrease of support values over GROUP 2 analyses, and longer MPT's. Analysis 9 resulted in a single, fully-resolved most parsimonious tree that recovered a monophyletic Saukidae that resolves many of the same genera and clades recovered in Analysis 8 (see the clade comprising *Prosaukia* and *Saukiella*, for example in Figure 11.2). However, in the case of Analysis 9, the inclusion of the Pytchaspididae as an outgroup resulted in character polarity that led to taxa considered to be derived plotting in basal positions (*Eosaukia* and *Lophosaukia*, for example plotting basally as a sister group to the Ptychaspididae), and taxa previously considered to be basal plotting in derived positions (*Prosaukia* and *Saukiella* for example) (see Figure 11.2). Moreover, the position of these clades in MPT's in GROUP 3 analyses is not in agreement with the evolutionary history of the Saukiidae as suggested by other authors (Lochman, 1956; Longacre, 1970; Ludvigsen and Westrop, 1983; Fortey and Chatterton, 1988; Edgecomb, 1992; Adrain, 2011), or with the stratigraphic occurrence of the fossils themselves (see section on stratigraphic consistency). For these reasons, we consider the cladistic hypotheses generated by analyses of GROUP 3 datasets to be unlikely. Further, the polarity of character states created by rooting trees with a Ptychaspididae outgroup is considered inferior to the polarity of characters created by rooting trees with a Pterocephaliid outgroup. Thus, according to our analyses, it is likely that the Saukiidae is a monophyletic group, that Saukiidae cladogenesis was via Pterocephaliidae and included a basal branch that also led to Dikelocephaliidae cladogenesis.

Much criticism has been leveled at Ulrich and Resser's (1933) taxonomic treatment of the saukiids, including criticisms that types for new taxa were based on specimens from multiple localities (e.g. Raasch, 1951); that many of their papers lack photographs for new species, have poor descriptions of taxa, or that they divided taxa too finely, etc (e.g. Sundberg, 2007); or, that many of their genera lack taxabases with which to distinguish them from other genera (e.g. discussion of *Prosaukia* in Ludvigsen and Westrop, 1983). However, in the preferred phylogenetic hypothesis presented herein (Figure 9.2), all of the saukiid genera that they erected hold up and are resolved. Indeed, these genera hold up across multiple datasets, and even with the rather severe polarity swings enforced by inclusion of ptychaspidid taxa.

However, the less-derived members of the saukiid clade (as revealed by these analyses) have relatively simple morphology, and thus, very few potential synapomorphies with which to distinguish them from the dikelocephaliids. Putative synapomorphies that define members of the Saukiidae and genera contained therein are mapped onto a simplified tree presented in Text-figure 1. Many of the character state changes represent parallelisms or reversals, and are not satisfactory as synapomorphies used to define genera. A monophyletic Saukiidae is defined by the following unambiguous changes: (5), a emarginated or w-shaped occipital furrow; (28) an anterior border that is not strongly upsloping; and (53), a marked decrease in the length of the preglabellar field relative to the Dikelocephaliidae.

Saukiella is defined by a transition from a true preglabellar field to a very short preglabellar field defined by a combined anterior border furrow and preglabellar furrow (see discussion in systematics section under *Saukiella*). *Prosaukia* is distinguished from *Saukiella* based on the palpebral midlength moving anterior of the glabellar midlength.

An important transition occurs above the stem to (*Prosaukia* + *Saukiella*); the loss of the preglabellar field is a synapomorphy that defines a taxonomic grouping that lies in a more derived position relative to the (*Prosaukia* + *Saukiella*) stem, and includes all remaining saukiids. This synapomorphy is interpreted to separates all less-derived members of the Saukiidae which possess a preglabellar field from the more derived members that have lost this feature, and thus defines a higher level taxonomic unit. We tentatively erect a subfamily-level Saukiinae, n. subfam. to include all Saukiidae genera that lack a preglabellar field, including: *Calvinella*, *Danzhaisaukia*, *Eosaukia*, *Linguisaukia*, *Lophosaukia*, *Mictosaukia*, *Saukia*, *Sinosaukia*, and *Tellerina* (see discussion in systematics section). The members of the Saukiidae that possess a preglabellar field are transferred into the subfamily Prosaukiinae n. subfam. Members of the Saukiidae transferred to this subfamily include: Anderssonella, Hoytaspis, Lichengia, Pacootasaukia, Prosaukia, and Saukiella. See discussion in systematics section.

The group comprising *Saukia* and *Mictosaukia* is defined by the possession of 4 axial rings (parallelism), while *Mictosaukia* is united by the following unambiguous synapomorphies: a strongly C-shaped transition from the lateral to the posterior librigenal furrow, and loss of a furrow on the genal spine.

The genus *Calvinella* is defined by (16) possession of an axial occipital spine (parallelism), and (45) emargination of the posterior pygidial margin (a character not shared by all members of the genus, and which is itself, a reversal). *Calvinella* is thus, a genus supported by only very tenuous synapomorphies.

Tellerina is supported by a number of synapomorphies, however, they are all parallelisms. These include: ridge ornamentation of the glabella (parallelism), a greatly reduced or absent S3 furrow (parallelism), slight elongation of cranidial frontal area, the length to width ratio of the pygidium decreases, and the length to width ratio of the glabella increases.

Synapomorphies that mark the transition to Gondwanan taxa (*Lophosaukia, Linguisaukia, Eosaukia, Danzhaisaukia*, marked on Text-figure 1 as Gondwana) include: non-confluent lateral and posterior librigenal furrows (reverses in some taxa), a decrease in the number of thoracic segments in the holaspid phase from 12 in Laurentian taxa to 11 in Gondwanan taxa, decrease in the width of the lateral librigenal border. In general there is also an extreme decrease in the length to width ratio of Gondwanan saukiids.

Measures of Stratigraphic Consistency.

Inclusion of stratigraphic data within cladistic analyses is termed stratophylogeny (Fisher, 1994), and is a technique that has provoked considerable controversy. Opponents of this approach argue that time is not an intrinsic property of organisms, and must therefore not be intermingled with biological or morphological data; that sampling error and incompleteness of the fossil record precludes stratigraphic information from being useful in cladistic analyses (Adrain and Westrop, 2001); or that unlike morphology, stratigraphic patterns are not the result of phylogeny (Sumrall and Brochu, 2003). Proponents argue that increased phylogenetic resolution results from inclusion of stratigraphic data, and that fewer trees are recovered leading to consensus trees with greater resolution (Fisher, 1994; Bodenbender and Fisher, 2003). This latter approach is not advocated here; no stratigraphic data was coded for direct inclusion in analyses. Rather, the composite section computed by CONOP9 is used as an independent assessment of phylogenetic hypotheses recovered by allowing direct comparison of cladograms with the CONOP computed global composite section.

Previous studies have suggested that the Saukia Zone of Laurentia is approximately coeval with, or encompasses the 'saukiid' zones of other paleogeographic continents (e.g. Ludvigsen and Westrop, 1985). For example, the *Sinosaukia impages* and *'Mictosaukia' perplexa* zones of Australia have been considered correlative with the middle and upper *Saukia* Zones of Laurentia respectively (Shergold 1980; Shergold 1990; Shergold 1991). Shergold (1980) made this correlation based on the global maximum dispersal of parabolinoidid trilobites, a tentative correlation based on similar evolution of the frontal (preglabellar) areas of pterocephaliids and *Haniwoides*, and on the occurrence of an unidentified species of *Prosaukia* in rocks from *Hapsidocare lilyensis* (Ivarian, according to Shergold 2007) subzone of the Burke River Structural Belt in Queensland interpreted as correlative with the *Ellipsocephaloide*s - *Idahoia* (upper Sunwaptan) Zone of Laurentia in which the first prosaukiids appear (see Longacre 1970).

Lee and Choi (2011) correlate their *Eosaukia* fauna with the Laurentian interval below the *Missisquoia typicalis* Subzone, including the lower Ibexian *Missisquoia depressa* Subzone and the upper part of the *Saukia* Zone based on the abundance of saukiid trilobites, and the correlation of the *Mictosaukia orientalis* Subzone of North China (which is itself correlative with the *Eosaukia* fauna of South Korea) with the *Missisquoia depressa* Subzone of Laurentia based on the occurrence of *Tangshanaspis* (Lee and Choi 2011, and references therein).

The order of appearance suggested by cladistic hypotheses and biostratigraphic sequence data are similar in some ways. Biostratigraphic data record the first and last appearance datums for a species in a sequence or many sequences of rock. However, the FAD (First Appearance Datum) and LAD (Last Appearance Datum) represent only the first and last appearances of a taxon in the rock record and are unlikely to represent its true first or last occurrence due to patchiness of the fossil record, preservation biases, uneven sampling, and systematic misattributions. Thus, species appear in the rock record, have a finite range through time, and then disappear from the rock record. The global FAD is assumed to represent a moment in time following the evolution of a taxon, and the LAD is assumed to represent a moment in time that precedes the extinction of a taxon. However, in reality, there is almost inevitably an interval separating the true first appearance of any taxon from its FAD, or its LAD from its extinction. Thus, the stratigraphic range of a taxon, when compared with ranges of other closely related taxa, can be thought of as representing the order of evolution of the fossil taxa contained within a sequence of multiple sequences or rocks.

Cladistics seeks to discover the historical relationships among a group of organisms by looking for the acquisition of shared, derived character states, called synapomorphies, and by subsequently ranking taxa according to how the set of synapomorphies is shared by members of the group. Cladistics is a method by which phylogenetic trees are constructed; these trees represent a branching pattern, based on synapomorphies, that represents our best understanding of the evolutionary history of the included taxa given the available evidence. Phylogenies then represent the branching order, or the order of evolution of taxa as they evolve and radiate from their last common ancestor (represented by the nodes on a tree). More correctly, phylogenies represent the polarity and change of the states of a set of characters that each included taxon is coded for. However, this group of character states represents the morphological attributes of the particular taxon for which it is coded, and thus, is a unique numerical string representing a particular taxon. The set of character states, when polarized by an outgroup taxon, thus contains within it information on the synapomorphies that will allow a particular taxon to be grouped with its closest relatives based on possession of these synapomorphies. The branching pattern of the most parsimonious (shortest) phylogenetic tree that emerges after cladistic analysis is the preferred hypothesis. Thus phylogeny seeks to represents the order of evolutionary appearance of taxa.

Both biostratigraphic and phylogenetic methods (when applied to fossil data), then, use the same basic data (taxa), to do similar things. Biostratigraphy uses ordinal taxon datums, based on first and last occurrences, co-occurrences, and repeating sequence of taxa to tell relative time in geological successions. Phylogeny uses fossils drawn from rock successions, and coded for the specific characters that they contain to rank the taxa in order of evolutionary appearance. Both methods suffer from potential sampling problems. Sedimentary facies shift through time depending on global water depth, ocean sediments are recycled, uplifted, and eroded, sedimentary rocks are buried, heated, and deformed, and the further you go backward in time, in general, the less sedimentary rock is available from which to sample for fossils. Cladistic analyses show only branching patterns, but homoplasies or convergence can confound the signal contained within a phylogeny.

However, the rocks from which the taxa are collected themselves contain an estimate of the evolution of taxa - the local first and last appearance of the taxa within the section from which they are collected. This is the only actual, physical evidence available with which to test phylogenies. When this occurrence data is composited globally, incorporating all observed local ranges, it has the potential to yield a method of testing phylogenies that is powerful in terms of its resolution.

Results of Stratigraphic Consistency.**—**When sections from Laurentia only (n=26; Canada, continental United States, and Mexico) are analyzed using CONOP, a very detailed composite section results with saukiid ranges that fit well with past workers' various definitions of the *Saukia* Zone of Laurentia (Winston and Nicholls, 1967; Longacre 1970; Stitt, 1971, 1977; Taylor and Halley, 1974; Miller et al., 1982) (see Figure 12). Both pterocephaliid and ptychaspidid taxa lie below the first appearance of saukiid taxa, with first saukiid taxon, the genus *Prosaukia*, appearing lowest in the composite section, followed in ascending order by *Briscoia* (a dikelocephaliid), *Saukiella*, *Saukia*, *Mictosaukia*, and finally *Calvinella* (several Laurentian genera, *Tellerina*, for example are not represented in Figure 12 because their stratigraphic ranges are not well known, or because they are not included in published range charts). A comparison of the CONOP composite section in Figure 12 with the preferred cladogram in Figure 9.2 reveals a similar pattern of taxon appearance. In this cladogram, the dikelocephaliids branch off below the first appearance of the saukiids, followed progressively by a clade comprising *Prosaukia* + *Saukiella*, a clade comprising *Saukia* + *Mictosaukia*, and in the most derived position for Laurentian saukiids, *Calvinella* (see Figure 12). Only one dikelocephaliid taxon, *Briscoia llanoensis*, occurs in more than two sections in the global composite, and its placement on the stratigraphic composite lies above that of *Prosaukia*. Such a pattern of cladogenesis, when compared with the order of stratigraphic first occurrence implies that that either: 1) the dikelocephaliids may have a long ghost lineage; 2) not enough sections currently are entered in the CONOP database for coexistence data to recover the correct composite placement for the dikelocephaliids;

or 3) our preferred cladistic hypothesis is wrong. Because there is a dearth of published range charts incorporating dikelocephaliids, these hypotheses cannot currently be explored.

Unfortunately, confidence intervals in our analyses are rather poorly constrained. This is because in taxa with relatively few occurrences, the position of the first and last occurrence within the computed composite section is likely to vary considerably within the set of equally good solutions, and may vary from run to run (Sadler and Cooper, 2003; Sadler, 2014 personal communication). However, CONOP minimizes the range extension needed to make all of the included local sections fit within a single computed composite section, with the best fit composite requiring the least amount of range extension (Wang et al., 2014). Thus, the computed composite, and the individual ranges of taxa in this composite can be thought of as estimates of the true ranges of included taxa, given the available data, and with almost certainly some range extension. However, there is precedence for using FAD and LAD datums to quantify time intervals - this is done routinely (albeit with great care); the base of the Cambrian is defined as the FAD of the trace fossil *Tricophycus pedum*, the guide event for the base of the Ordovician is the FAD of the conodont *Iapetognathus fluctivagus* - indeed, the geological time scale is built upon such FAD and LAD events of taxa (Peng et al., 2012). Such stratigraphic controls are now being used to constrain cladistic hypotheses, and to estimate taxon longevities (e.g. Hopkins 2012; Webster and Sadler, NSF proposal and final report).

When a global composite section is built incorporating all sections and taxa from Laurentia and elsewhere (Figure 13; 54 local sections, 1115 taxa), the resulting composite section reveals a pattern that is inconsistent with the preferred cladogram (Figure 9.2). For example, the genera *Eosaukia*, *Linguisaukia*, *Lophosaukia*, *Taebeksaukia*, and *Mictosaukia* are all in the upper, relatively derived portion of the preferred cladistic hypothesis (Figure 9.2); in the composite section, the ranges of these taxa all lay below *Prosaukia misa*, the stratigraphically lowest taxon recovered in the composite section in which only Laurentian taxa are included. The composite section in Figure 13 more strongly supports the Ptychaspididae outgroup cladogram in Figure 6.2 (compare Fig. 6.2 with Figure 13). This likely results from a lack of sections that include taxa known from both Laurentia and elsewhere. In order to distinguish dissimilarity of faunas due to provinciality from dissimilarity due to age, it is necessary to examine two contrasting objective functions (Sadler and Sabado 2007.) The "LEVEL" objective function effectively treats faunal dissimilarity as provinciality, whereas the "SEQUEL" objective function operates as if dissimilarity is attributable to difference in age; i.e. LEVEL interleaves dissimilar faunal successions and SEQUEL separates them.

Paleobiogeography.

Cladistic methods have been widely applied to the study of fossil organisms and their distribution both spatially and temporally, and across widely varied clades (see summary discussion in Lieberman, 2003). Recent approaches to paleobiogeography have increasingly relied on pre-existing phylogenetic hypotheses in conjunction with detailed information on the temporal and spatial distribution of included taxa to infer patterns of change in taxonomic distribution through time. Perhaps the greatest strength of cladistic paleobiogeographic approaches lies in their ability to identify detailed changes in the historical geographic and stratigraphic ranges of taxa. Because the taxonomic histories of taxa (geographic, temporal, and environmental distribution) are integral to their phylogeny, cladistic hypotheses can be used to inform about a variety of paleogeographic issues.

While cladistic paleobiogeographic methods have been used with increasing frequency in recent years, they have only rarely been applied to Cambrian organisms (e.g. Lieberman, 1998). Trilobita are an obvious candidate for such an integrative approach, because they are morphologically distinct and geographically widespread, and are much used in Cambrian biostratigraphy. One relatively new cladistic biogeographic method that has been applied to trilobites is a modified version of Brooks Parsimony Analysis (mBPA) (see Lieberman and Eldredge, 1996; Lieberman, 2000, 2003). This technique characterizes patterns of vicariance and geodispersal using a multi-step process that begins by mapping paleogeographic occurrences of each terminal taxon onto a given cladogram. Standard Fitch optimization is then used to recover the ancestral area-state of each node on the tree for each character, given the area-state(s) of each terminal taxon on the tree topology on which they occur. In Fitch parsimony optimizations, as applied to biogeography, nodes represent characters, each of which may have any of the area-states in which the terminal taxa occur. The result Fitch optimization is a tree onto which the terminal taxa have been mapped as a series of numbers indicating their presence in the area-states in which they occur, and nodes (common ancestors of terminal taxa) optimized for their ancestral area-states given the paleogeographic distribution of the terminal taxa (Fitch, 1971; Lieberman and Eldregde, 1996; Wiley and Lieberman, 2011). The Fitch optimization is then translated into several matrices where the “taxa” are regions in which the biological species included in the cladistic analysis occur, and the “characters” represent nodes on the cladogram that are coded for presence or absence of taxa from discrete area-states or regions (Lieberman, 2000). These matrices were then coded and run through TNT. The resulting cladograms represent the 'relatedness' of the paleogeographic areas on which the original taxa occur. Continent- or global-scale expansion or contraction in the paleogeographic ranges of taxa through time inferred by this method are interpreted to represent episodes of barriers to gene flow falling (geodispersal, *sensu* Lieberman and Eldredge, 1996), or emplacement of such barriers leading to the splitting of such ranges and speciation (vicariance), respectively. Through a comparison of the topologies of the paleobiological and mBPA (area) cladograms recovered, it is theorized that patterns and timing of vicariance and dispersal events can be discerned (Brooks et al., 1981; Brooks, 1985; Lieberman and Eldredge, 1996; Lieberman, 2000).

Cladistic analyses of the Saukiidae have revealed two main phylogenetic hypotheses: saukiid cladogenesis occurring in Laurentia with saukiids and dikelocephaliids derived from the same common ancestor (Figure 4.2); or saukiid cladogenesis occurring in Gondwana with the eosaukiids contributing the ancestral stock (Figure 6.2). The CONOP computed global composite section that incorporates all local FAD and LAD of taxa that occur in two sections or more strongly suggest that saukiid cladogenesis may have occurred in Gondwana, possibly in Australia or North China (see Figure 13).

However, if the assertions made by proponents of cladistic paleobiogeographic methods are true, and vicariance is maintained by wide ocean basins, and especially considering the preference of saukiids for shallow shelfal environments, then it might be expected that the more preferable phylogeny would be the one which minimizes the number of episodes of transoceanic migration. This hypothesis was tested using cladistic paleobiogeography methods, including both Fitch optimizations alone in order to look at the number and direction of migrations, and with mBPA to characterize the relatedness of the regions in which the saukiids occur. Trees produced by an mBPA of a vicariance matrix, where paleobiogeographic areas have a sister relationship are interpreted as having more recently been separated from each other by barrier emplacement, (i.e. – they are closely paleobiogeographically related. Branches that are more distal from one another are interpreted as having less paleobiogeographic relatedness, and thus, were separated from each other farther back in time (Lieberman, 2003).

Results of Fitch Parsimony Optimization.—Phases one and two of the standard Fitch parsimony optimization (Fitch 1971; Wiley and Lieberman, 2011) was performed on the cladograms represented in Figs. 4.2 and 6.2 in order to ascertain which of the two outgroup hypotheses (pterocephaliid versus ptychaspidid) minimizes the total number of migrations necessary to explain the actual distribution of fossils included in each. The results of these optimizations are given in Figures 14 and 15.

The first Fitch optimization (Figure 14) was computed using the cladogram and distribution of terminal taxa in Figure 4.2 (pterocephaliid outgroup, qualitative and gap-weighted characters). This optimization reveals that at minimum, 11 migration events are necessary to explain the paleogeographic distribution of the fossil species included in the pterocephaliid outgroup cladogram (see Figure 14). Of these eleven migration events, three involve dispersal to two or more regions outside of the home range of the ancestral species; such large-scale range expansions are 'geodispersal' events, *sensu* Lieberman and Eldredge 1996. However, if a comparison is made between the migrations inferred from this optimization and our understanding of the distribution of paleocontinents during late Cambrian time, the dispersal events labeled D1 in Figure 14 represents movement from S. China to Oman and to North China, events that could be explained by dispersal or progressive range expansion along shallow water corridors between these areas all lying near or on core Gondwanan terranes. Node D2 in Figure 14 should not represent an episode of true transoceanic migration because the last common ancestor of *Diemanosaukia miserabilis*, according to this optimization, was present in South China. *Dimeanosaukia miserabilis* is found in Australia and Antarctica, both which were part of core Gondwana during late Cambrian time. Additionally, most paleogeographic reconstructions place South China slightly outboard from core Gondwana and just to the west of Australia (Scotese et al., 1986; McKerrow et al., 1992; Cocks and Torsvik, 2002; Scotese, 2004). Thus, no large, deep ocean basin separated these regions during the late Cambrian and this distribution could be explained by gradual range expansion along shallow subtidal or shelfal gradients. The inferred range expansion event labeled D3 in

Figure 14 represents an expansion in the range of the ancestral taxon of *Eosaukia walcotti* to also include Australia; as the ancestral taxon of *E. walcotti* was also inferred to be present in North and South China, and Arabia, this range expansion also need not require trans-oceanic migration. For the same reason, the event labeled D4 in Figure 14 necessitates only one true trans-oceanic dispersal, that from North or South China to Kazakhstan.

Considering the distributions at the ancestral nodes discussed above in conjunction with the distributions of the terminal taxa, we interpret the Fitch optimization of this cladogram to necessitate only five episodes of true trans-ocean basin dispersal. These episodes of dispersal generally proceed from Laurentia outward (no dispersal events directed toward Laurentia), and include a major radiation from Laurentia to South China that results in the gradual spread of saukiids across Gondwana from S. China to Australia and Antarctica, on to Oman and North China, and eventually on to cross the Iapetus toward Kazakhstan. The earlier dispersals of *Pacootasaukia* and *Anderssonella* to Australia, and of *Mictosaukia* to North China apparently allowed the development of endemic faunas in these regions that did not participate in the later radiation event that populated core and outbound regions of Gondwana with saukiids.

The second Fitch optimization (Figure 15) was computed using the distribution of terminal taxa on the tree topology given in Figure 6.2 (ptychaspidid outgroup, qualitative and gap-weighted characters). This second optimization attempted to determine which of the two main cladistic hypotheses necessitates the least number of transoceanic migrations, and may therefore represent the more parsimonious solution regarding migrations. Results of this second analysis imply a minimum of 14 migration (see Figure 15). Of these 14 events, D1 necessitates movement from North to South China, and D3 and D4 in Figure 15 are the same as in Figure 14, involving the movement of ancestral taxa to areas in close connection during the late Cambrian; thus none of these are interpreted as representing true trans-oceanic migrations. Additionally, two of the dispersals at D2 in Figure 15 represent similar dispersals necessitating only movement along shallow shelfal environments; however at this node, there is a dispersal toward Kazakhstan.

Considering these distributions, we interpret the Fitch optimization of this cladogram to necessitate seven separate episodes of true trans-oceanic migration. These episodes of dispersal generally proceed from North China to Kazakhstan, on to South China, Australia and Arabia, followed by a radiation to Laurentia which also had later taxonomic interchange with Gondwana. In this scenario, an endemic North China saukiid taxon gradually colonizes Gondwana and then radiates to Laurentia. There are no movements from Laurentia to North China, but three separate dispersal outward from Laurentia, one resulting in the ancestral stock of *Mictosaukia* moving to North China and (subsequently expanding its range to include Laurentia), a second involving the ancestor of *Pacootasaukia* and *Lichengia* migrating to Australia, and a third involving the migration of *Hamashania* to North China. In this scenario, migrations leaving Laurentia are more frequent, and involve movement to (and from) the eastern parts of Gondwana, while there is only one migration from South China.

Given the results above, we prefer the scenario that minimizes the number of trans-oceanic migrations, or the Fitch optimization based on the Pterocephaliidae outgroup cladogram (Figure 14). Further paleobiogeographic analyses were performed using mBPA on the preferred cladogram in Figure 4.2. The results of these are given below.

A number of gyre-like currents probably operated in both the northern equatorial Panthalassic Ocean and southern equatorial Iapteus Oceans during late Cambrian time (Wilde, 1991; Brock et al., 2000). Presuming a similar global windfield distribution on the Cambrian as on the modern Earth, strong eastward (westerly) currents would dominate in the northern hemisphere Panthalassic Ocean around 60° because of a presumed lack of landmasses at this latitude in much the same way as the strong westerly Antarctic Circumpolar current in the modern Southern Ocean. In the southern hemisphere of the late Cambrian, such westerly currents would be inhibited by Gondwanan terranes such as South America and Africa, and thus would not be able to form. However, the hypothesized northern gyres could have facilitated movement of trilobite larvae if they managed to become entrained in the flow, especially the presumably stronger northern Panthalassic gyres.

Considering the preferred Fitch optimization presented in Figure 14, the distribution of the included taxa and the migration polarities inferred from the cladogram on which it is based, the dispersals can provide additional details on oceanographic surface currents during the late Cambrian. For example, the distribution of the dikelocephaliids requires at least one episode of transoceanic dispersal to explain

Hamashania in North China. Dikelocephaliids in Laurentia are widespread, but are most common in western Laurentia. The most commonly reconstructed paleogeographic position for North China during the late Cambrian is to the North of Australia, and so the most parsimonious way to explain the distribution of *Hamashania* would be to invoke a westward dispersal toward the eastern coastal regions of Gondwana, where the genus could spread to North China and also to Australia where it is also found (Shergold, 2007).

Lichengia simplex and *Pacootasaukia simplex* are found in central Australia in the Pacoota Sandstone of the Amadeus Basin in the Northern Territory. The dispersal event between the ancestral stock of *Lichengia* and the dikelocephaliids hypothesized in Figures 9.2 and 14, is a dispersal from Laurentia to Australia. Because *Lichengia* is found both in Australia and Indochina (Taratao Island, Thailand) and *Pacootasaukia* in Australia, either an eastern or western dispersal seems equally likely. However, the genus *Lichengia* is found only in Australia and peninsular Thailand, and not other coastal areas of Gondwana or North or South China. Such a shared distribution argues for closer geographic ties between Australia and Indochina. Because *Lichengia* and *Pacootasaukia* are found only in Australia and Thailand and not China (*L. onigawara* has been reassigned to *Prosaukia brizo*), it seems more likely such a limited distribution could be explained by a westward dispersal from Laurentia.

Similarly, *Anderssonella* is found only in Australia and the North China, and this the dispersal necessitated by the cladogram in Figure 9.2 appears to have been westward from Laurentia because of the lack of this taxon in South China or other coastal areas of Gondwana.

The dispersal necessary to explain the distribution of *Saukia* and *Mictosaukia* appears more complex; *Mictosaukia* is also hypothesized to have radiated outward from Laurentia according to the cladogram in Figure 9.2 (see also, Figure 14). The genus appears in Australia, North China, South China, Afghanistan, Turkey, and Oman..

The next dispersal on the Fitch optimized tree in Figure 14 is polarized from Laurentia toward South China. This dispersal results in a hypothesized radiation in South China followed by a gradual transition toward various terranes on Gondwana. Because many of the taxa in a derived position relative to the inferred dispersal on the tree in Figure 14 occur only or predominantly in South China, we interpret the dispersal event responsible for this distribution as leaving Laurentia and moving eastward.

These hypothesized dispersal events suggest that the dominant direction of larval saukiid trilobite dispersal may have been westward from the shallow seas surrounding Laurentia across the Panthalassic toward the eastern margins of Australia, Antarctica, and North China. The tree topology of our preferred cladogram (Figure 9.2), when optimized for the paleogeographic distribution of terminal taxa suggests that dispersal polarity from Laurentia to Australia and North China was dominant and happened repeatedly, while only a single dispersal event appears to be more easily explained by invoking an eastward dispersal. This suggests that the currents may have been stronger on the western margins of Laurentia than those on the eastern margins, leading to most dispersals from Laurentia toward Gondwana following a westward trajectory.

***modified Brooks Parsimony Analysis (mBPA).*—**While Brooks Parsimony Analysis in various modifications has been employed with evident success in tracking evolutionary host-parasite relationships (e.g. - Brooks and McLennan, 2003; Domínguez-Domínguez et al., 2006), and in the assessing the relationship of geographic regions inhabited by terrestrial organisms (e.g. - Bouchard et al., 2005; Sigrist and Carvalho, 2009), its application to these problems is not uncontroversial (Ebach and Humpheries, 2002; Siddall and Perkins, 2003; Sidall, 2005). For example, one application of modified Brooks Parsimony to Cambrian trilobites has yielded the surprising implication that the geographic distribution of certain early Cambrian trilobites requires that the clade first evolved in the late Neoproterozoic, some 580 million years ago (Lieberman 2002). This conclusion is based on the reasoning that common ancestry implies an original shared *contiguous* distribution (i.e. origin on a single landmass that later fragmented). Indeed, invoking oceans as barriers to gene flow in taxa that are fully aquatic and marine may be unrealistic given recent studies on island biogeography.

Sessile cnidarians, mollusks, and (mostly) mobile arthropods in the marine realm; and vagile mammals, reptiles, amphibians (perhaps most dramatically), insects, spiders, birds, and sessile plants of the terrestrial realm have all managed to colonize most if not all of the available ecological niches, both subaerially and subaquaeously on the widely dispersed islands of the Pacific Ocean. Indeed, even the seemingly impenetrable barriers to extremely specialized environments have been overcome by dispersal; non-marine shrimp of the genus *Paratya*, for example, have managed to overcome the saline environments that surround their freshwater fluvial habitats and to disperse broadly throughout islands of the Pacific (Page et al.,2005). Dispersal in this case is hypothesized to occur via periodic flushing of young larvae, or by larvae of more seawater-tolerant species of *Paratypa*, by seasonal floods into the open ocean where this water may remain buoyant for some time facilitating short 'island-hopping' dispersals (Page et al.,2005).

Indeed, barriers to dispersal are even more extreme than the example of paratypid shrimp in the case of spiders. Also found broadly throughout the Pacific region, spiders do not have a larval stage and are not aquatic, yet even they have managed to overcome the barrier presented by a deep, wide ocean basin (Gillespie, 2002).

Proponents of using mBPA for studies of trilobite distribution make the case that patterns of observed range expansion across multiple marine clades arise due to the elimination of barriers to marine taxa, perhaps due to relative sea-level rise or fall, to the collision of formerly separate tectonic plates, or to episodes of continental rifting (Lieberman and Eldredge, 1996; Lieberman, 2000; Lieberman 2003; Rode and Lieberman, 2005; Wiley and Lieberman, 2011). Lieberman and Eldredge (1996) and Lieberman (2003) point out that similar patterns in both vicariance and geodispersal trees may be indicative that the geological processes responsible for vicariance were cyclical (invoking sea-level change). Conversely, incongruous patterns in vicariance and geodispersal trees indicate unique geological events such as continental collisions (Lieberman, 2003).

Implicit in the vicariance paradigm is that ocean basins act as barriers to species movement - they separate the barriers cited by proponents of mBPA (continents, tectonic plates, and islands); thus, they must be accorded equal weight as biogeographic barriers to dispersal. However, as discussed previously, nearly all animals that inhabit the oceans have either a vagile adult form, a free-floating planktonic larval stage, or a pre-, or post-fertilization free-floating embryonic stage; hence, ocean basins (even deep, wide ones) must also be accorded the possibility of *facilitating* dispersal events, and a strong Gulf Stream-like current could facilitate many traditional dispersals leading to a false geodispersal signal. Thus, the assumptions made in interpreting both the vicariance and geodispersal mBPA area cladograms may lead to spurious interpretations of these trees in groups of marine organisms with vagile adult phases and/or planktonic larval phases.

Results of mBPA.—The vicariance analysis coded from the cladogram in Figure 4.2 (Pterocephaliidae outgroup, qualitative and gap-weighted character data) resulted in three most parsimonious trees of 122 steps, with a C.I. of 0.893 and a R.I. of 0.581. The strict consensus of this tree is Figure 16.1. The geo-dispersal analysis coded from the cladogram in Figure 4.2 resulted in a single most parsimonious tree of 118 steps, with a C.I. of 0.864 and a R.I. of 0.579. The tree is Figure 16.2.

The topology of the vicariance tree (Figure 16.1) indicates a sister relationship between (North and South China), (Kazakhstan and Australia), and (Oman, Laurentia, and Antarctica). This topology suggests that barriers to trilobite migration between Oman, Laurentia, and Antarctica) were removed more recently than those between (Kazakhstan and Australia) and (North and South China). These results suggest a closer relationship between the taxa of North and South China than either of these regions' taxa to Australia. This is surprising, considering most paelogeographic reconstructions place

North China to the north and east of Australia, while South China is placed slightly to the south and to the west of Australia (e.g. Scotese et al., 1986; McKerrow et al., 1992; Cocks and Torsvik, 2002; Scotese, 2004). If the more typical paleogeographic placement of North and South China is true, then it would follow that one of the Chinese terranes should be more closely related to Australia in terms of its trilobite biota than it is to the other Chinese terrane because the position of Australia would lie between them. The results of the mBPA in Figure 16.1, instead, support a placement with the two Chinese terranes more closely proximal to each other than either North or South China is with Australia. A similar position for the North and South Chinese terranes was proposed by McKenzie et al (2011), in which the position of the North China block was proposed to straddle India and Australia based on the provenance of populations of detrital zircons and endemic trilobite populations. Such a position of these two Chinese terranes is supported by the vicariance tree in Figure 16.1.

The purported relatedness between Kazakhstan and Australia is perhaps expected, given their reconstructed paleogeographic positions and reconstructed surface paleocurrent directions in upper Cambrian time (Scotese et al., 1986; Wilde, 1991; McKerrow et al., 1992; Cocks and Torsvik, 2002; Scotese, 2004). The purported relationship between Arabian, Laurentian, and Antarctic faunas, however, is unexpected. Antarctica and Arabia are both components of core Gondwana, Arabia lies to the south and west of Australia, while Antarctica lies just south of the equator directly to the south of Australia. Thus, both would be expected to have a closer taxonomic affinity to Australia than to Laurentia. However, paleoceanographic surface current reconstructions suggest a strong westward surface current existed along the western margin of Laurentia. A direct, westward current would transport larval trilobites to the eastern margin of Antarctica, and these trilobites. This is suggested by the vicariance tree in Figure 16.1; however, no support for this hypothesis is currently exists within any of our cladistic hypotheses or paleobiogeographic data.

The geo-dispersal tree given in Figure 16.2 is more fully resolved than the vicariance tree, and indicates that barriers to species movement were removed more recently between Antarctica and (Kazakhstan and Australia) than they did between Laurentia and Arabia, and that barriers separating North and South China from all of these areas were removed even further back in time. While the area relationship between North and South China, and Arabia are consistent with paleogeographic reconstruction for these terranes, it is interesting to note that Laurentia is resolved in a position indicating that barriers to gene flow were removed further back in time (less derived position on the tree in Figure 16.2) than barriers between (North and South China) and Antarctica and Australia.

In light of these mBPA analyses, and the timing of the vicariance and dispersal events they resolve, it may be necessary to consider whether ocean basins, even very wide and deep ones, are barriers to dispersal, or whether episodes of dispersal occur routinely enough via ocean surface currents, for example, to significantly degrade any signal of 'geodispersal'. The minimum number of dispersals necessary to explain the distribution of upper Cambrian saukiid trilobites in our cladistic analyses is five; thus the hypothesis that few migration or dispersal events are responsible for the observed distribution of the Saukiidae is not supported. Five dispersal events in a data set that includes just fifty taxa suggests that one dispersal even occurs for every ten species originations in the Saukiidae and closely related taxa, or that trans-oceanic migrations were not a trivial part of saukiid species' histories.

Perhaps most compelling from a dispersability standpoint, in the early ontogenetic stages of development, saukiids possessed an asaphoid protaspis. This particular type of larval stage attained a size of up to several mm in length in asaphoids, before going through a rather dramatic metamorphosis to the much more adult-like meraspis stage (Fortey, 2001). This peculiar asaphoid protaspis in Asaphida (the order to which the saukiids belong) has been interpreted as an adaptation that allowed asaphiids to have a prolonged planktonic larval stage (Speyer and Chatterton, 1990), resulting in increased dispersibility in the saukiid trilobites, and thus, dramatically increased likelihood of transoceanic dispersal events.

SYSTEMATIC PALEONTOLOGY

Prior to this study, there were over 290 named species and subspecies of saukiid trilobites assigned to the family Saukiidae Ulrich and Resser 1930 globally, many of which are based on fragmentary or highly incomplete material. Indeed, in Ulrich and Resser (1933) alone, there are 102 named species, nearly all new species. These species are distributed throughout thirty genera (Jell and Adrain, 2003). Of these genera, *Caznaia* (Shergold, 1975) and *Lophoholcus* (Öpik, 1967) are most likely ptychaspidids; *Anderssonella* (Kobayashi, 1936) and *Galerosaukia* (Shergold, 1975) possess characters consistent with the Pterocephaliidae, but the position of *Anderssonella beauchampi* in cladistic analyses herein lies close to the ptychaspidids when the outgroup includes both pterocephaliids and ptychaspidids, but is more closely allied with *Prosaukia* when analyzed with either outgroup individually. This suggests that *A. beauchampi* may have characters derived by convergence. *Hamashania* has a more dikelocephaliid cranidial morphology with a long preglabellar field and upturned anterior border - although the sagittally ovate pygidial morphology of this species differs distinctly from members of both the Saukiidae and Dikelocephaliidae.

Liquania was established based on a single, damaged cranidium from Shaanxi, North China. It is also distinctly saukiid in appearance, with a mildly w-shaped SO furrow, and an S1 furrow that is continuous across the glabella (see plate 64, figure 9 of Zhou et al. 1982). However, it is not included in herein due to the extreme fragmentary nature of the specimen - the occipital node is damaged, the fixigena, anterior and posterior limbs and most of the anterior margin are not preserved; thus its taxonomic position cannot be determined at this time. *Mareda* (Kobayashi, 1942a) is an invalid junior homonym of the lepidopteran (moth) genus *Mareda* Walker, 1855 and has subsequently been reassigned to the genus *Saluderella* Özdikmen, 2006; the genus *Mareda* was erected based on pygidia only, but Sohn and Choi (2005) note the similarity of these pygidia to pygidia of *Hamashania*. These authors stop short of assigning *Mareda* to the family Dikelocephaliidae, instead preferring to leave it unassigned (Sohn and Choi, 2005).

Metacalvinella Li and Yin, 1973 is distinctly saukiid. Lee and Cho (2011) referred *Metacalvinella latilimbata* (not morphologically similar or related to *Eosaukia latilimbata* Lu 1956) to *Eosaukia rectangula* (see Lee and Choi, 2011), and this specimen will serve as the neotype *pro tem* for this species until it is hoped the type material is found. *Mictosaukioidia* (Lu and Zhou, 1990) has been referred to *Eosaukia* by Lee and Choi (2011); however, unfortunately, after the death of Lu Yanhao, the saukiid material from the 1990 publication has subsequently been misplaced; no material currently exists, type or otherwise, that the present authors are aware of available for study. It is hoped that the original material can be relocated, or that new material from the localities in Lu and Zhou (1990) can be collected, and neotypes designated.

Paracalvinella Zhou and Zheng, 1980 has a parallel sided glabella, extremely large palpebral lobes, a palpebral furrow that is confluent with at the axial furrow at the anterior of the lobe, transglabellar S1 and S2 furrows, pustulated crandium, an occipital spine, and a preglabellar field (although in their original diagnosis, Zhou and Zheng indicate that it does not; see pl. 2, fig. 13 of Zhou and Zheng, 1980). These are all characters that are more in line with an attribution to *Prosaukia*. However, because the genus is apparently known from a single sclerite only (cranidium), it cannot be included in our analysis due to the extreme incomplete nature of the genus.

Pileaspis Sun, 1990 is also saukiid in appearance. It has a w-shaped occipital furrow, transverse, connected S1 furrow, posteriorly-directed and interrupted S2 furrows, palpebral lobe midpoint located anterior of the glabellar midpoint and quite far from the axial furrow (wide fixigenae). It also appears to have a true preglabellar field. On closer inspection of Sun's (1990) plates, the convex posterior part of the anterior cranidial border may be defined by a very shallow and wide anterior border furrow, and with a strongly impressed preglabellar furrow superposed on it; thus this genus may have a combined furrow and not a true preglabellar field (this species was not examined in person for this study). *Pseudocalvinella* (Qiu 1984) was synonymized with *Mictosaukia* Shergold 1975 by Lee and Choi (2011). phylogenetically, *Pseudocalvinella spinosa* is indistinguishable from *Mictosaukia striata*, which has taxonomic priority.

The type species of *Stigmaspis* Nelson, 1951, *Stigmaspis hudsonensis* is distinctly saukiid, but material is effaced and insufficiently complete. The cranidium of *S. hudsonensis* distinctly tapers anteriorly, has no preglabellar field, anterolateral abaxial portions of the anterior border furrow that are angled anterolaterally toward the cranidial corners, and palpebral lobes located anterior to the glabellar sagittal midpoint. The associated free cheek in Nelson's (1951) material is also poorly-preserved, and the arrangement of lateral and posterior librigenal furrows cannot be assessed. Nelson (1951) gives occurrence data for this species as co-occurring with *Prosaukia*; Berg (1953) indicates it occurs within the same 2.5" member with *Ptychaspis miniscaensis* and *Prosaukia misa*. This co-occurrence implies that by the evolution of the earliest definitive saukiid trilobite, that the group leading to the Saukiidae had already diverged into two main morphological groups, one with a preglabellar field, and one without. The morphological resemblance of *S. hudsonensis* to some members of the genus *Eosaukia* should be emphasized in this light, because the evolutionary trend of gradual reduction of the preglabellar field in Laurentian saukiids is well-correlated stratigraphically. This early saukiid could represent an early ancestor of the Gondwanan saukiid genera, or conversely, a Gondwanan *Eosaukia* that had managed to disperse to Laurentia. In either case, *S. hudsonensis* bears a striking morphological similarity to species of *Eosaukia*. However, due to the extreme rarity of this species, its highly incomplete nature, and to the effacement of the sclerites known, we cannot include this species in our analysis.

Thailandium Kobayashi, 1957 has a distinct, raised anterior border and a distinct preglabellar field. Shergold (1991) included this genus in Saukiidae, noting the subparallel-sided glabella, relatively wide palpebral area, small palpebral lobes, transglabellar preoccipital furrows, and preglabellar field, and noted that Kobayashi's type species, *T. sulum* could be considered a small-eyed *Prosaukia*. However, other morphological features of Kobayashi's material are problematic for this placement: the cranidial posterior limb has only the faint indication of a furrow, the associated free cheek of *T. solum* indicates that the eye is very small, and there is no visible posterior librigenal furrow present. Moreover, our review of *Prosaukia* indicates that *Prosaukia* has anteriorly-divergent anterior cranidial facial sutures. As suggested by Shergold, a thorough review of the Thai material is necessary in order to diagnose this genus. *Thailandium solum*, the type species, is provisionally included within Saukiidae herein because of the morphological departures outlined above, and in particular, in the characters of the librigenae. Shergold's (1991) material is saukiid in appearance, and may represent a Gondwanan species of *Prosaukia*.

Morphological characters and morphometric data was collected from specimens housed in the following collections: American Museum of Natural History, AMNH; Chicago Field Museum, PE; Museum of Comparative Zoology, Harvard University, HMCZ; New York State Museum, NYSM; Paleontological Research Institution, PRI; Royal Ontario Museum, ROM; Smithsonian Institution Museum of Natural History, USNM; University of Tasmania Geology Department, UTAS; University of Wisconsin, Madison Geology Museum, UWGM; University of Minnesota Geology Museum, UMPC; Weiss Earth Science Museum, University of Wisconsin-Fox Valley, WESM; and Yale Peabody Museum, YPM.

Family DIKELOCEPHALIIDAE Miller, 1889

Genus BRISCOIA Walcott 1924

BRISCOIA SEPTENTRIONALIS Kobayashi 1935

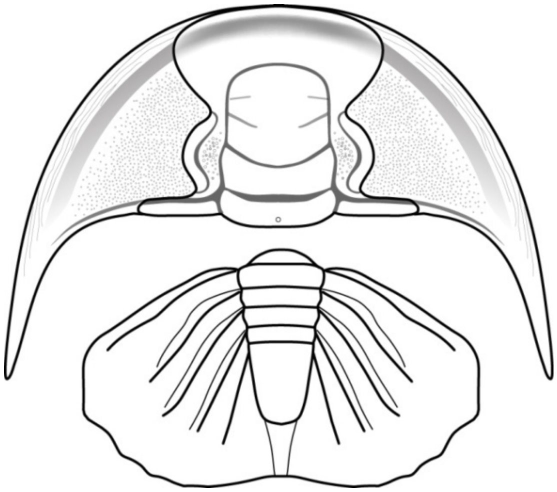
Text-Figure 2

Briscoia septentrionalis KOBAYASHI, 1935, p. 51, pl. 9, figs 10–17; PALMER, 1968, p. B59, pl. 15, figs. 1–5.

*Briscoia robust*a KOBAYASHI, 1935, p. 52, pl. 9, fig. 18.

Briscoia mertiei KOBAYASHI, 1935, p. 53, pl. 10, figs. 6, 7.

Discussion.—It is often very difficult to place trilobite occurrences in a general stratigraphic succession due to differences in stage, or biozone nomenclature. *Briscoia septentrionalis* when described by Palmer (1968), was given an occurrence in the lower member of the Jones Ridge Limestone, and falling within the "Trempealeauan-1 Fauna". Because of many problems of stratigraphic consistency, the Trempealeauan 'stage' has been superseded by the Sunwaptan Stage (Ludvigsen and Westrop, 1985), leading to potential problems with zonal correlation. For example, Palmer's (1968) "Trempealeauan-1 Fauna" contains the following taxa: "*Briscoia*" *elegans, B. septentrionalis, Chuangiella intermedia, Hungaia pacifica, Hungaia* sp., *Lauzonella*? *tripunctata*, *Pseudagnostus clarki*, *Pseudagnostus* sp., *Pseudosaukia* cf. *P. brevifrons*, *Rasettia* cf. R. *capax, Richardsonella nuchastria, Richardsonella* sp., *Richardsonella* sp. 1,



Text-figure 2. Reconstruction of *Briscoia septentrionalis.*

Richardsonella? sp. 2, *Richardsonella* sp. 4, *Tatonaspis alaskensis*, and *Tatonaspis*? sp. Because very few of these taxa are biostratigraphically useful, assigning the Jones Ridge material to a particular biostratigraphic zonal scheme is difficult. However, the *Rasettia magna* Subzone (lower part of the *Saukiella pyrene* Zone) of Stitt (1977) contains *Rasettia capax*, and so the material from Palmer's "Trempealeauan-1 Fauna is tentatively placed in the *Rasettia magna* subzone.

Occurrence.—East central Alaska, Jones Ridge Limestone, lower member ("Trempealeauan-1 Fauna" of Palmer, 1968).

Genus DIKELOCEPHALUS Owen 1852

Diagnosis.—Dikelocephalid trilobites with a single pair of posterolateral pygidial spines; pleural segments are equally divided or have expanded propleural bands.

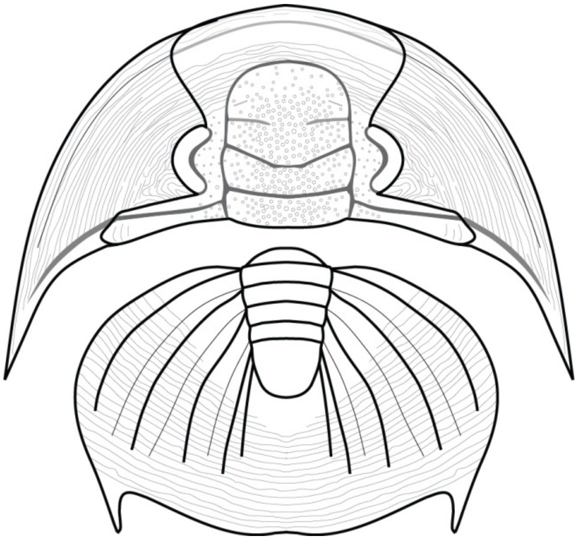
Type species.—Dikelocephalus minnesotensis Owen 1852, from the St. Lawrence Formation, Fairy Glen, Washington County, Minnesota.

DIKELOCEPHALUS MINNESOTENSIS Owen 1852

Text-Figure 3

Dikelocephalus minnesotensis OWEN, 1852, p. 574, pl. 1, figs. 1, 2, pl. 1a, figs. 3, 6; HUGHES, 1994, p. 53, figs. 46, 47, pls. 1–8, 10; figs. 14, 15, pl. 11; STITT AND STRAATMANN, 1997, fig. 8.21, 8.22; ADRAIN AND WESTROP, 2004, p. 10, pl. 1, figs. 1–26; see HUGHES (1994) for complete synonymy list.

Type material.—USNM 17863, lectotype; 447020, 447021, paralectotypes.



Text-figure 3. Reconstruction of *Dikelocephalus minnesotensis* based on information and specimens published in Hughes (1994).

Discussion.—Hughes (1994) noted that the emargination of the posterior pygidial margin probably represented an upward arch of the dorsal pygidial surface posterior to the axis rather than an actual inflection of the margin; thus, this character (emargination of the posterior of the pygidium) is coded as absent for this taxon. See Hughes (1994) for comprehensive synonymy, and an exhaustive treatment of this taxon.

Occurrence.—Southern Alberta, *Illaenurus* Zone, Mistaya Formation (limestone); southwestern Montana, *Illaenurus* Zone, Sage Member, Snowy Creek Formation (limestone); central Texas, *Saukiella norwalkensis* Subzone, *Saukia* Zone, San Saba Member, Wilberns Formation (limestone); south central Wisconsin, southeastern Minnesota, and northeastern Iowa, *Saukia* Zone, Reno Member and upper part of Mazomanie Formation (Tunnel City Group) (sandstone), and St. Lawrence Formation (fine sandstones and shales); south central Oklahoma, *Saukiella serotina* Subzone, *Saukia* Zone, Signal Mountain Formation (limestone); also recorded from Colorado (shale) and Nevada (limestone), stratigraphic details poorly known (Hughes, 1994).

DIKELOCEPHALUS FREEBURGENSIS Feniak 1948

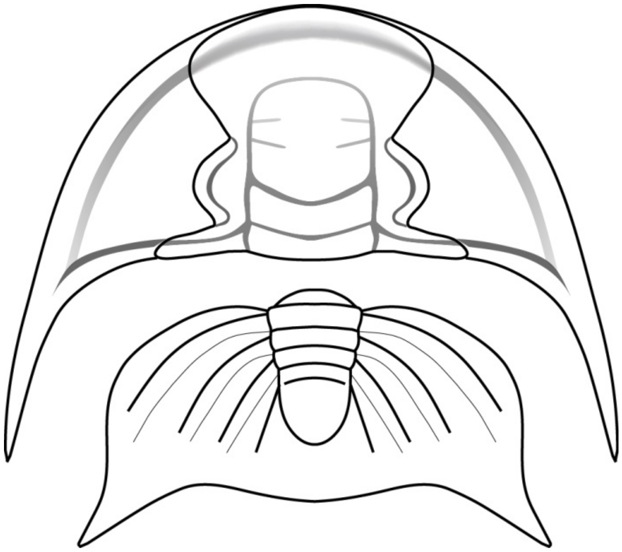
Text-Figure 4.

Dikelocephalus freeburgensis FENIAK *IN* BELL, FENIAK, AND KURTZ, 1952, p. 195, pl. 35, fig. 4, pl. 38, figs. 4a–e; HUGHES, 1994, pl. 9, figs. 1–6, 17–20.

Type material.—UMPC 6660e, holotype; UMPC 6660f, paratype.

Diagnosis.—A species of *Dikelocephalus* with distinct librigenal lateral furrows. Pygidium transversely rectangular (length to width ratio - approximately 0.51, n=1), with long pleural spines; distance from terminal piece posterior to posterior pygidial margin much less than in *D. minnesotensis*.

Discussion.—Hughes (1994) remarked on the dearth of specimens of *Dikelocephalus freeburgensis* with which to compare with *D. minnesotensis*, and statistical lack of characters with which to distinguish these species from one another. However, the specimens that are available (two cranidia, two librigena, and two pygidia see plate 38, figs. 4a–e of Bell et al, 1952; plate 9, figs. 1–6, 17–20 of Hughes, 1994) are morphologically distinct from *D. minnesotensis* to warrant retention as a valid species. Aside from the marked morphological differences in the pygidia of these species (greater length and distinctly different orientation of the pygidial pleural spines, and longitudinally more compressed, subquadrate pygidial shape in *D. freeburgensis*), Hughes (1994) noted that statistical growth differences may occur between dikelocephaliid species in the St. Lawrence Formation, and the Tunnel City Group (in which *D. freeburgensis* occurs). Cranidial differences include a slightly higher glabellar length to width



Text-figure 4. Reconstruction of *Dikelocephalus freeburgensis*.

ratio in *D. freeburgensis* (1.36 compared to 1.24 in *D. minnesotensis*), and a more convex, upturned anterior border in *D. freeburgensis*. A PCA of the 28 geometric morphometric landmark (GML) points (Figure 18) was performed on well-preserved cranidia of *D. minnesotensis* (n=10), and all currently known cranidia of *D. freeburgensis* (n=2). This analysis reveals a consistent morphospace relationship between all specimens of *D. minnesotensis*, while all specimens of *D. freeburgensis* fall well outside of the morphospace occupied by *D. minnesotensis* (see Figure 18). Together, these morphological and morphometric differences suggest that *D. freeburgensis* is not a taphonomic or morphological variant of *D. minnesotensis*, but a valid species of *Dikelocephalus*.

Occurrence.—South central Wisconsin, southeastern Minnesota, *Dikelocephalus postrectus* Zone, Reno Member (Tunnel City Group, localities F10, F55.1F, F57.4B of Bell et al.,1952).

HAMASHANIA PULCHERA Kobayashi 1942

Text-figure 5

Hamashania pulchera KOBAYASHI, 1942A, p. 38, figs 1–4; SOHN AND CHOI, 2005, p. 198, figs 3a–g; SOHN AND CHOI, 2007, p. 302, figs. 4a–c.

Platysaukia euryrachis KOBAYASHI, 1960, p. 407, pl. 19, fig. 12, text-fig. 13b.

Mareda mukazegata KOBAYASHI, 1960, p. 407, pl. 19, figs 31–32, text-fig. 14b; DUAN ET AL., 2005, p. 123, pl. 52, figs. 17–18.

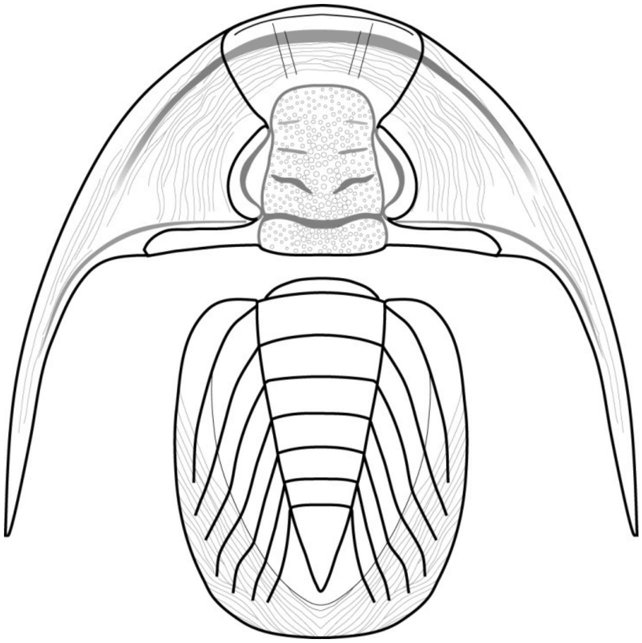
Mareda sinuata GUO AND DUAN, 1978, p. 456, pl. 2, fig. 21; DUAN ET AL., 2005, p. 123, pl. 21, figs. 14–17, text-fig. 7–5.

Mareda busiris (Walcott); ZHANG AND JELL, 1987, p. 245, pl. 12l, fig. 6.

Mareda pulchera (Kobayashi). DUAN ET AL., 2005, p. 124, pl. 21, figs. 10–12, pl. 52, fig. 15.

Diagnosis.—A species of *Hamashania* having smooth glabella and pygidia with obsolete interpleural furrows (Sohn and Choi, 2005).

Discussion.—Sohn and Choi (2005) revised the genus *Hamashania* in 2005 based on a review of the type material and new material from the Taebaeksan Basin, Korea. At that time, they recognized that the type species of *Platysaukia*, *P. euryrachis* was an incompletely preserved specimen of *Hamashania*; thus the genus *Platysaukia* is a junior synonym of *Hamashania* (Sohn and Choi, 2005). Shergold's (1991) material from the Pacoota Sandstone was referred to the new genus *Pacootasaukia* Sohn and Choi 2005. *Hamashania* possesses a very unusual, axially elongated pygidium (see Text-Figure 4; fig. 3, Sohn and Choi, 2011). No complete, articulated specimens of *Hamashania* exist, however, a pygidium and a cranidium were recovered from the same bedding plane in Shandong, China (Choi.D.K., pers. comm., 2011); and so it appears that this unusual pygidium does belong to this species. The unusual, longitudinally-elongate pygidium of *Hamashania* is an important synapomorphy for the genus; all other dikelocephalid genera possesses ovate, transversely elongate, subcircular or subquadrate pygidia, often with



Text-figure 5. Reconstruction of *Hamashania pulchera*. Note the sagittally elongate pygidium. This condition is unknown in any other dikelocephaliid.

pleural spines. Interestingly, in 3-dimensionally-preserved material from the Taebeksan Basin of Korea, the lateral librigenal doublure coincides with the dorsal lateral border furrow, implying that the longitudinally-oriented pygidium could not be positioned beneath the cephalon to produce a fully encapsulated condition when the trilobite enrolled. Moreover, there is no evidence to suggest *Hamashania* could enroll.

Family SAUKIIDAE Ulrich and Resser 1933

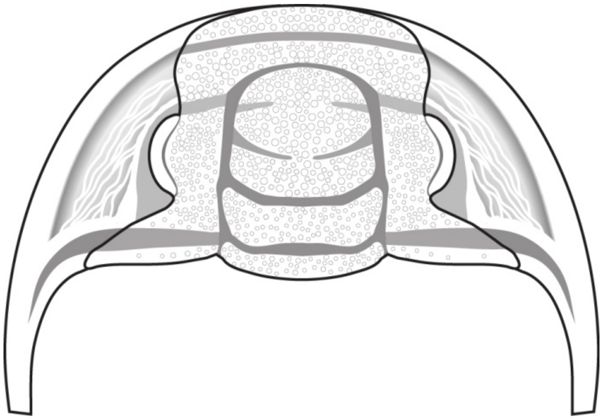
Genus ANDERSSONELLA Shergold 1975

Type species. — *Anderssonella beauchampi*, from the upper Cambrian (early Payntonian *Pseudoagnostus quasibilobus* with *Tsinania nomas* Assemblage-Zone), Chattsworth Limestone, Black mountain, Queensland, Australia (by original designation).

ANDERSSONELLA BEAUCHAMPI Shergold 1975

Figure 19.1-19.3; Text-Figure 6

Anderssonella beauchampi SHERGOLD, 1975, p. 119, pl. 20, figs 1–5, pl. 21, figs 1–2, text-fig. 46.



Text-figure 6. Reconstruction of *Anderssonella beauchampi* based on specimens CPC 11749 (holotype) and CPC 11750–11752, 11755a.

Types.—CPC 11749 (holotype).

Diagnosis.—A species of *Anderssonella* with strongly granulose cranidium; anterior cranidial border with irregular ridge-like ornament composed of linked granules. Preglabellar field short (sagittally), markedly convex, separated from glabella by narrow preglabellar furrow. Low ocular ridges of fixigenae present on fixigenae. Librigenae with distinct subocular groove laterally adjacent to prominent, raised diverticulum; prominent caecal network associated with diverticulum. Pygidium transversely ovate; with broad, concave posterolateral border. Four axial rings.

Discussion.—Lochman (1956) considered *Anderssonella* to be close to the morphological condition of the ptychaspidid ancestral state, and *Consapis* as representing the ancestral stock from which the saukiids evolved, but did not consider either of these genera as being closely related to the Pterocephaliidae. In our cladistic analysis, *Anderssonella* plots in various places depending on the outgroups that are included in the analyses.

When all taxa are included in analyses, and multiple ptychaspidid species are included as outgroups, *A. beauchampi* plots consistently as basal to the ptychaspidids (see Figures 7.1 and 7.2); thus, Lochman's (1956) hypothesis on the descent of ptychaspidids from *Anderssonella* may well be grounded. However, when the ptychaspidids are removed from the analyses because of the polarity swings enforced on ingroup taxa by their inclusion (see discussion in section on cladistic analyses), *Anderssonella beauchampi* plots basally to most *Prosaukia* and as a sister species with *Prosaukia misa* and *Hoytaspis speciosa* (see Figure 9.2). Interestingly, *A. beauchampi* did not group with closely with the Pterocephaliidae in our analysis as might be expected by the possession of well-developed ocular ridges (see Figure 19.1, Text-Figure 5), a character often found in pterocephaliids. Ocular ridges are found in some members of the Ptychaspididae as well, but are not generally well-defined in *Ptychaspis*; thus outgroup selection may exert a polarization in characters that that groups *Anderssonella* with the included pterocephaliids due to no *ptychaspidid* that also possesses this character having been included in our analyses. Other characters uniting *A. beauchampi* and *Prosaukia misa* include a lack of confluence of the lateral and posterior librigenal furrows (compare Figure 19.2 with Figures 27.6 and 27.7). Shergold (1991) also noted that *Anderssonella* has a pygidium that is morphologically similar to *Prosaukia*. Indeed, both *A. beauchampi* and *Prosaukia misa* both have a transversely ovate pygidium which lacks a distinct pygidial border furrow (the included ptychaspidids all have a distinct pygidial border furrow). Unfortunately, because the only pygidium assigned to *A. beauchampi* (Figure 19.3) is damaged, it is unknown whether this species also has a postaxial ridge as is the case in all known *Prosaukia*. In other species of *Anderssonella* where the posterior of the pygidium is known, a distinct postaxial ridge is present, and extends from the terminal piece to the posterior margin of the pygidium (see *A. fengtianensis*, the type species of the genus, pl. 83, fig. 11 in Lu et al., 1965).

Genus CALVINELLA Walcott 1914

Calvinella WALCOTT, 1914, p. 388.

Type species.—*Dikelocephalus spiniger* (Hall, 1863), from late Cambrian sandstones, Trempealeau, Wisconsin.

Diagnosis.—A genus of Saukiidae lacking a preglabellar field; abaxial part of anterior border furrow straight, extending from glabellar shoulder nearly transverse to angled anterolaterally; relatively long axial occipital spine in all species. Pygidia with distinctly unequally-divided lateral pleural segments; propleurae longer (sag.), especially distally.

Discussion.—Of the fifteen species and subspecies listed in Ulrich and Resser (1933), Raasch (1951) recognized only four: *Calvinella spiniger*, *C. pustulosa*, *C. walcotti*, and *C. wisconsinensis*. The librigenae of all of these species are very similar; all have lateral and posterior border furrows that meet and merge before continuing into the genal spine, more as a continuation of the posterior margin than the lateral one (evidenced by the merged furrow being slightly displaced laterally). The main morphological differences between species of *Calvinella* lie in characters of the cranidia and pygidia.

Calvinella has few synapomorphies that distinguish it from *Tellerina* and other species of Saukiidae. In the head region, *Tellerina* differs from *Calvinella* by its possession of a very much wider lateral librigenal border, raised, anastomosing ridge ornamentation of the cephalon, and by the lack of an occipital spine. These differences are rather robust in comparison with the apomorphies available within *Calvinella* used to define species. The main species-diagnostic features of *Calvinella* cranidia relate to the orientation of the abaxial part of the anterior border furrow. As in *Tellerina*, the anterior of the glabella is pushed entirely past the medial part of the anterior border furrow, creating an anterior border furrow that is discontinuous (interrupted by the glabellar anterior) and connects to the axial furrow at the anterolateral corners of the glabella. The angle of the abaxial portion of the anterior border furrow (ABF) is a key diagnostic feature. In *C. spiniger*, the angle of the ABF is quite low, from nearly transverse (86.1°) to approximately 73.9°, and the anterior border itself is relatively long (sagittally), while the pygidium is transversely ovate with a relatively long axis, four axial rings, a postaxial ridge extending to the posterior margin, and completely lacks any inflection of the posterior pygidial margin. *Calvinella walcotti* also has a low angle abaxial part of the ABF, but in this species, the anterior border itself is not as long (sagittally); the pygidium is distinctly subcircular, again with a relatively short axis, four axial rings, and well-defined postaxial ridge extending nearly to the posterior margin, but with a distinct inbend in the medial part of the pygidial posterior border. In *C. wisconsinensis*, the abaxial part of the ABF extends distinctly anterolaterally at an angle of approximately 55-65°, the pygidial axis is perhaps slightly longer, and there is no inflection of the posterior pygidial margin. *Calvinella pustulosa* differs in having a distinct prosopon comprising rather large pustules covering the glabella; one of the two pygidia assigned to this species by Ulrich and Resser (1933) (MPM 19410) also has 4 axial rings, is transversely ovate, and also appears to have a pygidial posterior margin with a medial inbend. Species synonymized by Raasch (1951) were those with no significant morphological departure from these four species; Raasch's taxonomic treatment is supported herein.

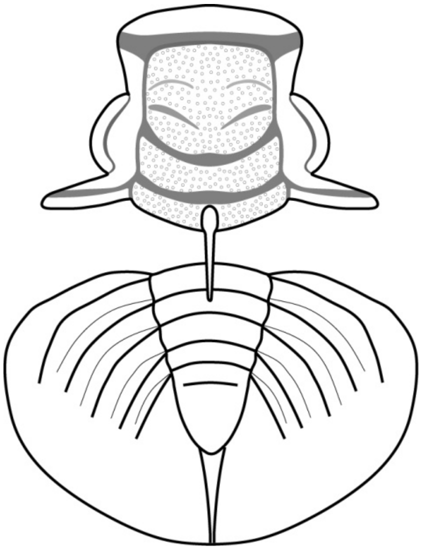
CALVINELLA OZARKENSIS Walcott 1914

Figure 19.4–19.5; Text-Figure 7

Calvinella ozarkensis WALCOTT, 1914, p. 389, pl. 70, figs. 1–6; ULRICH IN BRIDGE, 1931, p. 216, pl. 19, figs. 8, 9, ?11; SHIMER AND SHROCK, 1944, p. 621, pl. 261, figs. 15, 16.

Types.—USNM 58674, holotype; 58677, 60055 syntypes.

Diagnosis.—A species of *Calvinella* with a long (sag.) anterior border furrow lying immediately anterior of glabella; a very wide, slightly anterolaterally-directed abaxial portion of anterior border furrow, an arcuate S3 furrow, and strongly pustulated prosopon.



Text-figure 7. Reconstruction of *Calvinella ozarkensis* based on specimens USNM 58674 (holotype) and USNM 58677, and 60055.

Discussion.—Material from Texas assigned to *C. ozarkensis* by Winston and Nichols (1967) was subsequently reassigned by Longacre (1970) to *C. prethoparia* due to many morphological differences (see discussion under *C. prethoparia* below; Longacre, 1970). The type material of *C. ozarkensis* figured by Walcott (1914) differs from all other species of *Calvinella* in the width of the anterior border furrow, its continuity across the anterior of the glabella (appearing almost to be a preglabellar field), and the robustness of the pustulation of the crandial prosopon (see Figure 19.4). Lochman (1970) remarked on the differences separating *C. ozarkensis* from *C. prethoparia*, including a frontal area separated by a faint border furrow into a preglabellar field and anterior border. A re-examination of the type material reveals that the very long (sag.) anterior border furrow (the entire width of the anterior border furrow may only be assessed at the anterolateral corners of the crinidium) is not completely bisected by the anterior of the glabella as it is in other species of *Calvinella*, but the medial part of the ABF lying directly anterior to the glabella is still intact; thus, in this species, a continuous anterior border furrow is still intact. The preglabellar part of the axial furrow combines with anterior border furrow at the glabellar anterior. Because the entire (sag.) length of the anterior border furrow can be measured only at the anterolateral corners of the cranidium, and because the portion of the anterior border furrow lying anterior of the glabella is shorter than the abaxial portion of the furrow, we consider the entire concave area lying immediately anterior of the glabella as representing a partial anterior border furrow; thus, there is no pre-glabellar field and this species can be referred unambiguously to *Calvinella*. The "faint anterior border furrow," mentioned by Lochman (1970), p. 47, is probably an effect of the preglabellar part of the axial furrow overprinting the anterior border furrow. *Calvinella ozarkensis* consistently plots in a basal position for this genus; thus, the forward-shifted position of the anterior border furrow likely represents a transitional state between the possession of a preglabellar field (as in *Prosaukia* and *Saukiella*) and a lack of this character together with an entirely interrupted anterior border furrow.

CALVINELLA PRETHOPARIA Longacre 1970

Figure 19.6-19.9; Text-Figure 8

Calvinella prethoparia LONGACRE, 1970, p. 45, pl. 6, figs. 7–12; WESTROP, 1995, p. 23, pl. 8, figs. 3–6.

Calvinella ozarkensis WINSTON AND NICHOLLS, 1967, p. 80, pl. 11, figs. 5, 9.

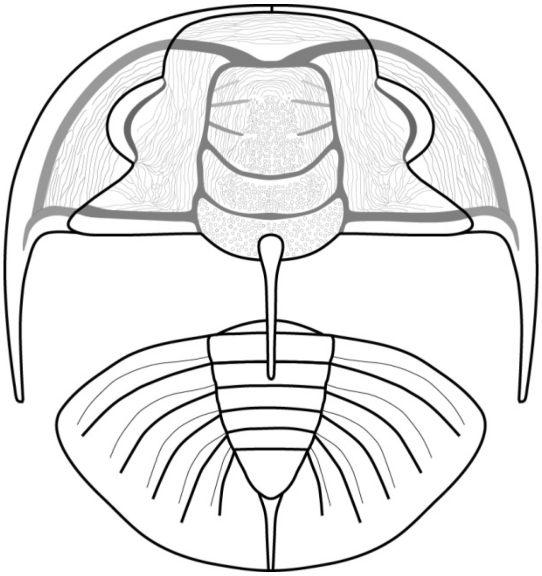
"*Calvinella*" *prethoparia* TAYLOR AND HALLEY, 1974, p. 27, pl. 2, figs 1–3.

"*Calvinella*" cf. *'C.' prethoparia* LANDING, WESTROP, KRÖGER, AND ENGLISH, 2011, p. 549, figs. 8f–8h.

Type material.—USNM 185874 (holotype).

Other material examined.—UNSM 186588–186590, 192282–192286.

Emended diagnosis.—A species of *Calvinella* with palpebral lobes rather widely spaced outward from the glabellar axial furrow; anterior branch of facial suture straight to gently convergent.



Text-figure 8. Reconstruction of *Calvinella prethoparia* Longacre 1970, based largely on USNM 185874 (holotype) and USNM 186588–186589, 192283–192285.

Discussion.—As noted by Taylor and Halley (1974), cranidia of *C. prethoparia* from the type locality (Wilberns Formation, San Saba member, central Texas) have more evenly pustulated cranidial prosopon than do specimens from New York, which have a combination of pustulated and anastomosing ridge ornament. However, in Longacre's figures specimens (USNM 192282, syntype), the same type of cranidial ornament noted by Taylor and Halley is present; thus apparent differences in cranidial prosopon between Texas and New York material are likely attributable to taphonomy.

Taylor and Halley (1974) suggested that cranidial characters of *C. prethoparia* are sufficient for the erection of a new saukiid genus; characters that these authors cited include: parallel rather than divergent preocular facial sutures; wide, flat, interocular fixigenae; triangular posterior fixigenae; and relatively short (exsag.) palpebral lobes that are centered anterior to the glabellar midpoint rather than centered posterior to the glabellar midpoint (see Figure 19.6). It is worth noting, however, that not all of these characters are correctly identified. For example, the midpoint of the palpebral lobes is anterior to, or even with, the occipital glabella longitudinal midpoint in *C. prethoparia*, *C. wisconsinensis*, and *C. spiniger*; it is located posteriorly to the glabellar midpoint in *C. ozarkensis*. Additionally, the ratio of the sagittal eye length to glabellar length is similar in these species of *Calvinella*; *C. spiniger*: 0.460, *C. ozarkensis*: 0.409, *C. prethoparia*: 0.425 *C. wisconsinensis*: 0.484; thus, this character (short palpebral lobes) falls within the variation observed within established members of *Calvinella*. The shape of the posterior limb can vary substantially among genera of Saukiidae, and even within genera; *Prosaukia stosei* has much more triangular posterior fixigenae than do other members of that genus. Thus, this appears to be a character that varies at low taxonomic levels. The wide lateral spacing of the palpebral lobes does differentiate *C. prethoparia* from other species of *Calvinella*, but *C. prethoparia* consistently groups within a monophyletic, but divided *Calvinella* in a position as a sister taxon to *C. ozarkensis*. Characters that unite *C. prethoparia* with other members of *Calvinella* include possession of an occipital spine in the holaspid, anterolaterally directed cranidial border furrows, transversely elliptical pygidium, and possession of a pygidial postaxial ridge (Figure 19.7). Thus, the wide spacing of the eyes may represent an species-level autapomorphy; and if this is the case, such wide eye spacing may also influence the shape of both the anterior and posterior cranidial fields. Additionally, in the CONOP computed composite section (Figures 12 and 13) *Calvinella prethoparia* consistently falls within the stratigraphic ranges of other species of *Calvinella*.

Occurrence.—Lower *Saukiella serotina* Subzone (at localities H-1 and H-3 of Taylor and Halley, 1974), lower Whitehall Formation, Washington County, N.Y; upper *Saukiella serotina* Subzone (at localities CC-61, 63 ; JR-529, 536; LCS-44, 45, 45.4, 45.8; and TC-1388, 1400 of Longacre, 1970), Wilberns Formation, San Saba member, central Texas.

CALVINELLA SPINIGER (Hall 1863)

Figure 20.1–20.3; Text-Figure 9

Dikelocephalus spiniger HALL, 1863, p. 143, pl. 10, figs. 1–3; HALL, 1867, p. 124, pl. 5, figs. 1-3.

Conokephalina spiniger BRÖGGER, 1886, p. 205.

Calvinella spiniger ULRICH AND RESSER, 1933, p. 220, pl. 37, figs. 18–29; pl. 38, figs. 1–3; SHIMER AND SHROCK, p. 621, pl. 261, figs. 13, 14; WESTROP, PALMER, AND RUNKLE, 2005, figs. 9.7, 9.8, 10.8–10.10.

Calvinella spiniger altimuralis ULRICH AND RESSER, 1933, p. 224, pl. 38, figs. 4-8.

Calvinella spiniger communis ULRICH AND RESSER, 1933, p. 225, pl. 38, figs. 9-28.

Calvinella spiniger communis mutation ULRICH AND RESSER, 1933, p. 225, pl. 38, figs. 26-28.

Calvinella spiniger postlevata ULRICH AND RESSER, 1933, p. 226, pl. 38, figs. 29–30.

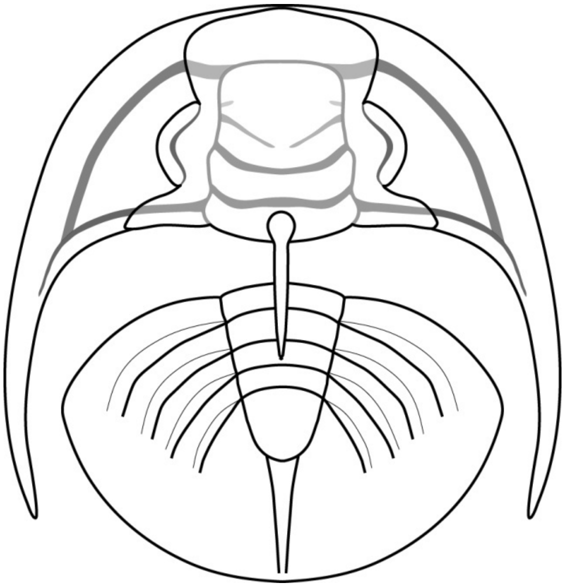
Calvinella clivula ULRICH AND RESSER, 1933, p. 228, pl. 38, figs. 31–33.

Calvinella sparsinodata Ulrich and Resser, 1933, p. 230, pl. 39, figs. 11–16.

Calvinella walcotti norwalkensis Ulrich and Resser, 1933, p.237, pl 39, figs. 31–34.

Type material.—AMNH 341A (lectotype), AMNH 341B (paralectotype).

Other material examined.—UNSM 58657–58660, 85276, 85292, 85297, 85299–85301; UWGM 664.



Text-figure 9. Reconstruction of *Calvinella spiniger* based on AMNH 341A, 341B (lectotypes), and USNM 85276.

Diagnosis.—A species of *Calvinella* with relatively long (sagittally) cranidial anterior border, abaxial parts of anterior border furrow directed only slightly anteriorly. Glabella with relatively long, posteriorly-directed, straight S2, discontinuous across medial part of glabella, prosopon unknown. Occipital spine long. Pygidium transversely ovate, length to width ratio approximately 0.66; four axial rings; long posterior margin with well-defined postaxial ridge extending all the way to pygidial posterior margin. Posterior pygidial margin without inflection.

Discussion.—Westrop et al.,(2005) re-examined Ulrich and Resser's (1933) lectotype, the cranidium on which Hall (1863) erected *Dikelocephalus spiniger*, and commented on the mild granulation of the cranidial internal mold. While several of the librigenae assigned by Ulrich and Resser (1933) to *C. spiniger* have subparallel, anastomosing wavy, raised ridge ornament of the librigenal field, usually expressed only on internal molds, no pustulation was observed on any of the cranidia reposited in the USNM or UWGM collections for *C. spiniger* itself, or any of the species synonymized with it. Two possible explanations exist for this seeming disparity between Hall's (1863) material and all other examples of *C. spiniger*: 1) preservation of the cuticle ornament necessitated fine-grained sand or silt due to small-scale nature of the prosopon, or 2) *C. spiniger* had no cuticular ornament and the lectotype assigned by Ulrich and Resser (Hall's own type material) is actually a known pustulated species, *C. pustulosa* or *C. ozarkensis*. The latter case seems rather unlikely; all well-preserved material examined during the course of this study revealed, at the very least, traces of cuticular ornament. The former explanation is much more parsimonious; the fine-scale nature of the prosopon in *C. spiniger* is evidenced by a lack or ornament in all but the finest-grained material, and then only in internal molds. Additionally, *C. pustulosa* can be discounted as the lectotype specimen based on its possession of abaxial parts of the ABF that are angled more anteriorly than those of *C. spiniger*, and *C. ozarkensis* has the medial part of the anterior border furrow intact and present immediately anterior to the glabella.

CALVINELLA WISCONSINENSIS Ulrich and Resser 1933

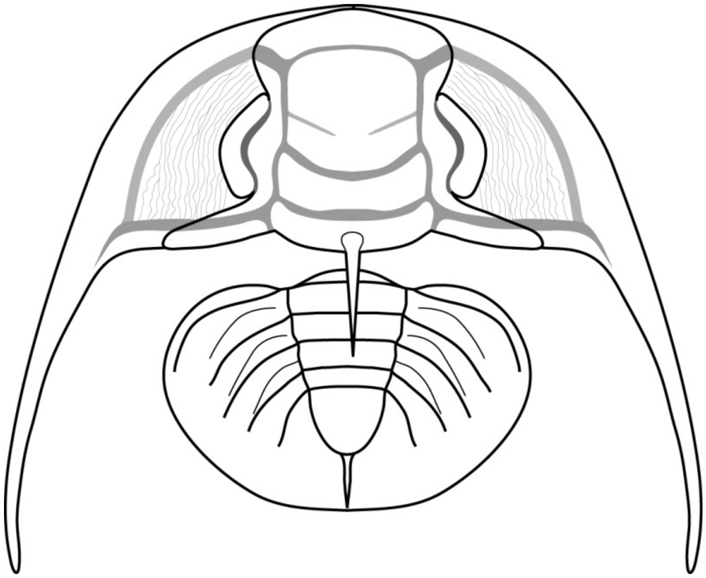
Figure 20.4–20.6; Text-Figure 10

Calvinella wisconsinensis ULRICH AND RESSER, 1933, p. 240, pl. 40, figs. 23–33; NELSON, 1951, p. 784, pl. 110, fig. 21.

Calvinella cf. C. wisconsinensis WESTROP, PALMER, AND RUNKLE, 2005, p. 86, figs. 9.1–9.6, 10.1–10.7

Other material examined.—USNM 85296, UWGM 4007/1–4007/8, additional un-numbered material in the USNM collections; UWGM 1056–1061, 1073–1085, 1107–1108, 1162–1163, 1178, 1385–1391.

Diagnosis.—A species of *Calvinella* with abaxial parts of preglabellar field oriented anterolaterally at approximately 55 to 65°. S2 faint, posteriorly-directed; S3 furrow not apparent.



Text-figure 10. Reconstruction of *Calvinella wisconsinensis* based on USNM 85296 and un-numbered USNM material.

Genus DIEMANOSAUKIA Jago and Corbett 1990

Type species.—*Diemanosaukia miserabilis*, from an un-named sandstone unit, Misery Hill, western Tasmania (by original designation).

Emended diagnosis.—A genus of Saukiidae with coarsely tuberculate prosopon; lacking a preglabellar field; glabella parallel-sided, extends to anterior border. Axial furrows deep; occipital and S1 furrows deeply impressed; S2 furrow shallow, posteriorly-directed; S3 furrow very shallow, anteriorly-directed. Palpebral lobe midlength located anterior of occipital-glabella midlength; palpebral lobes located away from axial furrow. Librigenae with broad genal spine bases; lateral and posterior librigenal border furrows separated by a low ridge; posterior border furrow extends into base of genal spine. Thorax of 13(?) segments. Pygidium transversely semi-elliptical; pygidial axis extends nearly to pygidial border; axis comprises 7 or 8 axial rings plus terminus; postaxial ridge absent; pleurae evenly divided by pleural furrows (after Jago and Corbett, 1990).

DIEMANOSAUKIA MISERABILIS Jago and Corbett 1990

Figures 20.7, 21.1–21.2; Text-Figure 11

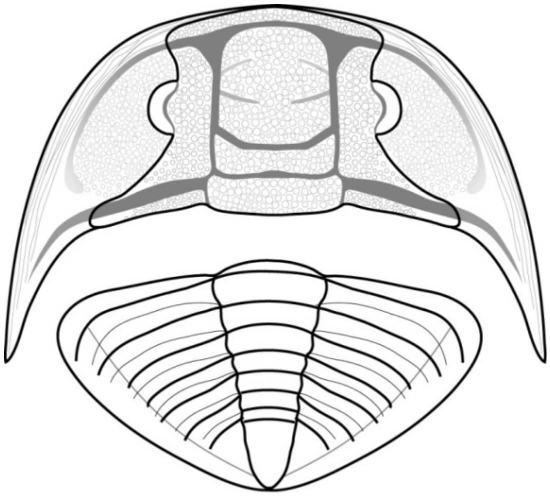
Diemanosaukia miserablilis JAGO AND CORBETT, 1990, p. 240, figs. 3A–3J, 4A–4J.

Saukiid cranidium, WRIGHT ET AL.,1984, p. 304, fig. 2A.

Saukiid free cheek, WRIGHT ET AL.,1984, p. 304, fig. 2D.

Type material.—UTAS 123926 (holotype).

Diagnosis.—Genus monospecific; same as for genus.



Text-figure 1. Reconstruction of *Diemanosaukia miserabilis* based on UTAS 123926 (holotype), and UTAS 123925–123933.

Discussion.—This monospecific genus is currently known only from Tasmania and Antarctica (Wright et al., 1984; Jago and Corbett, 1990). In Australia, *D. miserabilis* is confined to the Payntonian (Jago and Corbett, 1990). In Antarctica, *D. miserabilis* occurs in the Trans Antarctic Mountains in Northern Victoria Land, near the Ross Sea. During Cambrian time, East Antarctica was connected to the southern margin of Australia, and the portion of northern Victoria Land where *D. miserabilis* occurs would have been located very close to western Tasmania. The co-occurrence of these taxa adds additional evidence supporting a strong linkage between eastern Antarctica and southern Australia, and particularly, the western margin of Tasmania and peninsular northern Victoria Land.

Jago and Corbett (1990) also noted the morphological similarity between saukiid material from Antarctica and *D. miserabilis*. At that time, those authors did not place the Antarctic material into synonymy with *D. miserabilis*, citing the markedly differing pygidium figured as saukiid in Wright et al., (1984). The two pygidia illustrated by Wright et al., (as ?saukiid pygidia, figs. 2B, 2C) are morphologically dissimilar to *D. miserabilis* pygidia (see Jago and Corbett, 1990), and are both damaged and incomplete. However, those authors gave no stratigraphic accounting of where the saukiid specimens are located within their section, so the pygidia figured by Wright et al., (1990, fig 2B, 2C) may not even be associated with the crandium. Data with the reposited specimens does not indicate any stratigraphic information, nor does it appear any stratigraphic section of this locality was ever published.

The cranidium illustrated by Wright et al., (1990) can be assigned to *D. miserabilis* based on the absence a preglabellar field, the wide spacing of the relatively small palpebral lobes away from the glabella, the tuberculated prosopon of the glabella and of the anterior border, parallel sides of the glabella, and the slightly posteriorly-angled abaxial portions of the anterior border furrow. Likewise, the free cheek illustrated by those authors can also be assigned to *D. miserabilis* based on the broad base of the genal spine, the low ridge separating the lateral and posterior librigenal border furrows, the pustulated librigenal field, and the parallel ridge ornamentation extending into the genal spine.

Other saukiid faunas living in Gondwana at this time had quite reduced pygidia, both in terms of the length to width ratio of the pygidia and in terms of the number of pygidial axial rings. *Diemanosaukia miserabilis*, however, has a relatively long pygidium with seven to eight axial rings. Jago and Corbett (1990) noted the similarity in gross morphology between *Diemanosaukia* and *Danzhaisaukia nitida*, including the lack of a preglabellar furrow, the wide base of genal spine, the lateral and posterior borders separated by a low ridge, the overall pygidial outline shape, and the rather high number of pygidial axial rings in both species. Those authors differentiated the two species based on much larger palpebral lobes in *Danzhaisaukia* than in *Diemanosaukia*, as well as the possession of 11 thoracic segments in the former species, and 13 in the latter. However, *Diemanosaukia* material is many times the size of the tiny specimens assigned to *Danzhaisaukia*; moreover, the ratio of the length of the palpebral lobe to the length of the glabella is known to change through ontogeny, so this particular character can only reliably used to differentiate between species in cases where an ontogenetic series is well known in both species (see Hughes, 1994 for a discussion on palpebral lobe length through ontogeny). The differing number of thoracic segments, however, cannot be discounted; as the number of thoracic segments are not know to vary in saukiid holaspids, this character reliably distinguishes these taxa from one another. The anterior of the cephalon is also rather distinctive in *Danzhaisaukia nitida* - the cephalic border is extended anteriorly into a short, triangular extension, similar to *Lophosaukia* and *Sinosaukia*; *Diemanosaukia* lacks this anterior projection of the cephalon. Even with these significant differences, *Diemanosaukia* plots in a position very close to, but in a more derived position than, *Danzhaisaukia nitida* and *Sinosaukia daliensis* in our cladistic analysis, and in the preferred cladogram, it nests within species traditionally considered as belonging to *Eosaukia* indicating that this genus is artificial (see Figure 4.2).

Jago and Corbett (1990) tentatively assigned their material from Misery Hill to the Payntonian, approximately equivalent to the upper part of the Sunwaptan in North America. Wright et al. (1984) assigned their saukiid material to the early Tremadoc based on the presence of the genera *Pseudokainella* and *Harpides(?)* However, the conodont assemblage recovered by Wright et al. (1984) is interpreted to span the latest Cambrian to earliest Ordovician, so the saukiids within these authors' sections may be in the Cambrian part of the section, but additional data is necessary to confirm this.

Genus EOSAUKIA Lu 1954

Type species.—Eosaukia latilimbata Lu, 1954 from the Sandu Shale, Guizhou, South China (by original designation).

Emended diagnosis.—A genus of Saukiidae with a strongly convex cephalon and lacking a preglabellar field. Cranidium subtrapezoidal; abaxial portion of anterior border furrow well-defined and angled anteriorly toward anterolateral corners of cranidium; three pairs of glabellar furrows present in addition to occipital furrow; S2 and S3 very narrow (transversely), S2 directed posteriorly, S3 directed anteriorly. Palpebral lobes generally shorter than 50% of glabellar length; prominent apodemes on underside of anterolateral corners of glabella. Librigenae with narrow lateral border and vincular notches on ventral posterior doublure. Pygidium micropygous, transversely ovate; axis with two to four axial rings; posterior border very narrow, rim-like. (after Lee and Choi, 2011).

Discussion.—The systematics of the *Eosaukia* have recently been reviewed by Lee and Choi (2011). We include synonymy information herein as reference for cladistic discussion in this paper. Any taxonomic disagreements with Lee and Choi (2011), revisions, or taxonomic treatments that were not specifically discussed by those authors are noted within the following sections.

EOSAUKIA ACUTA (Kuo and Duan *in* Kuo, Duan, and An, 1982)

Text-Figure 12

Calvinella acuta KUO AND DUAN IN KUO, DUAN, AND AN, (in part) 1982, p. 19, pl. 3, fig. 12, non fig. 11.

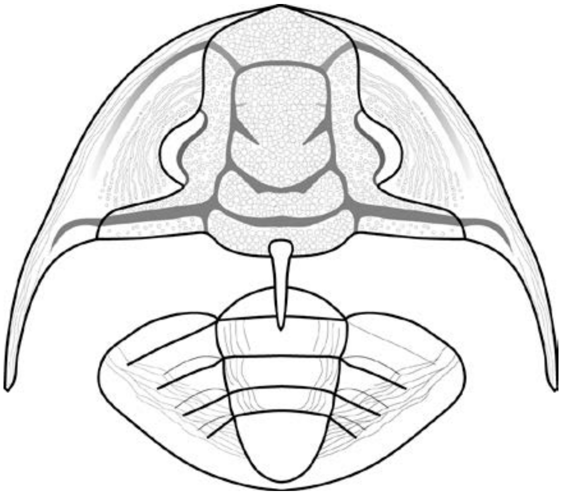
Eosaukia acuta LEE AND CHOI, 2008, p. 220, fig. 2; LEE AND CHOI, 2011, p. 288, figures 3.4, 7.

Calvinella triangula QIAN, 1985, p. 81, pl. 17, figs. 12–14.

Mictosaukia striata QIAN, 1986 (in part), pl. 71, fig. 7.

Calvinella micropora QIAN, 1986, (in part), pl. 72, fig. 7.

Diagnosis.—A species of *Eosaukia* with an elongate, triangular anterior cranidial border area, and an occipital spine. Librigena narrow, lateral and posterior librigenal border furrows not confluent; lateral border furrow shallows and terminates anterior of genal angle. Genal spines not advanced. Pygidium with three axial rings; two low ridges present on terminal piece connect to the posteriormost (third) axial ring.



Text-figure 2. Reconstruction of *Eosaukia acuta*, based on SNUP3146–3151.

EOSAUKIA ANGUSTILIMBATA (Qian 1986)

Figure 21.3–21.6; Text-Figure 13

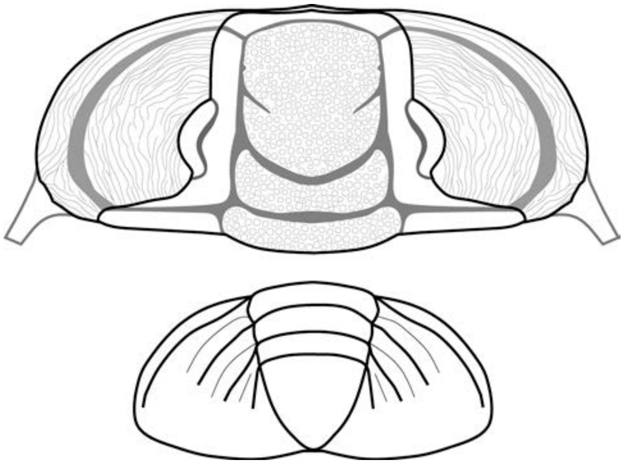
Mictosaukia angustilimbata QIAN, 1986, p. 276, pl. 71, figs. 8–11; pl. 72, figs. 1–5; text fig. 107.

Eosaukia angustilimbata LEE AND CHOI, 2011, p. 296, appendix 1.

Type material.—NIGPAS 98774 (holotype).

Other material examined.—NIGPAS 98766–98772, 98775.

Diagnosis.—A species of *Eosaukia* with S3 furrow expressed only as semicircular indentation on glabella adjacent to the axial furrow anterior to S2. Posterior librigenal margin gently curved forward; lateral and posterior librigenal furrows confluent, strongly curved or C-shaped at confluence. At least ten vincular notches on ventral librigenal lateral and posterior doublure. Pygidium with three axial rings; terminal piece subtriangular, extends nearly to posterior pygidial margin. Posterior pygidial margin transversely flat or quadrate.



Text-figure 3. Reconstruction of *Eosaukia angustilimbata*, based on NIGPAS 98774 (holotype), 98766–98772, 98775.

Discussion.—This species has an S3 glabellar furrow, but the furrow is defined only by a semi-circular indentation along the axial furrows anterior to S2. The orientation of this furrow cannot be ascertained in the present material.

A re-examination of the type material revealed only three well-defined pygidial axial rings, not the four reported by Qian (1986), although there is a very faint indication of an additional furrow lying posterior to the third axial ring. The transversely subquadrate shape of the posterior pygidial margin is unique to this species in the *Eosaukia*, all other members of which have a rounded pygidial posterior margin.

However, the ten ventral vincular notches in the ventral side doublure of the librigenae of *E. angustilimbata* indicate that this species of saukiid, like other members of the genus *Eosaukia* was capable of sphaeroidal enrollment. Vincular notches are a coaptative structure in trilobites that help to facilitate sphaeroidal enrollment. Sphaeroidal enrollment is characterized by the interaction of the pleural tips of the thoracic segments with notches in the ventral side of the cephalic doublure (Whittington, 1997). Because of the mechanical, dovetail-like nature of the interaction of these sclerites, the resulting encapsulization is thought to have been strong, creating a robust posture that could resist predation (Bergström, 1973). Because all articulated species of *Eosaukia* known have eleven thoracic segments, the ten vincular notches *E. angustilimbata* would necessarily imply that *E. angustilimbata* used a very strong flexure of its anteriormost thoracic segment to facilitate enrollment. Even within species of Saukiidae in which ventral morphology of the head region is known, details of the coaptative structures remain vague. For example, there does not appear to be a vincular furrow in *E. angustilimbata*; and other species of *Eosaukia* show only vague indications of a very shallow vincular furrow (see fig. 6.9 and 6.14 of Lee and Choi, 2011). Perhaps due to the relatively small size of the pygidium and the conterminant hypostome [see *Linguisaukia spinata*, plate 12, fig. 1 of Lu and Zhou, 1990 for hypostome attachment details (sadly, specimens in this publication are now lost)], it may not have been possible for the pygidium to have been tucked in far enough to have necessitated a furrow.

The development of the vincular structures may have occurred immediately following the postmolt stage, when the cuticle was still pliable before calcite crystal reprecipitation. During the postmolt stage, arthropods are most vulnerable to predation; it is hypothesized herein that during this interval, *Eosaukia* species tightly enrolled, and that the relatively thick pleural tips were impressed into the thinner, pliable ventral cephalic doublure. After the exoskeleton hardened, the vincular structures would be a permanent part of the hardened cuticle. The implication of this hypothesis is that vincular notch counts could be quite variable depending on how tightly individuals of a species enrolled immediately post-ecdysis; individuals may exist within a single species that have no vincular structures, or that have variable numbers, or that all have a similar number. A study of a great many ventrally preserved librigena of a single species of *Eosaukia* are necessary to more fully understand whether this is a character that varies from individual to individual or not. Thus, while the presence of vincular structures is one of the character that currently unites the *Eosaukia*, (this character is not known in all species within this genus due to lack of ventrally preserved material) it is a distinct possibility that the phylogenetic signal recorded in this character is purely behavioral.

EOSAUKIA BELLA (Walcott 1906)

Figure 22.1; Text-Figure 14

Ptychaspis bella WALCOTT, 1906, p. 585; WALCOTT, 1913, p. 180, pl. 17, fig. 9; KOBAYASHI, 1931, p. 180, pl. 22, fig. 6.

Calvinella bella KOBAYASHI, 1933b, p. 253; HSIANG *IN* LU, CHANG, CHU, CHIEN, AND HSIANG, 1965, p. 449, pl. 88, fig. 5.

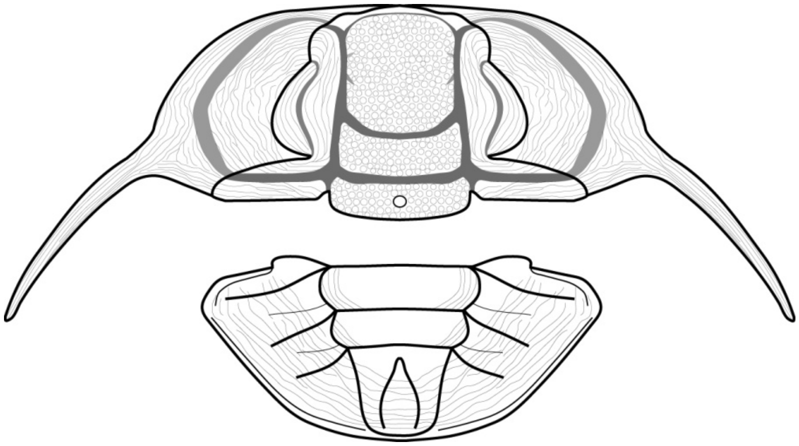
Sinosaukia bella RESSER, 1938b, p. 43.

Mictosaukia bella SHERGOLD, 1975, p. 143; SHERGOLD, 1991, p. 23; ZHANG AND JELL, 1987, p. 237, pl. 117, fig. 10; pl. 118, fig. 5.

Eosaukia bella LEE AND CHOI, 2008, p. 220, fig. 2; LEE AND CHOI, 2011, p. 287, figs. 3.3, 6.

Type material.—USNM 58124, holotype.

Emended diagnosis.—A species of *Eosaukia* with densely tuberculate glabella; genal field ornamented with lirae. Cranidial anterior border very short; palpebral lobes relatively long and wide; occipital node present, occipital spine absent. Genal spines long, inflected, diverging posteriorly before gently curving adaxially; genal spines advanced. At least seven vincular notches on posterior part of lateral librigenal doublure. Pygidium strongly convex; axis wider than 40% of pygidial width, with two axial rings and a terminal piece bearing two distinct longitudinal ridges. (After Lee and Choi, 2011).



Text-figure 4. Reconstruction of *Eosaukia bella* based on SNUP 3006, 3123–3124, 3129–3130, 3135, 3137 (see fig. 6 of Lee and Choi, 2011).

Discussion.—Shergold (1975) placed this species within *Mictosaukia*, and noted the similarity between *E. bella* and *Mictosaukia perplexa* from western Queensland, Australia, citing only the slightly granulose nature of an exfoliated glabella to distinguish *M. perplexa* from *E. bella*. Lee and Choi (2011) placed *M. perplexa* into *Eosaukia*, but they also retained *E. perplexa* Shergold 1975 as a valid species, but offered no morphological basis with which to support this opinion. Indeed, *E. perplexa* is morphologically very similar to *E. bella*. Shergold's material is exfoliated, as is the holotype. However the holotype of *E. bella* (Figure 22.1) bears a piece of the original cuticle that is clearly tuberculate, whereas in Shergold's (1975) material, the entire glabella is entirely exfoliated. The associated librigena of *M. perplexa* are strikingly similar to *E bella*; both possess confluent lateral and posterior librigenal furrows, the posterolateral confluence of these furrows anterior to the genal angle widens, shallows, and is C-shaped, the librigenal field and lateral border are covered in raised, anastomosing lirae, and both have vincular notches in the posterior librigenal doublure (the primary taxabase for *Eosaukia*). In *E. perplexa*, there appear to be eight notches; in *E.bella* there are at least six to seven. The anterior cranidial border also appears to be slightly longer (sagittally) in *E. perplexa* than in *E. bella*. Because of these minor morphological differences, we retain *E. perplexa* as a valid species of *Eosaukia*; however, all of these noted differences are very minor - it is therefore possible that all are due to taphonomic effects.

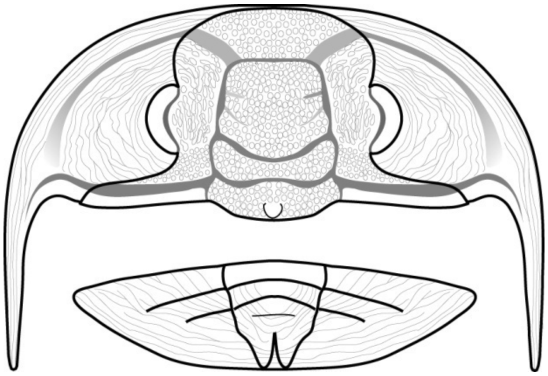
EOSAUKIA LATILIMBATA Lu 1954

Figure 22.2–10.3; Text-Figure 15

Eosaukia latilimbata LU, 1954, p. 127 (p. 145, English translation), pl. 1, figs. 5–6; LU, 1957, p. 284, pl. 147, fig. 11; LU ET AL.,1965, p. 443, pl. 86, fig. 14; LUO, 1974, p. 657; YIN AND LEE, 1978, p. 515, pl. 171, fig. 7; LU AND ZHOU, 1990, p. 32, pl. 10, figs. 1–3; LEE AND CHOI, 2011; p. 297, appendix 2.

Type material.—NIGPAS 7226 (holotype)

Other material examined.—NIGPAS ytf-0139, NIGPAS 7227.



Text-figure 5. Reconstruction of *Eosaukia latilimbata*, based on NIGPAS 7226 (holotype), 7227, ytf-0139.

Emended diagnosis.—Cranidium densely tuberculate. Glabella tapering anteriorly; S3 short (transversely), very shallow, transeverse; distinct occipital node present, occipital spine absent. Genal spines very slightly advanced. Transversely elliptical pygidium with three or four axial rings; two short (sag.) triangular ridges on terminal piece, originating from terminal axial ring.

Discussion.—This species is difficult to diagnose for several reasons. Shergold (1991) noted that both of the articulated specimens currently known are sagittally compressed, or telescoped. Both specimens have damage to the anterior part of the cephalon, and the cranidium of the holotype specimen has been distorted and no longer retains its original relief (Shergold, 1991). Because of distortion to the specimen, the original cranidial relief, the shape of the anterior part of the glabella and the arrangement of the glabellar furrows, all characters that are key in diagnosing *Eosaukia* properly, cannot be reliably diagnosed. Additional, non-articulated, material was described by Lu and Zhou (1990); however, after that paper's senior author died, those specimens (which were unfortunately never reposited) went missing, leaving only the photographs in the 1990 publication.

Lee and Choi (2011) included this species in their revised *Eosaukia* as well, and emphasize the presence of vincular structures on the ventral librigenal border as an apomorphy for this genus. However, there is currently no ventrally-preserved material available to confirm the presence of vincular notches, and the issues outlined above compound this problem further. Characters that currently unite *E. latilimbata* with the *Eosaukia* include: a very short micropygous pygidium with only three or four axial rings, and the presence of two short spines on the terminal piece extending from the posteriormost axial ring.

This species very closely resembles other species of *Eosaukia*, especially *E. rectangula* and *E. walcotti*. *Eosaukia walcotti* has a tuberculated cranidium, but the scale of tuberculation is finer, and a distinct occipital spine is present (see figures in Zhu, 2011), thus, this species can be ruled out as a conspecific. *Eosaukia latilimbata* also co-occurs in the same outcrop with *E. rectangula*, with the stratigraphic occurrence of *E. latilimbata* within the stratigraphic range of *E. rectangula* (see range chart, Lu and Zhou, 1990, p. 4). Moreover, the diagnoses of these two species are very similar: both possess strongly anterolaterally directed abaxial portions of the ABF, both are articulated and possess eleven thoracic segments, and have sagittally compressed pygidia of three to four pygidial axial rings. Lee and Choi (2011) refer Lu and Zhou's (1990) material to *Eosaukia rectangula*, but do not discuss the reasons for this assignment; this may be because a detailed examination of Lu and Zhou's material is not possible because of its loss. Even a cursory comparison of Lu and Zhou's (1990) plate 10, figs. 1–3 (*E. latilimbata*) with plate 10, figs. 4–10 (*E. rectangula*) reveals very little difference between these specimens. Both cranidia have rather robust, subtriangular posterior limbs, the length of the anterior borders are similar, and the abaxial portion of the anterior border furrow is at a similar angle in all cranidia (Lu and Zhou, 1990). The only major differences between these cranidia discernible from these photographs are: 1) the larger eye in one specimen assigned to *E. latilimbata* (Lu and Zhou, 1990, pl. 10, fig. 1), and 2) another cranidium assigned to *E. latilimbata* has discernible pustulation (Lu and Zhou, 1990, pl. 10, fig. 2). The larger eye is explained by the much smaller size of the cranidium in figure 1 (eye function is dictated by a minimum size threshold; eye allometry is well known in dikelocephaliids, see Hughes, 1994), while the lack of expressed tuberculation could be explained by it having been very low relief, specimens having been effaced, representing internal molds, or missing due to taphonomic effects. According to Lu and Zhou (1990), the surface of the cranidia of *E. rectangula* is granulated, but the photographs, unfortunately, do not show this character in detail. Lu and Zhou further cite the presence of 5 to 6 axial rings in *E. rectangula*, specifically as a character differentiating it from *E. latilimbata*; unfortunately, only four axial rings are visible in the photographs of *E. rectangula*. Moreover, both currently known specimens of *E. latilimbata* are known to be sagittally compressed (Shergold, 1991); this compression may be obscuring the true morphometric ratios and morphological features of *E. latilimbata*.

Additionally, because all currently known material of *Eosaukia rectangula* has been lost, there is no holotype material on which to base a specific diagnosis, and detailed comparison with other species is not possible. Unfortunately, because of this, detailed comparative work with other members of the genus is severely restricted, and the concept of *Eosaukia rectangula* is of limited value systematically. It is hoped that this type material will be found and that the status of this species can be further reviewed.

Occurrence.—Lower Furongian Sandu Shale, Guizhou, south China (type); Baoshan Formation, Yunnan, south China.

EOSAUKIA MICROPORA (Qian 1985)

Text-Figure 16

Calvinella micropora QIAN, 1985, p. 81, pl. 18, figs. 1–9; DUAN ET AL.,1986, p. 49, pl. 7, figs. 1–7; QIAN, 1986, p. 281, pl. 72, figs. 6–7, 9–10; pl. 73, figs. 2, 6, 11; text-fig. 109.

Eosaukia micropora LEE AND CHOI, 2008, p. 220, fig. 2; LEE AND CHOI, 2011, p. 284, figs. 3.2, 5.

Calvinella granulosa ZHANG AND WANG, 1985, p. 474, pl. 143, figs. 2–4.

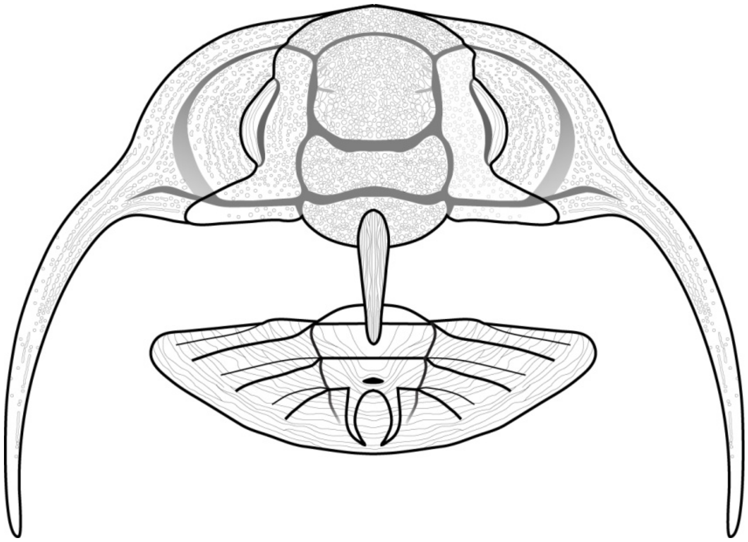
Calvinella latilimbata DUAN AND AN *IN* DUAN, AN, AND ZHAO, 1986, p. 49, pl. 7, figs. 8–10.

Mictosaukia aff. *walcotti* (MANSUY) ZHOU AND ZHANG, 1985, p. 106, pl. 5, figs. 11–12.

Scolosaukia lanceata SUN, 1990, p. 104, pl. 1, figs. 4–6.

Scolosaukia micropora (QIAN), SUN, 1990, p. 105, (in part) pl. 1, figs. 8–9, 12, non 10, 11.

Emended diagnosis.—A species of *Eosaukia* with long occipital and genal spines. Cranidium densely tuberculate, except on occipital spine and palpebral lobes which are ornamented with lirae. Palpebral lobes small, semicircular. Librigena with slightly advanced genal spine; lateral librigenal margin inflected at origin of genal spine resulting in recurvature of genal spine. Pygidium transversely elongate; axis approximately 30% of pygidial width, with two axial rings and a terminal piece bearing two longitudinal ridges. (After Lee and Choi, 2011).



Text-figure 6. Reconstruction of *Eosaukia micropora*, based on SNUP 3007, 3109–3110, 3118, 3121.

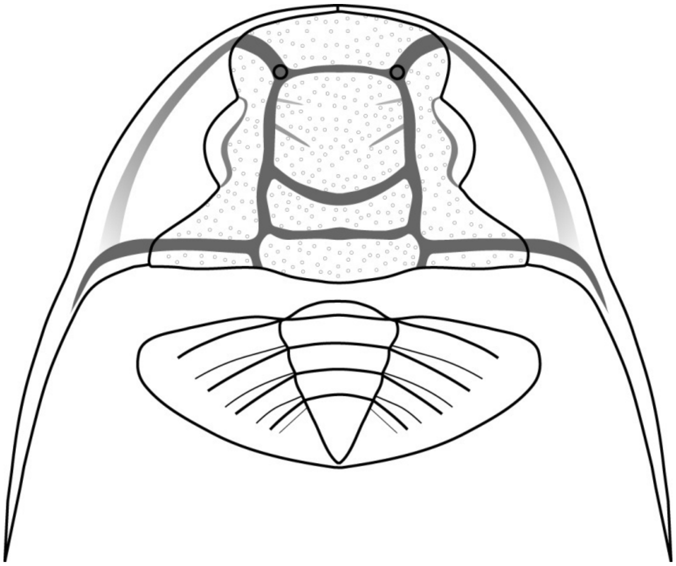
Occurrence.—Mictosaukia-Fatocephalus Zone, Jilin, North China (Qian, 1986; Duan et al.,1986); Fengshan Fm., Hebei, North China (Sun, 1990); *Eosaukia* fauna, South Korea (Lee and Choi, 2011).

EOSAUKIA RECTANGULA Lu and Zhou 1990

Text-Figure 17.

Eosaukia rectangula LU AND ZHOU 1990, p. 32, pl. 10, figs. 4–10.

Discussion.—Unfortunately, because of the loss of all known material of this species, detailed comparative work was not possible. This species was coded and measurements were made based entirely upon published descriptions and photographs. *Eosaukia rectangula* is included in the phylogeny because of its highly complete exoskeleton, to illustrate the close link with *E. latilimbata*, and to help polarize characters within the genus *Eosaukia*.



Text-figure 7. Reconstruction of *Eosaukia rectangula* Lu and Zhou 1990, based on figs. 4–10 in Lu and Zhou (1990).

EOSAUKIA WALCOTTI (Mansuy 1915)

Figure 22.4–10.6; Text-Figure 18

Ptychaspis walcotti MANSUY 1915, p. 22, pl. 3, figs. 16a–16b, pl. 4, figs. 1a–1z; SUN 1924, p. 68, pl. 5, fig. 2; KOBAYASHI 1931, p. 183, pl. 22, figs. 18, 19.

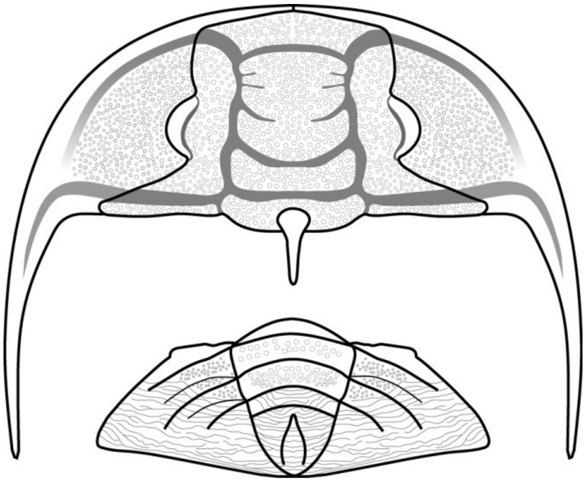
Calvinella walcotti KOBAYASHI 1933a, p. 254; LU 1957, p. 285, pl. 148, fig. 5; LU ET AL 1965, p. 451, pl. 88, figs. 13–16; LI AND YIN, 1973, p. 30, pl. 2, fig. 3; YIN AND LEE, 1978, p. 517, pl. 171, fig. 4.

"Calvinella walcotti" SUN AND XIANG, 1979, p. 11, pl. 3, fig. 11; ZHU, 1982, p. 295, pl. 1, figs 7–8; pl. 2, fig. 6; pl. 3, fig. 1.

Eosaukia walcotti KOBAYASHI 1956, p. 281, pl. 40, figs. 1–4; ZHU, 2011, pl. 13, figs. 1–15; pl. 14, figs. 1–8; pl. 15, figs. 1–21.

Eosaukia sp. cf. *E. walcotti* SHERGOLD 1991, p. 22, pl. 5, figs. 10–19.

Mictosaukia walcotti SHERGOLD 1975, p. 143.



Text-figure 8. Reconstruction of *Eosaukia walcotti* (Mansuy 1915).

Diagnosis.—A species of *Eosaukia* with an occipital spine and fine pustulation of cranidium. Posterior limbs triangular. Glabella narrows anteriorly; S2 furrow distinct, posteriorly-directed, straight; S3 furrow short, shallow, transverse; very faint, slightly forward-direct S4 present in well-preserved cranidia. Librigenae with lateral and posterior border furrows not confluent; lateral border furrow shallows and ends anterior of genal angle; posterior border furrow extends into genal spine. 11 thoracic segments;

very long dorsal axial spine extends posteriorly from thoracic segment 5 toward pygidium. Pygidium transversely ovate; three pygidial axial rings; two stout triangular ridges on terminal piece; terminal piece extends to pygidial posterior margin.

Discussion.—Shergold included *Eosaukia walcotti* in *Mictosaukia* when he revised these species in 1975, but cited no diagnostic morphological reason for doing so. Shergold (1975, p. 143) noted in the diagnosis for the new genus *Mictosaukia*, however, that the "... lateral and posterior marginal furrows terminate together in front of the genal spine base," without either furrow extending into the genal spine itself; this is one of the key morphological characters of *Mictosaukia* that carries phylogenetic signal. Shergold (1991) included this species in *Eosaukia*, noting the presence in *E. latilimbata* of posterior librigenal furrows that terminate prior to the base of the genal spine. In describing *E.* sp. cf. *E. walcotti* recovered from the Pacoota Sandstone in Australia, Shergold (1991, p. 22) notes that "...weak posterior border furrows continue into the base of the genal spine, but are not confluent with the lateral furrows. New articulated material recently described by Zhu (2011, unpublished doctoral thesis, three specimens reproduced herein as Figures 10.4–10.6) from South China near the type locality for *Eosaukia walcotti* indicates that the arrangement of librigenal furrows as described in Shergold (1991) is correct (see Figure 10.4). Because it appears that Mansuy's original (1915) material may be lost, the new Chinese material (currently not reposited) is exceptionally important, and we urge that it be reposited in the NIGPAS collections so that lectotype material can be designated. This new material shows all of the characters that were obvious in Mansuy's 1915 (slightly deformed) material; an occipital spine, the pustulated cranidial prosopon, non-confluent lateral and posterior librigenal furrows, and the short (sagittally), transverse pygidium (see Figs. 10.4–10.6). Additional characters that could not be detected in the photographs in Mansuy (1915) include the pustulated prosopon of the librigenae, the eleven articulated thoracic segments, the long axial spine inserting in thoracic segment five, and the two elongate-triangular pygidial spines on the terminal piece (see Figs. 10.4–10.6). Together, these characters indicate that a more correct systematic placement for *E. walcotti* is within *Eosaukia*, and we confirm Lee and Choi (2011) placement therein.

However, the current placement within *Eosaukia* is also not without systematic problems. One of the synapomorphies revealed for this genus by our analyses is the presence of vincular structures on the posterior part of the librigenal ventral doublure. These structures (see Figure 21.5 for an example in *E. angustilimbata*). Such structures are currently unknown in *E. walcotti*, even where limited ventral preservation exists. This could be due to lack of preservation, a very limited number of vincular structures, or to true absence. It is not currently known if this type of coaptative structure is actively coded for during development (genotypic), or passively constructed in the post molt phase by a combination of enrollment and pliable cuticle (phenotypic) (see discussion also above under *E. latilimbata*). Even with the lack of this character, *E. walcotti* is united with the *Eosaukia* by lack of a preglabellar field, possession of three glabellar furrows, a sagittally compressed pygidium with four or less axial rings, and generally, possession of two triangular ridge-like processes on the pygidial terminal piece that are in connection with the posteriormost pygidial axial ring.

Genus LICHENGIA Kobayashi 1942a

Type species.—*Lichengia onigawara* Kobayashi 1942, from the late Cambrian (Fengshanian) Licheng Formation, Shangyaochen, Licheng, Shanxi, north China.

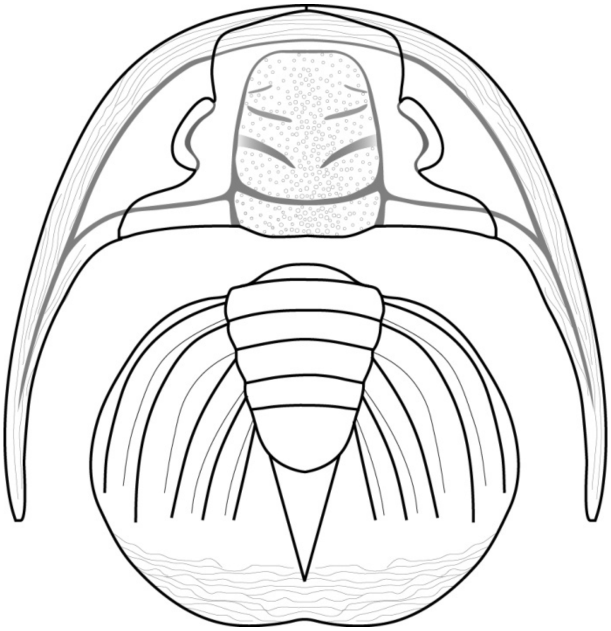
Discussion.—See Shergold (1991) for a complete discussion of this genus.

LICHENGIA SIMPLEX Shergold 1991

Figure 23.1–23.2; Text-Figure 19

Lichengia simplex SHERGOLD, 1991, p. 27, pl 4, figs. 1–7.

Type material.—CPC26771 (holotype), CPC26772-26862 (paratypes).



Text-figure 9. Reconstruction of *Lichengia simplex* Shergold 1991, based on specimens CPC 26771, 26775- 26776, 26779.

Diagnosis.—A species of *Lichengia* with up to four pairs of pre-occipital, sagittally-discontinuous glabellar furrows; glabellar anterior truncate or gently indented. Lateral and posterior librigenal border furrows confluent, confluence occurs substantially within genal spine; combined librigenal furrow extends considerable distance along genal spine; subcircular to subtrapezoidal pygidium with five axial rings; terminal piece rounded. Wide, triangular postaxial ridge extends from posterior terminal piece nearly to posterior pygidial margin. (After Shergold, 1991).

Discussion.—The gross morphological resemblance of this genus to the Laurentian genus *Prosaukia* was noted by Shergold (1991); it has a distinct preglabellar field, a rather flattened glabellar anterior, and a subcircular pygidium with many axial rings and a distinct postaxial ridge, all characters shared with *Prosaukia*. *Lichengia simplex*, however, is unique among saukiid species in possessing an S1 furrow that is interrupted across the medial part of the glabella. The configuration of the genal spine furrow is also unique; the lateral and posterior librigenal furrows are confluent as in many members of *Prosaukia*, but in *Lichengia simplex*, the point of confluence of these furrows is shifted posteriorly well into the genal spine. Additionally, *L. simplex* has definitively yoked librigenae, a character that Fortey and Chatterton (1988) consider derived.

In our analysis, *L. simplex* plots between *Saukiella* and *Briscoia*, due to the shared presence of the preglabellar field. This node is also close to *Hamashania*, a dikelocephaliid that also possesses an interrupted S1 furrow, and to *Dikelocephalus minnesotensis* a dikelocephaliid that is also known to have yoked librigenae through at least part of its ontogeny (see Hughes, 1994). Thus, due to the intermediate nature of the characters that it possesses, the position of *L. simplex* on the tree appears to be well-founded.

Genus LINGUISAUKIA Peng 1984

Type species.— Linguisaukia spinata Peng 1984.

Diagnosis.—A genus of Saukiidae differentiated by possession of small, arcuate palpebral lobes located posterior to glabellar midlength. Glabella parallel-sided or narrowing very slightly anteriorly; preglabellar part of axial furrow relatively wide, evenly concave; two pairs of pre-occipital furrows only, S3 absent. Anterolateral corners of cranidium subtriangular; abaxial portions of anterior border furrow straight, extend anterolaterally to cranidial corners. Relatively flat anterior cranidial border extended anteriorly into a triangular process; anterior of this process acutely rounded. Occipital spine present, very long. Librigenae with anterior prong, or flag-like process at the anterior; genal spine very long, longer than body in articulated examples. Pygidium transversely ovate; 3 axial rings present; lateral pleurae unequally divided. Terminal piece extends to posterior pygidial margin; slight invagination of axial pygidial posterior margin.

Discussion.—This genus is grossly similar to other genera of Saukiidae that have an anteriorly-directed process of the anterior cranidial border: *Danzhaisaukia*, *Lophosaukia*, and *Sinosaukia*. All four of these genera occur in south China (*Lophosaukia* also occurs in Australia), all have an anteriorly-directed process at the anterior of the cranidium, all are pustulated, and all with the exception of *Danzhaisaukia* have rather short (sagittally) pygidia with low counts of axial rings and terminal pieces that reach the pygidial posterior margin. However, all are morphologically incompatible with *Linguisaukia*. *Danzhaisaukia* is dissimilar to *Linguisaukia* in that the glabella of the former is more parallel sided, the palpebral lobes are much more anteriorly-located, the cranidial anterior limbs of the facial suture are divergent forward, lacks an occipital spine, and the posterior limbs are much more triangular. *Lophosauki*a has small, posteriorly-situated palpebral lobes, but is dissimilar in having an anterior glabellar lobe that lies below the level of the occipital lobe, a strongly inscribed preglabellar furrow that undercuts the anterior lobe of the glabella, and a downsloping triangular extension of the cranidial anterior border; it also lacks an occipital spine (see Figures 23.3 - 24.4). *Sinosaukia* has markedly posteriorly-directed posterior limbs of the cranidium, and a glabella that is either parallel-sided, or expanding anteriorly. Additionally, all three of these genera lack an occipital spine and have librigenae in which the lateral and posterior border furrows are not confluent; *Linguisaukia* has both of these conditions in addition to very long, gracefully curving genal spines and thus represents a distinct genus.

LINGUISAUKIA SPINATA Peng 1984

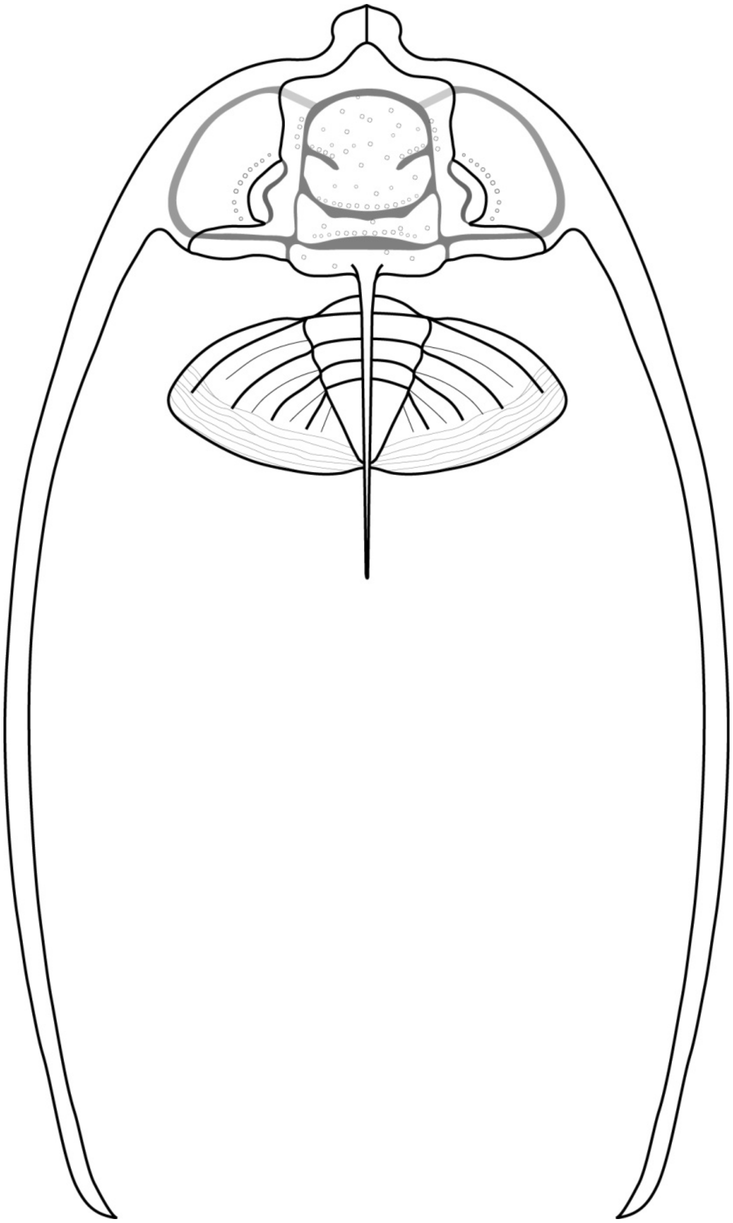
Figure 23.4–23.5; 24.1–24.2; Text-Figure 20

Linguisaukia spinata PENG, 1984, p. 347, pl. 6, figs. 4–8; LU AND ZHOU, 1990, p. 35, pl. 12, figs. 1–7, pl. 13, figs. 1–6.

Liguisaukia affinis PENG, 1984, p. 348, pl. 7, figs. 3–7; Lu and Zhou, 1990, p. 36, pl. 13, fig. 7.

Type material.—NIGPAS 83080a, 83080b (holotypes).

Other material examined.—NIGPAS 83078–83079, 83081–83082; 83088–83089, 83091–83092.



Text-figure 20. Reconstruction of *Linguisaukia spinata* Peng 1984, based on NIGPAS 83080a, 83080b (holotypes), 83078–83079, 83081, and photographs of lost material in Lu and Zhou 1990.

Diagnosis.—As per genus.

Discussion.—Peng (1984) named two species of *Linguisaukia* from outcrops in western Hunan, but noted in his original description of the second of these, *L. affinis,* that there were very few differences with which to differentiate them. Peng (1984) noted a parallel-sided glabella in *L. affinis*, in addition to the generally wider nature of the glabella. In the type specimen of *L. affinis* (NIGPAS 83088), there is significant damage to the left side of the crandium (see Figure 23.5), so the width of the glabellar lobes cannot be assessed accurately. However, the left axial suture can be traced along the left side of the glabella, and in relationship to the right axial furrow, the glabella tapers anteriorly. The apparent relative difference in width of the glabella between these species could be due to differences in the taphonomic factors (for example, differing sedimentation rates between outcrops might lead to variation in the amount of flattening experienced by exoskeletal sclerites). Because the parallel-sided nature of the glabella was the principle taxabase for *L. affinis,* and this can be demonstrated to be inconsistent with the type material, we synonymize *L. affinis* with *L. spinata*.

Beautifully preserved, fully-articulated material described and illustrated by Lu and Zhou (1990), and which was accessioned to the NIGPAS repository but never reposited, has subsequently been lost following the death of the senior author of that study. This is a tremendous loss for upper Cambrian trilobite paleontology in general, and for China in particular because this material was not only fully-articulated, but many specimens were also preserved in their ventral aspect, revealing the nature and articulation of the hypostome, as well as many other key diagnostic characters that could have helped refine the relationships of this group.

Genus LOPHOSAUKIA Shergold 1972

Type species.—*Lophosaukia torquata* Shergold 1972, from the Gola Beds, Momedah Creek, 19 km east-northeast of Black Mountain, Western Queensland, by original designation.

Diagnosis.—A genus of Saukiidae with anterior cranidial border reduced to a triangular area, either strongly sloping adventrally, or lying in a nearly horizontal plane. Anterior facial sutures subparallel to very slightly divergent. Preglabellar furrow deep, undercuts glabella frontal lobe; preglabellar field absent. (After Shergold, 1972).

Discussion.—Shergold (1972) discussed many of the Gondwanan taxa that resemble *Lophosaukia*, including *Sinosaukia*, noting that this latter genus was most probably the closest relative of *Lophosaukia*. Species of *Lophosaukia* have a triangular anterior projection (often downsloping) of the cephalic border, a glabellar anterior lobe that curves ventrally so that it lies below the level of the occipital lobe with a very deep preglabellar furrow that undercuts the anterior glabellar lobe (Shergold, 1972). Additionally, the prosopon of the glabella is usually very strongly developed. The genal spines of *Lophosaukia* generally have an inflection near the lateral origin of the spines so that they diverge slightly, and then converge posteriorly, giving the lateral margin of the genal spine a sinuous appearance. Pygidia of *Lophosaukia* are transversely ovate, sagittally compressed, and comprise very few (2 or 3) axial rings with the terminal piece extending all the way to the pygidial posterior margin.

As noted previously, among Gondwanan Saukiidae taxa, there are other genera in addition to *Lophosaukia* that possess a triangular process of the anterior cephalic border. *Sinosaukia* has a convex anterior border, with a glabellar anterior lobe that does not lie significantly below the level of the occipital ring. Additionally, the preglabellar furrow in *Sinosaukia* is much shallower, has a concave bottom, and does not undercut the anterior glabellar lobe. The genal spine in *Sinosaukia* can also have an inflected, sinuous lateral margin, but generally converge much more strongly posteriorly than do genal spines of *Lophosaukia*. Both species have similar pygidia.

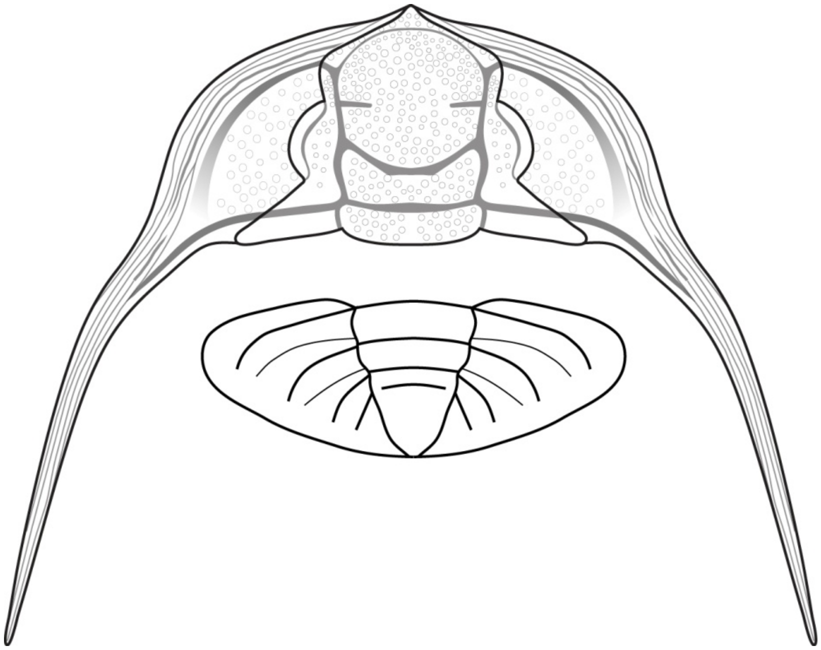
Linguisaukia has a more strongly developed preglabellar furrow than does *Sinosaukia*, both in terms of its width and depth, but the furrow is more evenly concave and does not undercut the glabellar anterior lobe. Additionally, *Linguisaukia* possesses a long occipital spine, a morphological feature not present in either *Sinosaukia* or *Lophosaukia*.

LOPHOSAUKIA TORQUTA Shergold 1972

Figure 23.3; Text-Figure 21

Lophosaukia torquta SHERGOLD, 1972, p. 62, pl. 18, figs. 1–6; text fig 18; SHERGOLD, 1975, p. 135, pl. 18, figs. 1–6.

Type material.— CPC 9765 (holotype).



Text-figure 10. Reconstruction of *Lophosaukia torquata* Shergold 1972, based on specimens CPC 9765–9766, 11779, 11781–11782.

Diagnosis.—A species of *Lophosaukia* with a short, acutely pointed, distinctly downsloping anterior cephalic projection. Glabella widens slightly anteriorly; cranidium strongly pustulated. Librigenal border with very strong subparallel striations; librigenal field pustulated. Pygidium with three axial rings.

Discussion.—*Lophosaukia torquata* is distinguished from other members of the genus based on the slight widening of the glabella anteriorly, the strong striation of the librigenal borders, and the short, acutely pointed and downsloping anterior projection. See Shergold (1972, 1975) for further discussion.

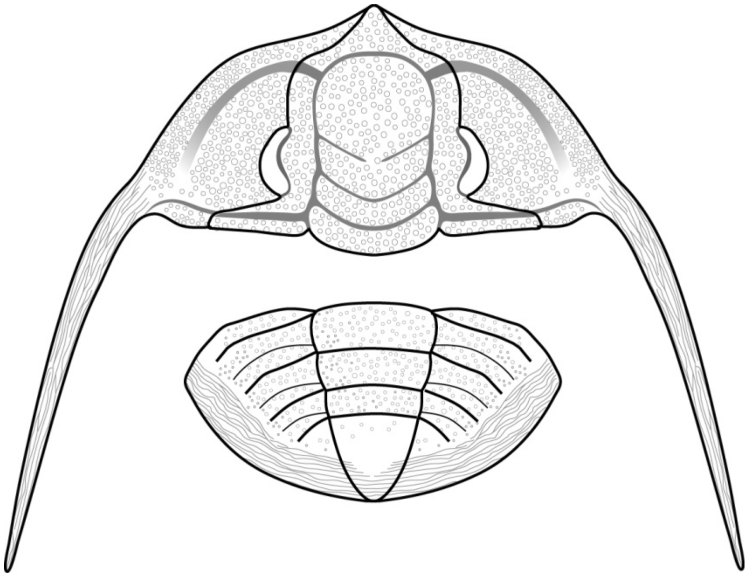
LOPHOSAUKIA JIANGNANENSIS Lu and Lin 1984

Figure 24.3–24.4; Text-Figure 22

Lophosaukia jiangnanensis LU AND LIN, 1983, pl. 3, figs. 5–8; LU AND LIN, 1984, p. 98, pl. 11, figs. 3–10.

Type material.—NIGPAS 83542 (holotype).

Other material examined.—NIGPAS 83535–83541.



Text-figure 11. Reconstruction of *Lophosaukia jingnanensis* Lu and Lin 1983, based on specimens NIGPAS 83542 (holotype), 83535–83541.

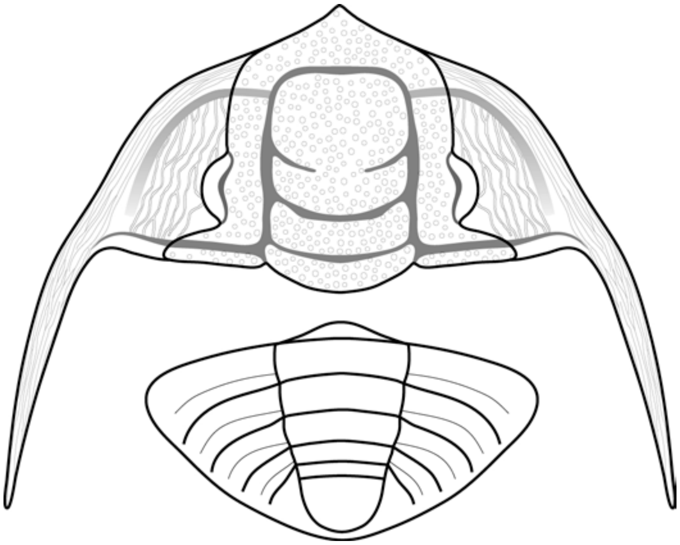
Diagnosis.—A species of *Lophosaukia* with a relatively long, obtusely rounded anterior projection of anterior cranidial border. Glabellar sides parallel. Librigenae with strongly pustulated lateral border; genal spine distinctly advanced; strong inflection present at lateral origin of genal spine. Genal spine strongly ornamented with anastomosing, raised subparallel ridges.

LOPHOSAUKIA RECTANGULATA Ergaliev 1980

Text-Figure 23

Lophosaukia rectangulata ERGALIEV, 1980, p.158, pl. 20, figs. 12–14.

Type material.—KGS 1950/325 (holotype).



Text-figure 12. Reconstruction of *Lophosaukia rectangula* Ergaliev 1980, based on KGS 1950/325 and 1950/327.

Diagnosis.—A species of *Lophosaukia* with a slightly flattened glabellar anterior. Palpebral lobes relatively widely-spaced away from axial furrow. Librigenal field ornamented with raised, wavy, anastomosing ridges.

Discussion.—The primary distinction between this species and *L. jingnanensis* and *L. torquata* is the ornamentation of the librigenal field. This species is also purported to possess an occipital median tubercle, but the specimens could not be secured to confirm these morphological characters. The articulated specimen, KGS 1950/327 was reported by Ergaliev (pl. 20, fig. 13, Ergaliev,1980) to have only eight thoracic segments. However, this crucial detail could not be confirmed from the published photograph of the specimen. It appears that the pygidium of the articulated specimen is displaced slightly from the thorax; additionally, the entire cephalon is rotated slightly counterclockwise from the orientation of the thorax (see pl. 20, fig. 13 of Ergaliev, 1980). Thus. while eight thoracic segments are preserved in KGS 1950/327, that number may be a minimum estimate of the total number of thoracic segments due to possible telescoping , or to segments being pushed beneath the cephalic or pygidial areas.

The distribution of this species is striking considering the range of other species of *Lophosaukia* known. Species of *Lophosaukia* are known from Australia, Kazakhstan, and North and South China. Thus, this genus had managed to disperse widely along core Gondwanan terranes and to cross the presumably shallow, narrow seas that separated these regions. Because this genus is not found in Siberia or Laurentia, this distribution argues for either a closer placement of Kazakhstan with terranes of core Gondwana, or alternatively suggests that a combination of westward ocean surface currents in combination with island arcs that may have been associated with the Panthalassic subduction zone allowed this genus to expand its range via 'island-hopping' to Kazakhstan.

Genus MICTOSAUKIA Shergold 1975

Type species.—Tellerina orientalis (Resser and Endo, *in* Endo and Resser 1937), from the Wanwan Formation, near Tawankou, Liaoning, North China.

Emended diagnosis.—A genus of Saukiidae with a slightly convex cranidium; glabella generally parallel-sided to slightly constricted in middle; preglabellar field absent; anterior border long (sag.); anterior border furrow nearly transverse abaxially. Palpebral lobe midpoint located posteriorly to glabellar mid-length, detached from axial furrows. Lateral and posterior librigenal furrows confluent, joining in a C-shaped bend; genal spine furrow absent; genal spines not advanced. Pygidium subisopygous; axis narrow, posterior border broad and concave. (After Lee and Choi, 2011).

Discussion.—This genus is most closely related to the morphologically similar Laurentian genus *Saukia*. The main morphological difference between *Mictosaukia* and *Saukia* is the arrangement of librigenal furrows; in *Mictosaukia*, the furrows are conjoined into a single border furrow with a C-shaped, or acutely-angled transition anterior to the genal angle. There is no trace of a furrow extending into the genal spine or its base. In this respect it is very similar to some species of *Eosaukia*, with which it has been confused. *Eosaukia* species have vincular notches on the ventral librigenal doublure; thus, if librigenae are preserved in the ventral aspect, distinction between these two genera can be made with considerable ease.

MICTOSAUKIA GLOBOSA (Robinson and Pantoja-Alor 1968)

Figure 24.6–24.7; Text-Figure 24

Saukia globosa ROBINSON AND PANTOJA-ALOR, 1968, p. 795, pl. 104, figs. 12–19.

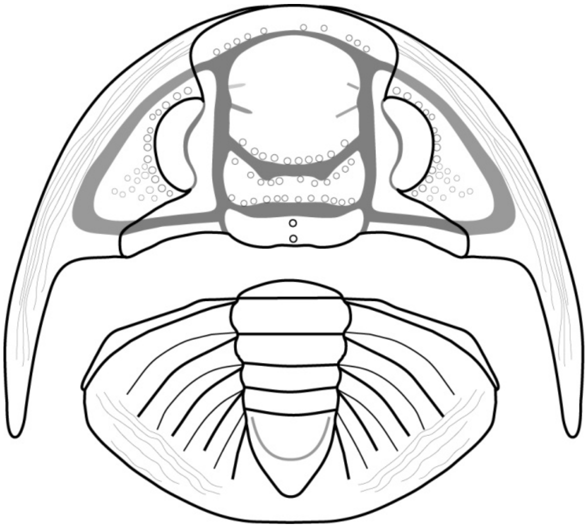
cf. *Mictosaukia globosa* SHERGOLD, 1975, p. 143; SHERGOLD, 1991, p. 23.

Saukia cf. *S. rotunda* LEE AND CHOI, 2008, p. 220, fig. 2.

Mictosaukia cf. M. *globosa* LEE AND CHOI, 2011, p. 282, figs. 3.1, 4.

Type material.—USNM 159043 (holotype).

Other material examined.—USNM 159041, 159042, 159044–159048, paratypes.



Text-figure 13. Reconstruction of *Mictosaukia globosa* (Robinson and Pantoja-Alor 1968), based on USNM 159043 (holotype), 159041, 159042, 159044–159048, and photographs in Lee and Choi (2011).

Diagnosis.—A species of *Mictosaukia* with two medial occipital nodes arranged along sagittal axis. Sides of glabella parallel. Anterior facial suture slightly divergent.

Discussion.—This species occurs both on the north China block (Korean peninsula) and Laurentia (Mexico) (see Robinson and Pantoja-Alor, 1968; Lee and Choi, 2011). *Mictosaukia* is a widely distributed genus, occurring in north China, south China, Afghanistan, Iran, Turkey, and Mexico (Lee and Choi, 2011), and the vast majority of the species assigned to this genus occur in areas within the north China block. This distribution suggests that *Mictosaukia* cladogenesis likely occurred in north China (due to most occurrences of the genus there), spread along northern coastal Gondwana into south China, along the western peri-Gondwana margin to Afghanistan, Iran, and Turkey, before dispersing at least once across the Iapetus to Laurentia. The observed distribution of *M. globosa* in both North China and extreme western Laurentia (but not in Kazakhstan) suggests that there may have been a eastward flowing northern Panthalassic current that carried saukiid larvae eastward depositing them on the western margin of Laurentia.

Occurrence.—Collections 16001d, 16002c, and 16000d of Robinson and Pantoja-Alor (1968), Tinu Formation, Oaxaca, Mexico; units SCO23 and 24 of Lee and Choi (2011), Dongjeom Formation, Taebaeksan Basin, Korea.

MICTOSAUKIA LUANHENSIS Zhou and Zhang 1978

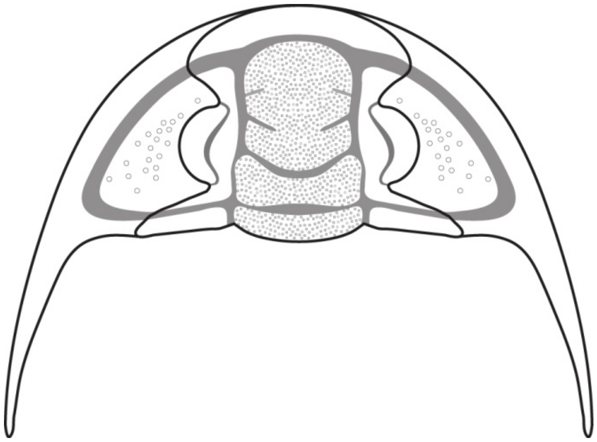
Figure 25.1–25.3, Text-Figure 25

Mictosaukia luanhensis ZHOU AND ZHANG, 1978, p. 8, pl. 1, figs. 18–21; ZHOU AND ZHANG, 1985, p. 104, pl. 7, figs. 8, 9; pl. 26, figs. 10–14; pl. 28, fig. 11; ZHANG AND WANG, 1985, p. 474, pl. 143, figs. 9–11; DUAN ET AL.,1986, p. 48, pl. 7, figs. 11–14; pl. 8, fig. 4; ZHU AND WITTKE, 1989, p. 228, pl. 13, fig. 12; ZHANG ET AL.,1996, p. 84, pl. 37, figs. 3–7.

Type material.—NIGPAS 46578 (holotype).

Other material examined.—NIGPAS 46578–46581, 78823–78824, 79094, 100028 (*M. striata)*.

Diagnosis.—A species of *Mictosaukia* with a finely-tuberculate cranidium. Anterior of palpebral lobe located close to glabellar axial furrow; anterior branch of facial suture strongly divergent. Abaxial portion of anterior border furrow extends slightly posterolaterally.



Text-figure 14. Reconstruction of *Mictosaukia luanhensis* Zhou and Zhang 1978, based on specimens NIGPAS 46578 (holotype), 46578–46581, 78823–78824, 79094.

Discussion.—Zhou and Wittke (1989) assigned a single cranidium from Tangshan, Heibei Province, North China to this species based on the density and size of tubercles covering the crandium. *Mictosaukia orientalis*, which co-occur with *M. luanhensis* in the same bed (Tzwh 22 of Zhou and Wittke, 1989) have a more strongly-diverging anterior facial suture in addition to the lack of ornamentation of the cranidial surfaces that is more typical of *M. orientalis*. The anterior branch of the facial suture in *M. luanhensis* is much less strongly divergent, and is nearly parallel to the axis of the cranidium; thus it is unlikely that the cranidium of *M. luanhensis* in Zhou and Wittke (1989) represents an extraordinarily-preserved *M. orientalis*. However, the anterior border in Zhou and Wittke's *M. luanhensis* specimen (NIGPAS 100028) is distinctly striated; a distinctly striated anterior border is a character of *M. striata*, a species that also occurs in North China in nearby Jilin province. *Mictosaukia striata* has more parallel-sided facial sutures, anterior border furrows that are closer to perpendicular to the body axis, and also has a densely tuberculated prosopon; all features that NIGPAS 100028 possesses. Thus, it is probable that the specimen assigned by Zhou and Wittke (1989) to '*M. luanhensis*' represents a specimen of *M. striata*.

MICTOSAUKIA ORIENTALIS (Resser and Endo *in* Endo 1931)

Figure 25.4–25.7; Text-Figure 26

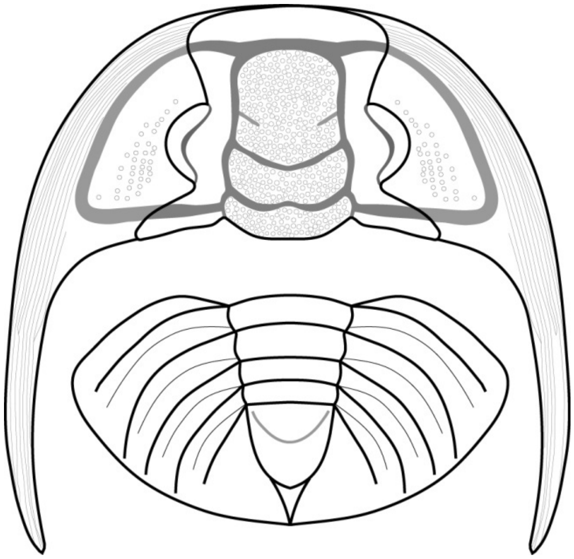
Tellerina orientalis RESSER AND ENDO *IN* ENDO, 1931, p. 89, text-fig. 38, figs. 1–7; RESSER AND ENDO *IN* ENDO AND RESSER, 1937, p. 293, pl. 57, figs. 1–7.

Tellerina paichaiensis KOBAYASHI, 1933, p. 130, pl. 13, fig. 9; LU ET AL., 1965 p. 455, pl. 89, fig. 12 (refigure of Kobayashi 1933 cranidium).

Mictosaukia orientalis SHERGOLD, 1975, p. 143; ZHOU AND ZHANG, 1978, p. 7, pl. 1, figs. 4–17; QIAN, 1985, p. 80, pl. 17, figs. 5–11; Zhang and Wang, 1985, p. 474; ZHANG AND JELL, 1987, p. 235, pl. 116, figs. 11–12; pl. 117, figs. 1–3; ZHU AND WITTKE, 1989, p. 228, pl. 11, figs. 12–13; pl. 13, figs. 8–11; pl. 14, figs. 1–6; LEE AND CHOI, 2011, p. 295.

Type material.—USNM 86927 (four syntypes).

Other material examined.—NIGPAS 78726, 78739–78742, 78760–78763, 78780–78783, 78821–78822, 78968–78970, 78994–78997, 79039, 79090–79093, 79119–79123, 100008–100009, 100024–100027, 100029–100034.



Text-figure 15. Reconstruction of *Mictosaukia orientalis* (Resser and Endo in Endo 1931), based on USNM 86927, NIGPAS 78726, 78994–78996, 79121, 79090, 79095.

Diagnosis.—A species of *Mictosaukia* with an anteriorly tapering glabella. Anterior facial suture divergent. Abaxial part of anterior border furrow angled slightly anterolaterally; furrow slightly divergent.

Discussion.—Several authors have placed *M. orientalis* into synonymy with *M. chinhsiensis* (Sun, 1924), including Shergold (1975), Zhu and Zhang (1978), and Zhu and Wittke (1989). Zhang and Jell (1987) stopped short of synonymizing these two species, but noted their similarity, as well as variability of certain characters within *Mictosaukia orientalis*, specifically the orientation of the abaxial part of the cranidial anterior border furrow, which can be anterolaterally- or transversely-directed (Zhang and Jell, 1987). The cranidia of the type material of *Mictosaukia orientalis*, (labeled *Tellerina orientalis*, USNM 86927), have a flat or slightly acuminate anterior cranidial margin, and the abaxial part of the anterior border furrows are anterolaterally directed at between approximately 15 to 17 degrees; thus, within the type material of this species (3 cranidia), the abaxial part of the anterior border furrow is not variable in its orientation. Additionally, the type material is largely exfoliated, so details of the prosopon are lacking. The type material for *M. orientalis* comes from the Fengshan Formation (Endo's Wanwan Fm), near Tawankou, Liaoning, North China.

Mictosaukia chinhsiensis has a much more rounded cranidial anterior margin, a longer (sagittally) preglabellar furrow, abaxial portions of the anterior border furrow that are transverse or slightly posteriorly-directed, a lower length-to-width ratio of the glabella, and a glabella which does not narrow anteriorly to as great an extent as does that of *M. orientalis*. *Mictosaukia chinhsiensis* is much more similar to *M. striata* in these morphological details; thus we prefer to retain both *M. orientalis* and *M. chinhsiensis* as separate, valid species.

MICTOSAUKIA STRIATA (Resser and Endo 1937)

Figure 25.8–25.9; 26.1–26.4; Text-Figure 27

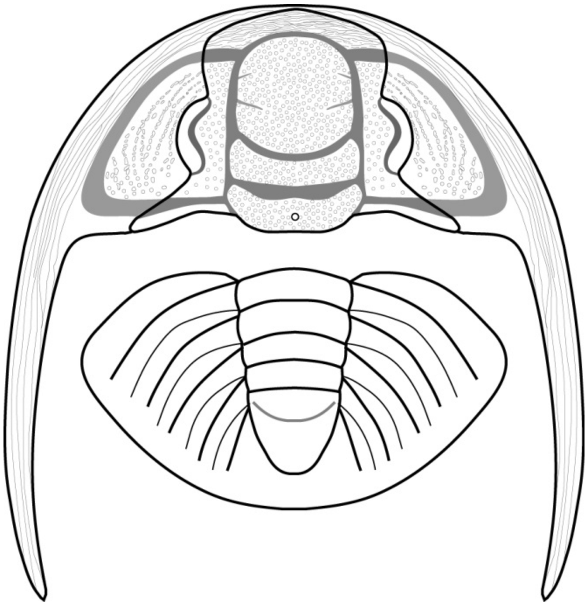
Calvinella striata, RESSER AND ENDO *IN* ENDO AND RESSER, 1937, p. 189, pl. 56, figs. 24, 25; LU ET AL., 1965, p. 450, pl. 88, figs. 8, 9 (refigure of Resser and Endo, 1937 material); YIN AND LEE, 1978, p. 517, pl. 171, fig. 3.

Mictosaukia striata, PENG, 1984, p. 350; ZHOU AND ZHANG, 1984, p. 104, pl. 1, fig. 4; pl. 4, fig. 13, pl. 7, figs. 1–3; pl. 11, fig. 4, pl. 12, figs. 4–7, pl. 28, figs. 24–25; QIAN, 1985,

p. 81, pl. 16, figs. 3–6; pl. 17, figs 1–4; ZHOU AND ZHANG, 1985, p. 104; QIAN, 1986, p. 278, pl. 71, figs. 1–7, text-fig. 108; ZHANG AND JELL, 1987, p. 237, pl. 117, fig. 9; LEE AND CHOI, 2011, p. 295.

Type material.—USNM 86768 (holotype).

Other material examined.—NIGPAS 78743, 78784, 78816–78818, 78884, 78898–78901, 79127–79128, 83096–83099, 98758–98765.



Text-figure 16. Reconstruction of *Mictosaukia striata* (Resser and Endo, 1937), based on specimens USNM 86768 (holotype), NIGPAS 78901, 83098, 98758–98759, 98761, 98764.

Diagnosis.—A species of *Mictosaukia* with sides of glabella parallel, median occipital tubercle; anterior branch of facial suture only very slightly divergent (subparallel).

Anterior border of cranidium with distinct, raised, subparallel ridges. Abaxial part of anterior border furrow transverse.

Genus PACOOTASAUKIA Sohn and Choi 2005

Type species.—*Platysaukia jokliki* (Shergold, 1991), from the late Cambrian Pacoota Sandstone, Amadeus Basin, Northern Territory, Australia.

Emended diagnosis.—Genus of Saukiidae with broad rectangular glabella; S1 continuous across glabella; broad gently convex preglabellar area may or may not be differentiated into vague anterior border and preglabellar field. Palpebral lobes separated from axial furrows by quite wide fixigenae. Pygidium transversely ovate; four to seven axial rings, well-defined pleural furrows, faintly incised interpleural furrows. (After Sohn and Choi, 2005).

Discussion.—See discussion in Sohn and Choi (2005).

PACOOTASAUKIA JOKLIKI (Shergold 1991)

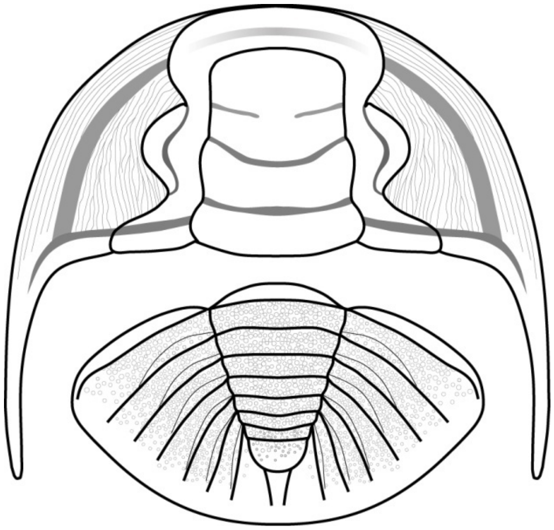
Text-Figure 28

Platysaukia jokliki SHERGOLD, 1991, p. 25, pl. 3, figs. 1–22; pl. 4, Figure 1.

Pacootasaukia jokliki SOHN AND CHOI, 2005, p. 201.

Dikelocephalus sp. ÖPIK, 1952, p. 1 (listed); ÖPIK IN JOKLIK 1955, p. 30 (listed).

Type material.—CPC26677 (holotype), CPC26678–6742 (paratypes).



Text-figure 17. Reconstruction of *Pacootasaukia jokliki* (Shergold 1991), based on CPC26677 (holotype), CPC26678–6742.

Emended diagnosis.—A species of *Pacootasaukia* with an anteriorly tapering occipital-glabella. Preglabellar area with only faint differentiation into anterior border furrow and preglabellar field; lacking any trace of preocular or laterally-continuous anterior border furrows. Pygidium transversely ovate to subcircular. (After Shergold, 1991).

Discussion.—Due to the type species of the genus *Platysaukia*, *P. euryrachis*, actually representing a poorly-preserved specimen of *Hamashania*, Sohn and Choi (2005) erected *Pacootasaukia* to contain valid saukiid species erected by Shergold (1991), but which he placed within the genus *Platysaukia* Kobayashi 1960. Because Sohn and Choi (2005) designated *Platysaukia* as a junior synonym of *Hamashania*, the two valid saukiid species that Shergold (1991) had assigned to this genus required reassignment to a valid genus. Thus, Sohn and Choi (2005) erected the genus *Pacootasaukia* to contain the two saukiid species displaced by this synonymy.

Overall gross morphology of this species is similar to that of the Laurentian genus *Prosaukia*, but *Pacootasaukia* is distinguished from all other species of saukiid by its shallow anterior border furrow which is prominent only in the area lying immediately anterior to the glabella; the lateral portions of the anterior border furrow are cryptic (see Shergold, 1991, plate 3, figs. 1–22).

Genus PROSAUKIA Ulrich and Resser 1933

Emended diagnosis.—A genus of Saukiidae typically with a subrectangular glabella that narrows slightly anteriorly. Anterior limb of facial suture convergent anteriorly. Cranidial frontal area divided into a preglabellar field and an inflated anterior cranidial border; preglabellar field lying distinctly below the level of the anterior border (in small holaspids). Pre-occipital glabellar furrows shallow or terminate before reaching axial furrow; S1 furrow complete across glabella medially, all other glabellar furrows interrupted across glabella. Pygidium transversely ovate, pleurae usually equally divided, distinct postaxial ridge present. (After Ludvigsen and Westrop, 1983).

Discussion.—Ulrich and Resser (1933) named a plethora of *Prosaukia* species, often based on very incomplete material, very slight morphological differences, material that had been collected from different intervals, at different outcrops, localities, and formations, and often paired cranidia and pygidia from such different stratigraphic intervals when naming species (Ulrich and Resser, 1933; examples given in Raasch, 1951; Lochman, 1956; Sundberg, 2007). Indeed, to illustrate the tenuous nature of their taxabases, *Prosaukia welleri*, described by Resser (1942) possesses all of the specific characters for *Saukia acuta*: swollen lateral occipital lobes, strong pustulated prosopon, a rounded glabellar anterior, and glabellar sides that distinctly taper anteriorly.

Raasch (1951) synonymized many of Ulrich and Resser's (1933) species, subspecies, varieties, and 'hybrids', but did so based largely on stratigraphic, rather than morphological criteria. Even so, the synonymy for *Prosaukia* listed in Raasch (1951) is in general agreement with the purely morphological treatment used herein. Of the 29 *Prosaukia* taxa erected by Ulrich and Resser (1933), Raasch (1951) considered only the following species as representing unambiguous species of *Prosaukia*: *P. ampla*, *P. beani*, *P. curvicostata*, *P. delecostata*, *P. dilata*, *P. halli*, *P. longa*, *P. longicornis*, *P. misa*, *P. tuburculata*, and *P. valida*. It should be noted that in addition to *P. ampla*, there is a species of *Saukiella*, *S. ampla* that shares the same species name. The following section gives a brief morphological discussion of each of these.

Prosaukia ampla Ulrich and Resser, 1933 (p. 157, pl. 27, figs 22–25) is morphologically similar to *P. longicornis* [compare Ulrich and Resser, 1933, pl. 27, figs. 12–21 (*P. longicornis*) with pl. 27, figs. 22–25 (*P. ampla*)]. There is no trace of cranidial ornament in either species, but librigenae attributed to *P. longicornis* have wavy, anastomosing, raised ridge-like ornamentation, similar to the ornamentation observed on a librigena attributed to *P. misa* (USNM 14490). Librigenae are not known from *P. ampla*, and the pygidia attributed by Ulrich and Resser (1933) to *P. ampla* are both incomplete. Both *P. ampla* and *P. longicornis* have occipital spines (although the length of these in *P. ampla* is unknown due to damage), and are thus morphologically distinct from *P. misa*. Ulrich and Resser (1933) report (p. 158) that they, "...have no reason to believe that the occipital spine [of *P. ampla*] can possibly have attained anything like the length commonly observed in *P. longicornis.*" This statement is indefensible from a systematics standpoint, because these authors did not possess any material of *P. ampla* with undamaged occipital spines to compare with *P. longicornis*. Ulrich and Resser (1933) also noted a slightly more curved nature of the glabellar furrows in *P. ampla* when compared to *P. longicornis*. However, in their plate 27, figs. 14, 18, and 19, *P. longicornis* has glabellar furrows that are curved to a similar extent to those of *P. ampla* in plate 27, fig. 22 (Ulrich and Resser, 1933), thus this character falls within the range of variation known in *P. longicornis*. Unfortunately, pygidia of these two taxa cannot be compared directly due to the damaged and incomplete nature of the pygidia assigned to *P. ampla*. Because of the lack of any taxabase with which to distinguish *P. ampla* from *P. longicornis*, we synonymize the former with the much more completely known species, *Prosaukia longicornis*.

Prosaukia beani Ulrich and Resser 1933 was erected based on a single cranidium (USNM 84571) that was purported to be pustulated by these authors. An examination of Ulrich and Resser's (1933) material reposited in both the USNM and UWGM suggests that preservation of prosopon in nearshore sandy facies in Minnesota and Wisconsin depends on: 1) the nature of the cuticular ornament (its scale), 2) the grain size of the sand in which the specimens were preserved, and 3) local taphonomic conditions. In nearly every species of saukiid, dikelocephaliid, ptychaspidid, and pterocephaliid trilobite examined during the course of this study, there is some trace of cuticular ornamentation preserved. Thus, even in saukiid species that 'lack' cuticular ornamentation, it is likely that they possessed ornamentation during life. The cranidial pustulation reported by Ulrich and Resser (1933), however, cannot be detected in a re-examination of the *P. beani* type specimen, even under oblique lighting and magnification. Ulrich and Resser (1933) also noted the damaged and incomplete posterior part of the occipital ring in this specimen. However, in spite of this missing cuticle, they still inferred that this cranidium possessed an occipital spine based on the assumed "... evident relations to *P. granosa* and *P. halli*," (Ulrich and Resser, 1933, p. 166). This specimen neither shows distinct cuticular prosopon, nor any indication of an occipital spine; in all other detectable ways, this cranidium is indistinguishable from *P. misa*, to which it is herein referred.

The cranidia associated with *Prosaukia curvicostata* are rather indistinct from other species of *Prosaukia* that occur in Wisconsin and Minnesota; the glabellar anterior is perhaps more rounded than in *P. misa*, the S2 furrows are very slightly impressed, posteriorly directed, and rather straight. A pair of very short, very faint S3 furrows are occasionally visible, and are angled anteriorly. The pygidium of *P. curvicostata*, however, is rather distinctive; it has four axial rings in the pygidium, pleural and interpleural furrows that are approximately equally divided and become nearly parallel with the sagittal axis in the posterior half of the pygidium. There is a slight median inflection of the posterior pygidial margin, a strongly expressed postaxial ridge that extends all the way to the pygidial posterior margin, and a very long posterior pygidial border that is approximately 50% of the sagittal pygidial length. The librigenae has a very wide lateral border, and a lateral librigenal furrow that shallows, but appears to make contact with the posterior border furrow; also, the lateral furrow is not distinctly C-shaped as is the case in *P. misa*. Semi-parallel ridges ornament a rather wide librigenal lateral border; no other ornament known. All of these features are similar to *Prosaukia hartti*, to which this species is referred. *Prosaukia hartti* has additional details of cuticular ornament as outlined below.

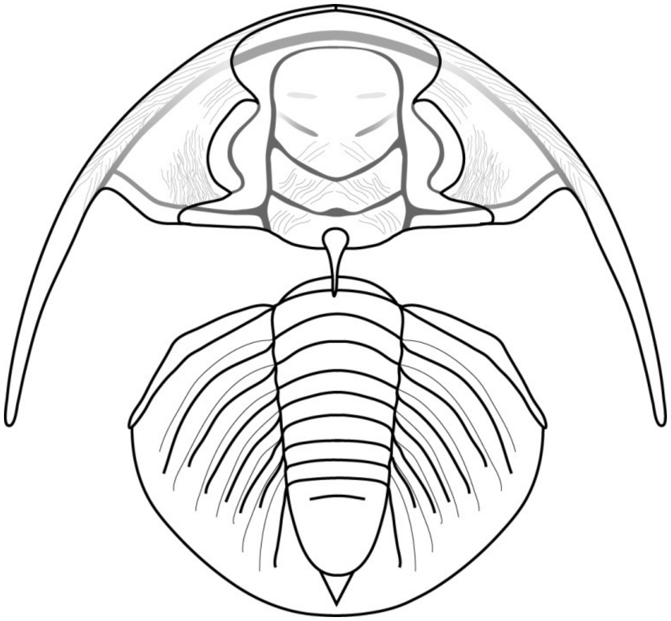
PROSAUKIA CORRUGATA Rasetti 1959

Figure 26.5–26.8; Text-Figure 29

Prosaukia corrugata RASETTI, 1959, p. 390, pl. 54, figs. 4–14.

Type material.—USNM 136962 (holotype).

Other material examined.—USNM 136963 (box listed as syntype, containing multiple figured and un-figured specimens), USNM 137142 (box with multiple un-figured specimens).



Text-figure 18. Reconstruction of *Prosaukia corrugata* Rasetti 1959, based on specimens USNM 136962 (holotype), 136963, 137142.

Diagnosis.—A species of *Prosaukia* with an occipital spine, closely-spaced fingerprint-like raised ridge prosopon on cephalon. Librigenae with lateral and posterior furrows confluent; posterior librigenal furrow continuing into base of genal spine. Pygidium with narrow axis; eight to ten axial rings.

Discussion.—This species of *Prosaukia* has a long, nearly circular pygidium with up to ten axial rings. Because pygidia where a count of axial rings can be made with accuracy are all fairly large, it is unlikely that such large pygidia of this species contain unreleased segments.

The frontal area of this species appears to vary throughout ontogeny. In small individuals, there is a distinct, slightly convex, furrow-bounded preglabellar field. In very large specimens, there is a relatively long (sagittally) convex preglabellar field defined at its posterior extent by a preglabellar furrow. Unfortunately, there are relatively few cranidia, and so a systematic ontogenetic study of the preglabellar field development is not possible at this time.

When Rasetti (1959) erected this species, he noted that it belonged to a group of prosaukiids described by Ulrich and Resser that lacked tuberculation and possessed an occipital spine. He further noted that comparison with the material from the upper Mississippi valley was not possible owing to the difference in lithology between the latter (sandstone) and Conococheague specimens (limestone) (Rasetti, 1959). However, a great many of the specimens from the upper Mississippi valley retain much of their original relief, and gross morphology can certainly be compared.

Prosaukia anomala Ulrich and Resser 1933, a similar, albeit more poorly known, species occurs in the Franconia Formation of Minnesota and Wisconsin. This species was referred to the invalid genus *Mareda* by Lochman (1956), and has subsequently been referred to *Suluderella* by Özdikmen (2006). However, in the very limited material of *P. anomala* known, the pygidium is quite similar to that of *P. corrugata* in its possession of ten axial rings and a distinct postaxial ridge extending to the posterior pygidial margin. Unfortunately, morphometric and shape analyses are not possible on the pygidia illustrated by Ulrich and Resser (1933) because of damage to both lateral margins. However, the angle of the interpleural furrow measured in different places along the axis in these species is similar [*P. corrugata*, USNM 136963, Rasetti (1959) pl. 54, fig. 6, between axial rings 1 and 2 = 28.5, between axial rings 5 and 6 = 54.1°; *S. anomala*, USNM 84572, between axial rings 1 and 2 = 37.1, between axial rings 5 and 6 = 57.2°].

The cranidia of these species differ markedly. The cranidium of the specimens attributed to *S. anomala* have an interrupted S1 furrow, rather large eyes, distinctly rounded glabellar anterior, and relatively short frontal area, and lack an occipital spine (see Ulrich and Resser, pl. 29, figs. 1–3); *P. corrugata* has a rather long occipital spine, uninterrupted S1 furrow, and eyes located much more rearward. Only one trilobite genus with a distinctly interrupted S1 furrow is included in our analysis, *Lichengia*, a Gondwanan taxa occurring in North China, Australia and Thailand. In our analysis, *Lichengia simplex* occupies a node between (*Saukiella* + *Prosaukia*) and the Dikelocephaliidae, indicating that it may be either a transitional saukiid or dikelocephaliid (see Figure 4.2). However, specimens of *S. anomala* recovered from the Franconia of Minnesota and Wisconsin do not co-occur on the same slabs, and so the cephalon many not represent a true association with the pygidia of this 'species'. Because of the lack of any real association between cephalic and pygidial sclerites of Ulrich and Resser's (1933) material, and because of the strong morphological resemblance in pygidia of *P. corrugata* and *S. anomala*, it is possible that the pygidium figured by Ulrich and Resser (1933) is conspecific with *P. corrugata*. However, more material is necessary for this attribution to be confirmed. We tentatively refer this pygidium to *?Prosaukia* c.f. *P. corrugata* in the interest of taxonomic stability.

Occurrence.—Upper Conococheague Limestone, Franklin County, Pennsylvania.

PROSAUKIA HARTTI (Walcott 1879)

Figure 27.1–27.4; Text-Figure 30

Conocephalites hartti, WALCOTT, 1879, p. 130.

Prosaukia hartti, Ulrich and RESSER, 1933, p.244; LUDVIGSEN AND WESTROP, 1983, p. 30, pl. 10, pl. 11, pl. 12, figs. 1–7; text-fig. 6.

Lonchocephalus calciferus WALCOTT, 1912, p. 270, pl. 43, fig. 9 (only).

Dicellocephalus hartti, WALCOTT, 1912, p. 273, pl. 44, figs. l–7a.

Dikelocephalus hartti, WALCOTT, 1914, p. 368, pl. 63, figs. 1–7a.

Tellerina hartti, ULRICH AND RESSER, 1930, p. 14.

Prosaukia curvicostata, ULRICH AND RESSER, 1933, p. 145, pl. 25, figs. 1–7; RAASCH, 1951, p, 142–143; NELSON, 1951, p. 778, pl 110, figs. 6, 16, 18.

Prosaukia demissa ULRICH AND RESSER, 1933, p. 147, pl. 25, figs. 17, 18.

Prosaukia subrecta, ULRICH AND RESSER, 1933, p. 148, pl. 26, figs. 2–8.

Prosaukia alternata, ULRICH AND RESSER, 1933, p. 149, pl. 25, figs. 8–12.

Prosaukia transrersa ULRICH AND RESSER, 1933, p. 150, figs. 13–16.

Prosaukia subconica ULRICH AND RESSER, 1933, p. 150, pl. 25, fig. 19.

Prosaukia subaequalis ULRICH AND RESSER, 1933, p. 151, pl. 26,. figs. 9–12.

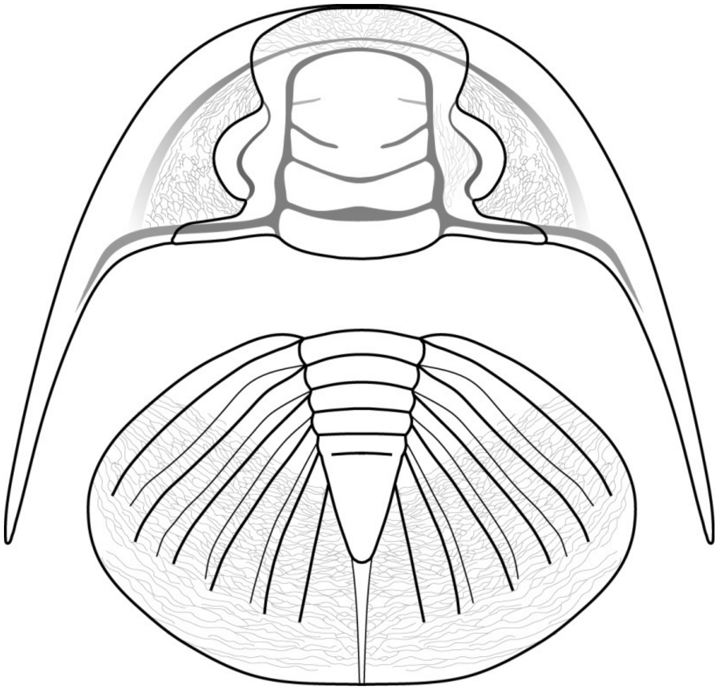
Briscoia hartti, KOBAYASHI, 1935, p. 51.

Saukia eboracensis RESSER, 1942 p. 49.

Prosaukia eboracensis, RASETTI, 1946, p. 541, pl. 1, figs. 17–19; FISCHER AND HANSON, 1951, pl. 1, fig. 5.

Types.—USNM 58571 (holotype).

Other material examined.—USNM 25749, 58572, 58575–58577, 59034, 328215; UWGM 1244–1246, 1282.



Text-figure 30. Reconstruction of *Prosaukia hartti* (Walcott 1879), based on specimens USNM 58571 (holotype), 25749, 58575–58577, 59034, 328215.

Emended diagnosis.—A species of *Prosaukia* with a slightly convex preglabellar furrow defined at its anterior by an anterior border furrow most strongly expressed laterally. Glabella wide, tapering anteriorly; occipital node present, occipital spine absent. Preoccipital glabellar furrows shallow before reaching axial furrow. Transversely ovate pygidium with five axial rings; four well-defined, and the last one weakly defined. A narrow postaxial ridge is present.

'PROSAUKIA' JINGXIANENSIS (Chien 1974)

Figure 28; Text-Figure 31

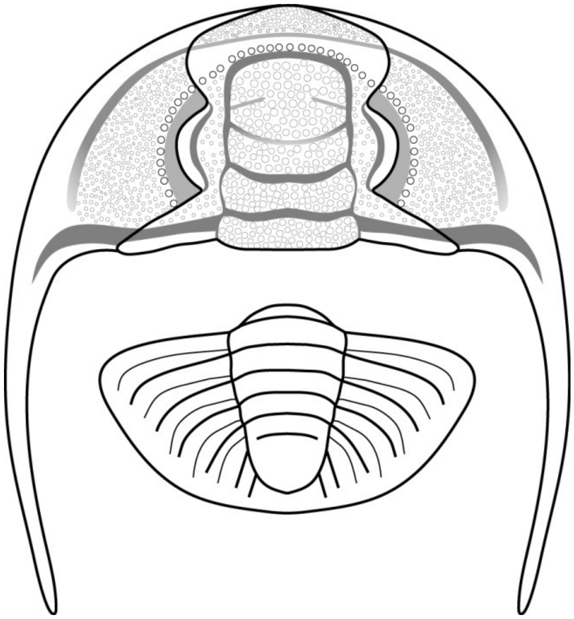
Saukia jingxianensis CHIEN, IN LU ET AL.,1974, p. 99, pl. 4, fig. 10; QIAN, 1985, p. 146, pl. 3, figs. 3–4, 6.

Prosaukia diversa CHIEN, IN LU ET AL.,1974, p. 100, pl. 4, fig. 11; QIAN, 1985, p. 148, pl. 4, figs. 3A, 3b, 6; pl. 5, figs. 2, 4.

Prosaukia diversa deformata QIAN, 1985, p. 149, pl. 4, figs. 1a–1d, 4; pl. 5, figs. 1, 3.

Types.—NIGPAS 23743 (holotype)

Other material examined.—NIGPAS 79342–79343, 79346–79350, 79360.



Text-figure 19. Reconstruction of *"Prosaukia" jingxianensis* (Chien 1974), based on specimens NIGPAS 23743 (holotype), 79342–79343, 79346–79350, 79360.

Emended diagnosis.—A species of *'Prosaukia'* with a short (sagittally), mildly convex preglabellar field with a curved, evenly-spaced single row of large tubercles extending across entire preglabellar field. Glabella parallel-sided, S1 and S2 continuous across glabella. Librigenae with distinct row of tubercles present, adjacent to palpebral lobes; lateral librigenal furrow shallows and disappears prior to posterior librigenal furrow, posterior librigenal furrow continues into base of genal spine. Thorax of eleven segments.

Discussion.—This species was originally described by Chien (1974) as a member of the genus *Saukia*. However, there are a number of problems with this assignment: *Saukia* has a glabella that distinctly narrows anteriorly, the librigenal lateral and posterior furrows are confluent, and fully articulated *Saukia* from the type locality have twelve thoracic segments. *'Saukia' jingxianensis* has a parallel-sided glabella, the librigenae have lateral furrows that shallow and terminate prior to the posterior border furrows, and possesses only eleven thoracic segments. While the number of thoracic segments within individual trilobite genera are known to vary (even within single species as in *Alocoplura konecki*), the number of thoracic segments is not know to vary within species of Saukiidae. Taken together, these morphological differences make a strong argument against this species grouping with *Saukia*, and allying it with *Prosaukia* instead, to which it is provisionally assigned.

In the holotype of *'Prosaukia' jingxianensis*, the anterior of the cephalon is partially compressed anteriorly, and so the true morphological details, particularly of the cranidial frontal area are partially obscured. In the two associated cranidia, NIGPAS 79242 and 79243, details of the crandial frontal area are slightly more visible. The anterior border is much longer in the isolated cranidia than it is in the holotype because the isolated material is not transversely compressed. There is a distinct, concave preglabellar furrow immediately anterior of the glabella. Anterior to this is a short convex area with a distinct row of large tubercles. Lying anterior to this, and visible only at the lateral margins of cranidia assigned to *'Prosaukia' jingxianensis*, there is a faint, but discernible anterior border furrow. The ABF is only traceable in these two cranidia of *'Prosaukia' jingxianensis* for approximately 1/3 of the length of the anterior border; however, the presence of the convex area and distinct row of tubercles running the length of the border indicates that this furrow is not interrupted by the glabellar anterior, and that the furrow necessarily divides the cranidial frontal area into a true preglabellar field and anterior border.

Specimens that have been assigned to *Prosaukia diversa* Chien are morphologically indistinguishable from *'Prosaukia' jingxianensis.* The only difference between these specimens is that material assigned to *Prosaukia diversa*, and *P. diversa deformata* has a slightly more distinct anterior border furrow than does material assigned by Chien to *'P' jingxianensis*. Both 'species' have a row of tubercles adjacent to the palpebral lobe on the librigenae, both have the same arrangement of librigenal furrows with the lateral librigenal border furrow shallowing before the genal angle and not converging with the posterior border furrow, and both have the same slightly convex preglabellar field with a single row of large pustules extending from facial suture to facial suture. Moreover, all three 'species' are found in southern Anhui province, and all originate from the Fengshanian Tancun Formation. Thus, we refer *Prosaukia diversa* Chien 1974, and *Prosaukia diversa deformata* Chien 1974 to *'Prosaukia' jingxianensis* Chien 1974.

PROSAUKIA MISA (Hall 1863)

Figure 27.5–27.8; Text-Figure 32

Dikelocephalus minnesotensis OWEN, 1852 (part). table 1A, fig. 1.

Dikelocephalus misa HALL, 1863, p. 144, pl. 10, figs. 4–5, 7–8.

Conokephalina misa (Hall) WALCOTT, 1914, p. 387, pl. 68, figs. 1–3.

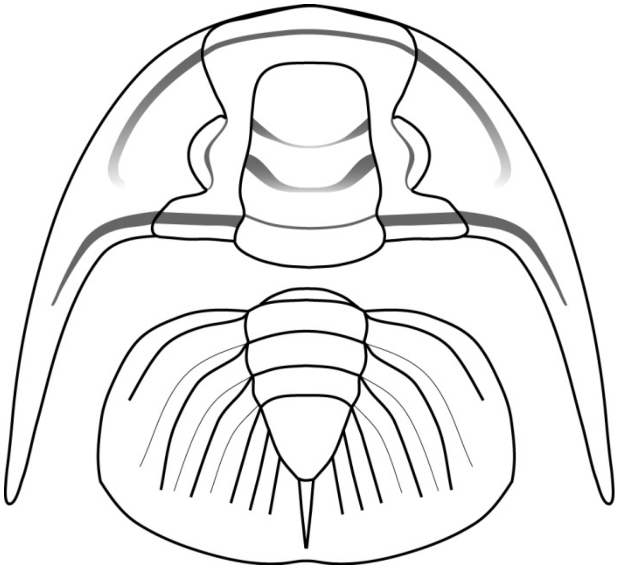
Prosaukia concava ULRICH AND RESSER, 1933, p. 145, pl. 26, fig. 1.

Prosaukia misa (Hall) ULRICH AND RESSER, 1933, p. 141, pl. 24, figs. 1–9; SHIMER AND SHROCK, 1944, p. 631, pl. 261, figs. 9–11; RAASCH, 1951, p. 142; BELL, FENIAK AND KURTZ, 1952, p. 192, pl. 38, figs. 1a– d; BERG, 1953, p. 567, pl. 61, fig. 1; GRANT, 1962, p. 994; WESTROP, 1986, p. 31, pl. 4, figs. 8–14; STITT AND STRAATMAN, 1997, pl. 7, figs. 24–26.

Prosaukia resupinata ULRICH AND RESSER, 1933, p.144, pl. 24, figs. 10–13.

Types.—AMNH 39109a (lectotype).

Other material examined.—USNM 14490, 58661, 84538–84540, 84548, 84541, additional un-numbered specimens; UWGM 1221–1223.



Text-figure 20. Reconstruction of *Prosaukia misa* (Hall 1863) based on specimens USNM 84538–84540, and un-numbered specimens in USNM and UWGM collections.

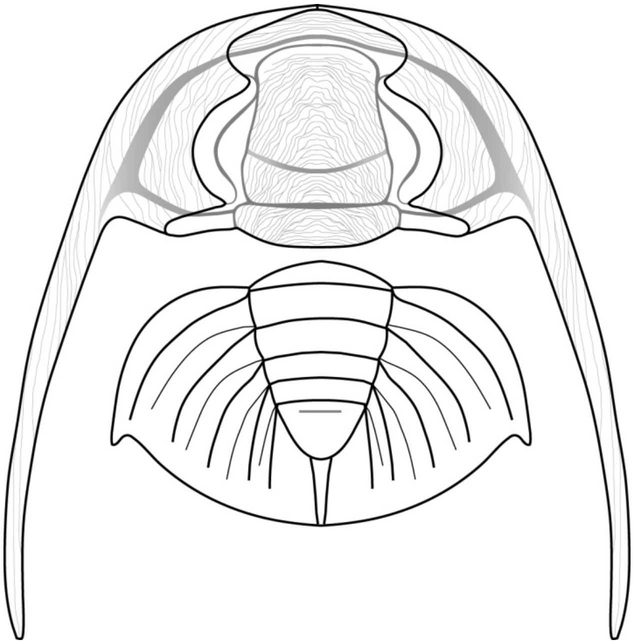
Discussion.—Several named species exist from shallow water sandy facies of the upper Mississippi valley that very closely resemble the morphology of *Prosaukia misa* (see discussion under the genus *Prosaukia*. *Prosaukia concava* Ulrich and Resser 1933 was erected solely on a single pygidium. Ulrich and Resser (1933) cite the following characters of *P. concava* that distinguish it from both *P. misa* and *P. halli*: 1) greater width and concavity of the lateral border, 2) distinctly upturned lateral border, and 3) pleural ribs unequally divided. However, the syntype of *P. misa* (USNM 084540) also has a slightly concave lateral pygidial margin, as does the syntype of *P. halli* (USNM 085663), which Hall originally assigned to *P. (Dikelocephalus) misa*. Additionally, this single, poorly-preserved specimen clearly shows vestiges of the pleural ribs nearly reaching the lateral pygidial margins (see pl. 26, fig. 1 of Ulrich and Resser, 1933), and together with effacement of the specimen could produce the seemingly wider margin. None of the characters outlined by Ulrich and Resser (1933) can be demonstrated convincingly, and moreover, because there are no other specimens in existence with which to compare other, very similar species with, we place this species into synonymy with *P. misa*.

PROSAUKIA OLDYELLERI Adrain and Westrop 2004

Figure 29.1–29.3; Text-Figure 33

Prosaukia oldyelleri, ADRAIN AND WESTROP, 2004, p. 11, pl. 2, figs. 1–39; pl. 3, figs. 1–41.

Type material.—SUI 99054 (holotype).



Text-figure 21. Reconstruction of *Prosaukia oldyelleri* Adrain and Westrop 2004, based on specimens in plates 2 and 3 in Adrain and Westrop (2004).

Diagnosis.—A species of *Prosaukia* with very long (sagittally) palpebral lobes; small marginal spines on anteriormost pleura of pygidium. Anterior of palpebral lobe reaches axial furrow; axial and palpebral furrow confluent. Anterior limb of facial suture strongly divergent. Occipital spine absent. Librigenae with slightly advanced genal spines; lateral and posterior librigenal furrows confluent. Short (sagittally) frontal area divided into short, flat bottomed preglabellar field, and convex, subtriangular anterior border.

Discussion.—This species of *Prosaukia* is the only known member of the genus to possess a pygidial pleural spine, a morphological character most often found in dieklocephaliids, but which also occurs in *Taebeksaukia*, a more derived genus found in

Gondwana. The palpebral lobes of this species are also confluent with the axial furrow, a autapomorphy unique among the Saukiidae, but one which also occurs in the dikelocephaliid genus *Hamashania*.

Occurrence.—Bullwhacker Member, Windfall Formation. Barton Canyon. Cherry Creek Range, Nevada.

Genus SAUKIA Walcott 1914

Type species.—*Dikelocephalus lodensis* Whitfield, 1880, p. 51; 1882, p. 188, pl. 10, fig. 14; p. 341, pl. 27, figs. 12, 13.

Diagnosis.—Glabella subrectangular, sides tapering anteriorly, may be medially constricted; up to three pairs of preoccipital glabellar furrows; S1 connected across glabella. Glabella anteriorly rounded or truncate; antero-lateral corners acutely or broadly rounded. Fixigenae narrow. Preglabellar field absent. Anterior border furrow confluent with at least the medial part of preglabellar furrow; anterior border of moderate length (sagittally). Librigenae with posterior and lateral border furrows confluent; genal spines long and slender. Pygidium transversely subelliptical, with strongly tapered axis; subequally divided pleurae die out on narrow, smooth, concave border. Surfaces granulate. (Lochman, 1970)

Discussion.—Both Lochman (1956) and Westrop (1986) commented on the similarity between the genus *Saukia* and other Laurentian members of the Saukiidae [see Lochman, 1956 for a thorough discussion of Ulrich and Resser's (1933) taxonomic problems related to *Saukia*]. *Saukia* is, as Lochman (1956) noted, distinguished from *Prosaukia* and *Saukiella* by the possession of a furrow-delineated preglabellar field in the latter taxa. Both Lochman (1956) and Westrop (1986) also pointed out the granular prosopon of *Saukia* as a further means of differentiating between *Saukia* and *Calvinella*. However, *Calvinella ozarkensis* possesses a densely tuberculate cranidium (see Figure 19.1), as does *Prosaukia stosei* (see Figure 28.4). Lochman (1956) and Westrop (1986) further point to the more equally divided pygidial pleurae and lack of occipital spine in *Saukia* help to distinguish it from the genus *Calvinella*.

SAUKIA ACUTA Ulrich and Resser 1933

Figure 29.7; Text-Figure 34

Saukia acuta ULRICH AND RESSER, 1933, p. 172, pl. 29, figs. 16–17; Shimer and Shrock, 1944, p. 633 , pl. 260, fig. 30.

Saukia obtusa ULRICH AND RESSER, 1933, p. 174, pl. 29, figs. 4–6.

Saukia angusta ULRICH AND RESSER, 1933, p. 177, pl. 29, fig. 8.

Saukia levigenata ULRICH AND RESSER, 1933, p. 186, pl. 30, fig. 6.

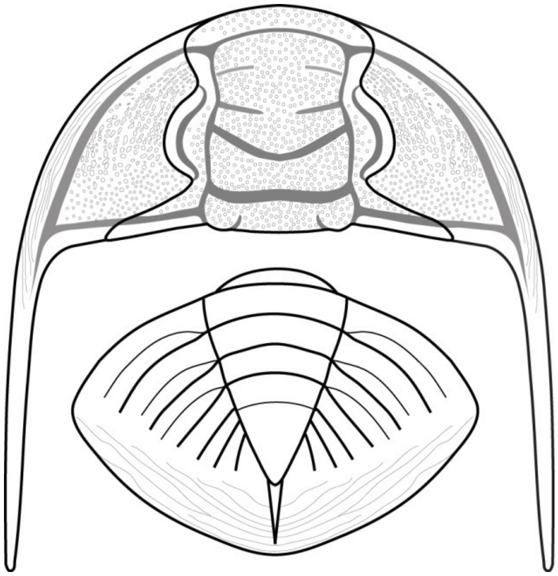
Saukia whitfieldi ULRICH AND RESSER, 1933 (pars), pl. 29, fig. 13.

Prosaukia welleri RESSER, 1942, p. 44.

Calvinella newtonensis WALCOTT, 1914, p. 389, pl 70, figs. 1–6.

Types.—USNM 58618 (holotype)

Other material examined.—USNM 58678–58679, 84574, 84576, 84578, 84581, 84589.



Text-figure 22. Reconstruction of *Saukia acuta* Ulrich and Resser 1933, based on specimen USNM 58618 (holotype), USNM 84581.

Discussion.—Prosaukia welleri, a species described by Resser in 1942 possesses the specific characters for *Saukia acuta*: swollen lateral occipital lobes, strong pustulated prosopon, lateral and posterior librigenal furrows confluent, strongly anteriorly tapering glabella with an evenly rounded anterior. The only major difference between *"P. welleri"*, and *Saukia acuta* is the presence of an occipital node. Because there are very few specimens attributed to *S. acuta*, and because the type material appears to be slightly flattened, this character may not have been preserved in the type material. Moreover, occipital tubercles and nodes are often not preserved even in well-studied species in which they are known to occur (Hughes, 1994). Thus, we do not consider the occurrence of an occipital tubercle in *"Prosaukia welleri"* to represent anything other than taphonomic; accordingly this species is referred to *S. acuta*.

Saukia obtusa is also very similar to the type material of *S. acuta*, with a few very minor differences. The terminal piece of the pygidium in *S. acuta* is triangular and terminates in a slender postaxial ridge, while the terminal piece in *S. obtusa* is obtusely rounded in USNM 84574 (Ulrich and Resser, 1933, pl. 29, fig. 6, syntype), it is much less so in the second syntype specimen (also USNM 84574, Ulrich and Resser, 1933, pl 29, fig 4). Additionally, the terminal piece of the syntype of *S. acuta* (USNM 84581, paratype, Ulrich and Resser, 1933, pl. 29, fig. 17) is damaged and cannot be fully described; this terminal piece is much less acute than that of the holotype. Moreover, the terminal pieces of both the holotype and syntype of *S. acuta* are damaged, thus the total number of axial rings present could be more than the four known in *S. acuta* sensu Ulrich and Resser, 1933. Considering these minor differences and the slight damage to the pygidia of *S. acuta* type material, we agree with Raasch's (1951) placement of *S. obtusa* with *S. acuta*.

Saukia leveginata appears to differ from *S. acuta* only in lacking lateral occipital nodes; it is referred to *S. acuta*.

Saukia angusta Ulrich and Resser (labeled *Saukia angustus* in reposited material in the USNM collections) differs from *S. acuta* only in the lack of well-defined occipital lateral nodes. However, the degree to which these lateral protuberances are preserved, even in Ulrich and Resser's (1933) type material for *S. acuta* is variable; in the holotype (see Figure 28.7) the left occipital lateral node is not preserved. Moreover, the single specimen assigned by Ulrich and Resser (1933) to *S. angusta* is very much smaller than any of the specimens assigned to *S. acuta*. Without a study on ontogenetic development in *S. acuta,* it cannot be ruled out that such structures were only developed in later (and thus, larger) ontogenetic stages. Raasch assigned this specimen to *S. lodensis*. However the orientation of the abaxial part of the anterior border furrow in *S. lodensis* is more anterolaterally-directed; in *S. angusta* Ulrich and Resser, this furrow is nearly transverse, as is the case in *S. acuta*, to which it is referred.

The articulated material of *S. acuta* may also not represent some key morphological characters accurately, specifically in the anterior cephalic region. The anteriormost part of the cranidium is damaged and cryptic in the syntype (USNM 84581), so the character, critically, of the anterior cranidial border furrow and its relationship with the preglabellar furrow cannot be assessed from this specimen. However, these regions in the holotype (USNM 58618) can be assessed with care. In the counterpart (negative) of the holotype, the free cheek on the right side is articulated with the cranidium and complete (this would be the left free cheek in the positive). The anterior of this librigena at its suture point with the anterior cranidial border transitions smoothly, and the position of the anterior librigenal furrow can be clearly seen at the border of the cranidium. The axial furrows have a distinct inbend near the anterior of the palpebral lobes (coincident with the position of S2), giving the glabella its distinctive 'hourglass' shape. The anterior corners of the glabella are acutely rounded, and the preglabellar furrow (and glabellar anterior) is evenly rounded across the anterior. The anterior border furrow on the part is only partially intact (left side of cranidial anterior), and appears to originate close to the maximal width of the pre-ocular area, although its precise position at the border is obscured. The anterior border furrow at the anterolateral corner of the cranidium is located away from the preglabellar furrow, but the anterior border furrow gradually approaches the preglabellar furrow as it moves toward the glabellar midpoint, and appears to merge with the preglabellar furrow by approximately 1/3 of the anterior glabellar width.

Many of the specimens illustrated as *Saukia* by Ulrich and Resser (1933) differ only minutely in the orientation of the abaxial part of the anterior border furrow. A detailed morphometric analysis of these cranidia from single collections is necessary to determine the degree to which the angle of these furrows vary within single bedding planes, collections, and species. If it is found that they do vary substantially, then there may be gradation between *S. acuta* and *S. lodensis* and status of the type material of the genus *Saukia* will have to be re-examined.

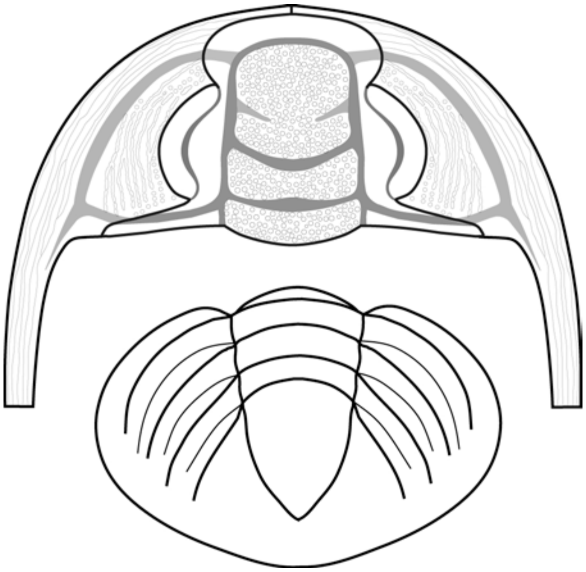
SAUKIA TUMIDA Ulrich and Resser 1933

Figure 29.8–29.9; 30.1–30.2 Text-Figure 35

Saukia tumida ULRICH AND RESSER, 1933, p. 192, pl. 30, figs. 11, 12; WINSTON AND NICHOLLS, 1967, p. 81, pl. 9, figs. 7, 9, 11; LONGACRE, 1970, p. 48, p1. 4, figs. 10, 11; STITT, 1971, p. 44, pl. 4, fig. 15.

Type material.—USNM 84592 (holotype).

Other material examined.—USNM 187921, 192243–192244, 185826–185828.



Text-figure 23. Reconstruction of *Saukia tumida* Ulrich and Resser 1933, based on USNM 84592 (holotype), 187921, 192243–192244, 185826–185828.

Diagnosis.—A species of *Saukia* with a markedly convex glabella; glabellar furrows deep, S2 furrow continuous across glabella. Strong pustulated prosopon of cranidium. Anterior border of cranidium strongly downsloping.

Discussion.—The type specimen for this species designate by Ulrich and Resser (1933) was erected based on a single cranidium from their location 87f (near Tunnel 2, 2 miles NW of Wilton, WI). Although preserved in sandstone, this cranidium preserves typical saukiid features, including granulated prosopon, but also characters atypical of *Saukia*, including a very strongly downsloping glabellar anterior that drops below the level of the remainder of the occipital lobe, as well as possessing a S2 furrow that shallows markedly axially, but is continuous transversely across the glabella; in these respects, this species is much closer to *Mictosaukia*. Differences between *S. tumida* and *Mictosaukia* include a furrow continuing into the base of the genal spine, and perhaps longer palpebral lobes in *S. tumida*.

Genus SAUKIELLA Ulrich and Resser 1933

Type species.—*Dikelocephalus pepinensis* Owen, 1852, p. 574, pl. 1, figs. 9, 9a, 9b.

Discussion.—Many authors have noted the difficulty in differentiating between *Saukiella* and *Prosaukia* (Longacre, 1970; Taylor and Halley, 1974; Shergold, 1975; Ludvigsen and Westrop, 1983; Westrop, 1986; Adrain and Westrop, 2004), an observation that compounds the task of assigning the plethora of species erected by Ulrich and Resser (1933) to valid species-bins. In his 1951 paper revising saukiid species from the upper Mississippi valley, Raasch recognized only five valid species of *Saukiella* from among the nineteen species and subspecies erected by Ulrich and Resser (1933); these were *S. frontalis*, *S. indenta*, *S. minor*, *S. pepinensis,* and *S. pyrene*. These assignments were made on the basis of morphology, and stratigraphic placement (Raasch, 1951). However, among these assignments, morphological characters appear to have sometimes been marginalized. As an example, Raasch synonymized *Saukiella norwalkensis* with *S. pyrene* and *S. indenta* for apparent stratigraphic reasons, while ignoring the differences in the librigenae of these species - specifically advancement of the genal spine in *S. norwalkensis*, a character absent in *S. pyrene*.

Indeed, there are very few morphological characters with which to differentiate *Saukiella* from *Prosaukia*. Lochman (1970) suggested that, for taxa that have a preglabellar field, the presence of an occipital spine, granular ornament, a subequally-divided frontal area, and non-confluent librigenal lateral and posterior border furrows are characters that differentiate *Prosaukia* from *Saukiella*. However, all of these characters are extremely varied throughout members of both genera. *Prosaukia hartti*, and *P. misa*, for example, both possess librigenae in which the lateral and posterior border furrows are not confluent; and neither of these species possess an occipital spine. While all species of *Saukiella* included in our analyses have librigenae with confluent border furrows, *Prosaukia corrugata* and *P. stosei* do as well.

The general dearth of morphological characters available with which to differentiate between *Saukiella* and *Prosaukia* has lead to the notion that these genera might be synonymous (Ludvigsen and Westrop, 1983; Westrop, 1986; Adrain and Westrop, 2004), or gradational, constituting a cline with distinct end members (Adrain and Westrop, 2004). The systematic placement of species into *Saukiella* or *Prosaukia* most often centers around the morphology of the frontal area of the cranidium. Ludvigsen and Westrop (1983, p. 29) suggested that possession of a "...distinct preglabellar field that stands below [the] level of inflated anterior border (at least in small holaspids)..." might be a synapomorphy that defines *Prosaukia*. However, *Saukiella pyrene* and *S. norwalkensis* both have an inflated anterior border that stands above a concave 'preglabellar field'. Adrain and Westrop (2004) further suggested confining *Saukiella* to taxa with a relatively long anterior cranidial border and a very short preglabellar field. To illustrate the very tentative and subjective nature of this potential apomorphy, in that same publication Adrain and Westrop (2004) then erect a new species of *Prosaukia*, *P.*

oldyelleri, and in the description of this new species state (on p. 11), "...unequally divided into short preglabellar field and longer, convex, subtriangular anterior border...".

Ludvigsen and Westrop (1983, p. 29) emended the diagnosis of *Prosaukia* to include a "...distinct preglabellar field that stands below level of inflated anterior border (at least in small holaspids)," noting that features of the frontal area are sufficient to differentiate *Prosaukia* from *Saukia*, *Tellerina*, and *Calvinella*, but not to differentiate between *Prosaukia* and *Saukiella.* Adrain and Westrop (2004) follow Ludvigsen and Westrop's (1983) diagnosis of *Prosaukia*, but suggest restricting *Saukiella* to only *S. pepinensis* and *S. junia* based on the suggested apomorphy for *Saukiella* of a relatively long frontal area with a short (sagittally) preglabellar field. This placement remains problematic, however, due to the arrangement of the frontal area of these species. *Saukiella junia* possesses both an anterior border furrow and a separate and distinct preglabellar furrow (see Figures 29.4–29.7). *Saukiella pepinensis* possesses a furrow lying immediately anterior to the glabella, but this furrow is narrower than the abaxial portion of the anterior border furrow. This furrow likely represents a combined preglabellar-anterior border furrow - and thus, not a true preglabellar field. A similar arrangement of the frontal area also exists in *Calvinella ozarkensis* (see Figure 19.4); however, in that case, the wide abaxial portions of the anterior border furrow are distinctly anterolaterally-directed, indicating at least partial interruption by the glabellar anterior, indicating that a preglabellar field is necessarily absent.

The morphology of the frontal area, then, and whether a true preglabellar field is present or absent becomes critical in establishing systematic and evolutionary linkages between genera. The question then logically becomes what is the definition of a preglabellar field? Harrington (1959) and Whittington (1997) define the preglabellar field as the area lying between the preglabellar and anterior border furrows. The implication of this definition is that a preglabellar field can only be present if both the anterior border furrow and preglabellar furrow can be detected. According to this definition, most *Prosaukia* species have a true preglabellar field, but there are clearly saukiid species that lack a preglabellar field, like *Eosaukia*, *Saukia*, *Tellerina*, etc. Thus, it is necessary in the evolution of saukiids for the progressive posterior migration of the anterior border furrow, which would have reduced the sagittal length of the preglabellar field. Confluence of the preglabellar and anterior border furrows would necessarily occur at some point during this transition, resulting in a preglabellar field that is more a combined furrow than space between two furrows. We suggest that the preglabellar field can represent either condition, but that in cases where a confluence of the anterior border and preglabellar furrows is suspected (as in *Saukiella*), that evidence of both furrows must be detectable. In *Saukiella*, potential sources of evidence for a combined furrow include:

1. The shape of the anterior border. The anterior border is defined by the anterior border furrow. Thus, if the anterior border is an approximately even arc shape, or with a very slight anterior deflection at the abaxial margins, then that border must by definition be defined by the anterior edge of the anterior border furrow. Thus, the anterior border furrow has not yet been interrupted by the glabellar anterior and a preglabellar field may be present;

2. The presence of a distinct preglabellar furrow. The preglabellar furrow is the anterior continuation of the glabellar axial furrows. If a distinct preglabellar furrow can be determined at the glabellar anterior (even if it lies within the anterior border furrow), confluence can be established, and thus, a preglabellar field must be present. As the preglabellar field may occupy all of the space anterior to the glabella, the area around the glabellar shoulders may contain traces of both furrows;
3. The relative width of the furrow lying anterior to the glabella. If a distinct preglabellar furrow cannot be determined, the width of the furrow may be an indication of whether the furrow is confluent. If the furrow lying anterior to the glabella is wider than the abaxial part of the anterior border furrow, it is likely that the furrow is a combination of the anterior border and preglabellar furrows;

it is suggested that at least two of these three criteria be used in establishing presence of a preglabellar field in Saukiidae. In taxa that lack a distinct anterior border furrow, the anterior extent of the preglabellar field is inferred to be represented by the inflection point between the flat area in front of the preglabellar furrow (preglabellar field) and the inflated anterior border (for example, *Dikelocephalus* and *Hamashania*).

We suggest that the preglabellar field in *Saukiella* represents a confluence of the anterior border furrow and the preglabellar portion of the axial furrow, and therefore does not represent a true preglabellar field, but an intermediate evolutionary state lying between a true, furrow-bounded preglabellar field, and its subsequent loss. We retain this character as representing a preglabellar field because it is a necessary evolutionary step from one state to another, and it is phylogenetically important for establishing character polarities. Thus, we suggest that 'confluent furrows of the frontal area' represents an intermediate evolutionary step from *Prosaukia* → *Saukiella*, and that this character represents an ordered transformation that occurred only once. We suggest that this character represents a synapomorphy uniting *Saukiella*.

SAUKIELLA JUNIA (Walcott 1914)

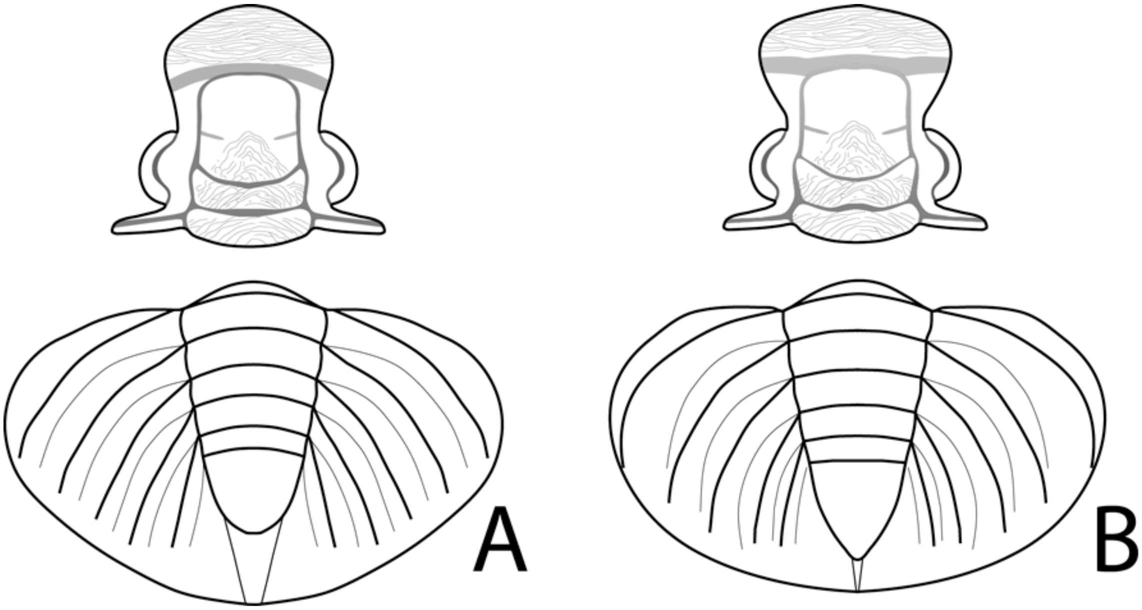
Figures 30.4–30.7; Text-Figure 36

Saukia junia WALCOTT, 1914, p. 378, text-fig. 17.

Saukiella junia, RESSER, 1938b, p. 43; WINSTON AND NICHOLLS, 1967, p . 81, pl. 9, figs. 8, 10, 12, 14, 22; LONGACRE, 1970, p. 50, p1. 5, figs. 12–21.

Type material.—USNM 60677 (holotype).

Other material examined.—USNM 185829–185833, 192266–192275.



Text-figure 24. Reconstruction of *Saukiella junia* based on specimens USNM 60677 (holotype), 185829–185833, 192266–192275. A) *Saukiella junia* variety A. Occurs stratigraphically above *S. junia* var B. B) *Saukiella junia* variety B. Occurs stratigraphically below *S. junia* var. A and stratigraphically above *Saukiella pepinensis*.

Diagnosis.—A species of *Saukiella* distinguished by a long (sagittally) cranidial anterior border, very short, flat to gently concave, furrow-like preglabellar field lying entirely below the level of the anterior border. S2 and S3 generally very weakly developed when present. Ovate pygidium with 5 axial rings.

Discussion.—This species has been considered by many authors to be quite variable in morphology (Winston and Nicholls, 1967; Longacre, 1970), with published descriptions separating specimens into two separate subspecies, a and b, based largely on the morphology of the glabella and frontal area. Winston and Nicholls (1967) define *S. junia sp. a* as possessing an elongate cranidium, parallel-sided and anteriorly rounded glabella, an evenly bowed anterior border furrow separating the frontal area into a long (sagittally) anterior border and a short preglabellar field; it occurs stratigraphically above species b. Species b is defined as having a shorter frontal area, the border furrow is fainter, transverse and separate from the border furrow, or curved and confluent with the border furrow. There are also minor described differences in pygidial morphology, primarily with the pleural furrows and the division of the pleurae (Winston and Nicholls, 1967).

Winston and Nicholls (1967) noted that *S. junia sp. b* occurs stratigraphically below material that these authors assigned to species a. However, these authors stopped short of erecting two separate species for this material, noting that within some collections specimens show morphologies that range between the end members (Winston and Nicholls, 1967). Longacre (1970) noted the acute similarity between *Saukiella junia sp. b* (lower, stratigraphically) and *S. pepinensis*, which has a stratigraphic range lying immediately below that of *S. junia sp. b.* This morphological similarity and stratigraphic order led Longacre (1970) to suggest that an evolutionary cline was represented by the sequence of *S. pepinensis* → *S. junia sp. b* → *S. junia sp. a*. Morphological changes in cranidia from *S. junia sp. b* to *S. junia sp. a* that Winston and Nicholls (1967) and Longacre (1970) noted up section in Texas include: a gradual elongation of the frontal area, transition from a poorly-defined to a more well-defined preglabellar field, a more arcuate as opposed to transverse anterior border furrow, and a more rounded glabellar anterior. Pygidial differences from *S. junia sp. b* to *S. junia sp. a* up section include: pleural furrow transitions from as firmly impressed as interpleural furrow to much less distinct, pleurae transition from less to more equally-divided, and pygidia higher in the section show a possible fifth axial ring (Winston and Nicholls, 1967; Longacre, 1970). Thus, it appears that sufficient characters exist for the formal recognition of two distinct subspecies.

SAUKIELLA NORWALKENSIS Ulrich and Resser 1933

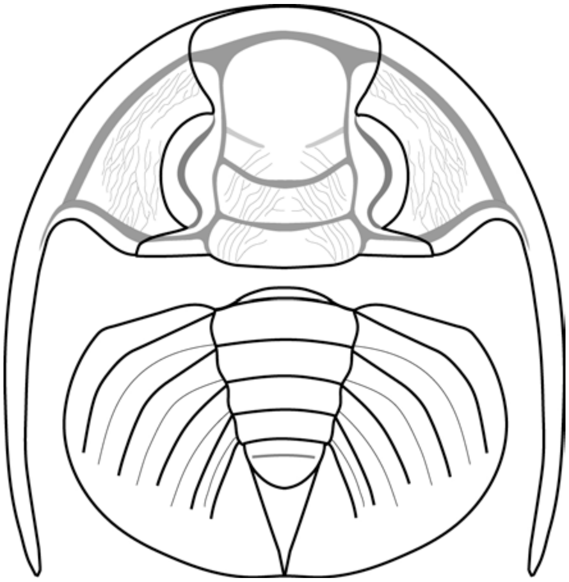
Figure 31.1–31.3; Text-Figure 37

Saukiella norwalkensis, ULRICH AND RESSER, 1933, p 209, pl. 36, figs. 5–27; WINSTON AND NICHOLLS, 1967, p. 82, pl. 11, figs. 6–8,12.

Saukiella pyrene, RAASCH (pars), 1951, p. 145.

Saukiella indenta, RAASCH (pars), 1951, p.145.

Other material examined.—USNM 85208 (box containing eight syntypes), 85209 (box containing seven syntypes), 825210 (box containing seven specimens), 825211, 185876–185879, un-numbered material; UWGM 1069–1072, 1106, 1224–1232, 1239.



Text-figure 25. Reconstruction of *Saukiella norwalkensis*, based on specimens USNM 85208–85211.

Diagnosis.—A species of *Saukiella* distinguished by relatively short cranidial border, and short preglabellar field defined by distinct anterior border furrow and preglabellar furrow. Librigenae with advanced genal spines, lateral librigenal border furrow continuing only to genal angle and confluent with posterior border furrow; furrow of genal spine absent; prosopon of anastomosing, wavy ridges subparallel to border furrow. Pygidium with 4 axial rings (sometimes an indication of a very weak fifth axial ring is present); terminal piece subtriangular, extends nearly to posterior border; weak postaxial ridge continues to posterior pygidial margin.

Discussion.—Raasch synonymized *Saukiella norwalkensis* with *S. pyrene* and *S. indenta* for apparent stratigraphic reasons [all specimens synonymized with *S. pyrene* occur in Raasch's (1951) Trempealeau Formation, Arcadia member, *Osceolia osceola* zonal unit;

while those synonymized with *S. indenta* occur in the Lodi member, *S. sublonga* zonal unit]. Raasch (1951) noted that cranidia, pygidia, and librigena assigned by Ulrich and Resser (1933) to individual taxa were often sourced from separate outcrops, and that these outcrops were often stratigraphically mis-assigned. However, in the case of *S. norwalkensis*, all but three of the fifteen specimens on which Ulrich and Resser (1933) based their concept of *S. norwalkensis* came from USNM locality 87e (1.5 miles northwest of Tunnel City, Wisconsin). Thus, there is no reason, for this taxon, to doubt that specimens came from separate localities. Unfortunately, the stratigraphic context in which individual specimens were collected from individual localities does not appear to have been important for Ulrich and Resser (1933).

Longacre (1970) agreed with Raasch (1951), and stated on p. 52, "From a comparison of the Texas collections with Ulrich and Resser's type material of all taxa in the synonymy, I conclude that the type material and the Texas specimens belong to one variable species, for which the appropriate name is Saukiella pyrene." However, Longacre (1970) provided no measurements, morphometrics, ratios, graphs, or other evidence to back up her claims.

Winston and Nicholls (1967) rejected Raasch's placement of *S. norwalkensis* into synonymy with *S. pyrene*, based on the parallel-sided nature of the Texas specimens, and the possession by most specimens of only a single glabellar furrow (although the specimens from Texas reposited in the USNM collections show a 2S and even the vague indication of a 3S furrow). The Texas specimens have wavy, sub-parallel, fingerprint like raised ridge cranidial prosopon - a character difficult to assess in the Wisconsin material preserved in sandstone (see pl. 11, fig. 6, 7 of Winston and Nicholls, 1967). Of all the specimens assigned by Ulrich and Resser (1933) to *S. norwalkensis*, only a few free cheeks (USNM 82507) show vague indication of linear, anastomosing features on the librigenal field; no indication of ornament exists on cranidia; thus a direct comparison of prosopon, in general, is not possible between Wisconsin and Texas specimens.

Morphologically, the cranidia that Ulrich and Resser assigned to *S. norwalkensis* are very similar to those of *S. pyrene* (compare pl. 36, figs. 5, 12, 13 with pl. 34; 35, figs. 1, 11); both have palpebral lobes located very close to the axial furrows, both have very large palpebral lobes, anteriorly narrowing glabellae, and similar glabellar furrows (transglabellar S1, S2 posteriorly-directed, interrupted, absent or very faint indication of S3). The orientation of the abaxial part of the anterior cranidial border furrow is marginally different; in many specimens of *S. norwalkensis,* these furrows often have a very slight forward deflection (see Figure 31.1), while those of *S. pyrene* are generally much more of a lateral continuation of the preglabellar part of the anterior border furrow (see Figure 30.4). This difference, however, is not always apparent. Moreover, the pygidia of both species are also indistinguishable - both have five pygidial axial rings, both are transversely ovate, both possess a triangular postaxial ridge that continues to the posterior pygidial margin (although a study of the variation within these two species is necessary to fully quantify minor differences).

Both species have librigenal fields ornamented with raised, anastomosing subparallel ridges, and both have confluent lateral and posterior margins. However, in *S. pyrene,* the posterior librigenal margin gradually transitions from the notch for the cranidial posterior limb into the base of the genal spine without significant anterior deflection; in *S. norwalkensis*, the genal spine is definitively advanced. This is a clear taxabase that differentiates these two taxa from one another.

Librigenae of other 'species' named by Ulrich and Resser (1933) show similarly advanced genal spines. For example, the free cheeks illustrated as *Saukiella indenta* (Ulrich and Resser, 1933, pl. 35, fig. 27; pl. 36, fig. 2), as *S. typicalis* (Ulrich and Resser, 1933, pl. 32, figs. 10, 11, 32), and *S. ampla* (Ulrich and Resser, 1933, pl. 33, fig. 29) all have advanced genal spines. However, Raasch (1951) considered both *S. ampla* and *S. typicalis* as junior synonyms of *S. pepinensis*, an opinion supported herein by the shared advancement of the genal spines, a rather short (sagittally) preglabellar field, and a rather long (sagittally) cranidial anterior border. Cranidia of *S. norwalkensis* can be distinguished from those of *S. pepinensis* based on the long anterior border, short preglabellar field, and palpebral lobes that are slightly more widely spaced away from the axial furrows.

SAUKIELLA PEPINENSIS (Owen 1852)

Text-Figure 38

Dikelocephalus pepinensis OWEN, 1852, p. 574, pl.1, figs. 9, 9a, 9b.

Saukia pepinensis WALCOTT, 1914, p. 381, pl. 67, figs. 1–13, 13a.

Saukiella pepinensis ULRICH AND RESSER, 1933, p. 202, pl. 33, figs. 22–24; SHIMER AND SHROCK, 1944, p. 633, pl. 260, figs. 31–33; RAASCH, 1951, p.

144; LONGACRE, 1970, p. 51, pl. 5, figs. 9–11; STITT, 1977, p. 44, pl. 4, fig. 2.

Saukiella ampla ULRICH AND RESSER, 1933, p. 199, pl. 3.3, figs. 28, 29.

Saukiella subgracilis ULRICH AND RESSER, 1933, p. 200, pl. 33, figs. 7–18.

Saukiella subgracilis hybrida ULRICH AND RESSER, 1933, p. 201, pl. 33, figs. 19–21.

Saukiella subgracilis parallela ULRICH AND RESSER,1933, p. 201, pl. 33, figs. 25–27.

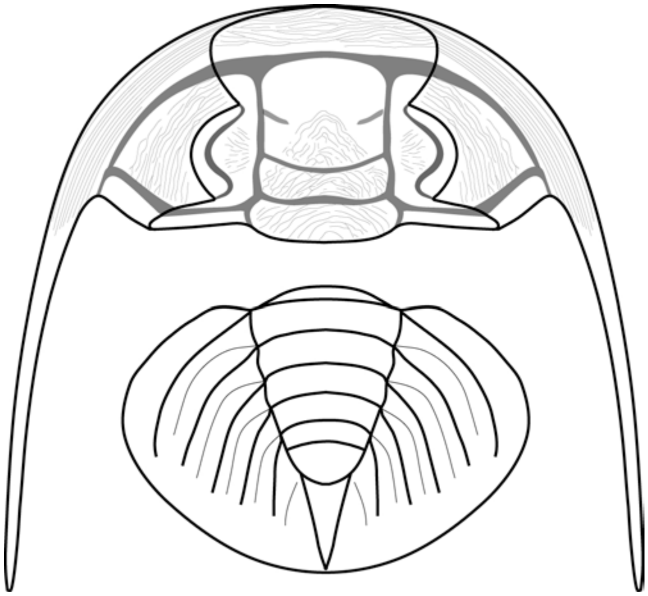
Saukiella typicalis ULRICH AND RESSER, 1933, p. 197, pl. 32, figs. 1–21; SHIMER AND SHROCK, 1944, p. 633, pl. 260, figs. 26–29; RICHTER AND RICHTER,1949, figs. 3a, b.

Saukiella typicalis convexa ULRICH AND RESSER, 1933, p. 197, pl. 32, figs. 22–29.

Saukiella typicalis subrecta ULRICH AND RESSER, 1933, p. 198, pl. 33, figs. 1–6.

Type material.—USNM 17868.

Other material examined.—YPM 6637, 8234, 37225, 37228, 73115, 154209; USNM 58629, 185823–185825, 192263–192265, UWGM 1202–1206, 1211–1214, 1217–1219, 1368–1371.



Text-figure 26. Reconstruction of *Saukiella pepinensis,* based largely on specimens USNM 58629, 185823–185825, 192263–192265.

Discussion.—As noted by Longacre, Raasch's (1951) synonymy left this as probably the most well-represented species of *Saukiella,* if not any species of Saukiidae. Minor differences abound within specimens attributable to *S. pepinensis,* with the shape of the glabella and morphology of the frontal area showing the most conspicuous variation. These variations are usually expressed as differences in the shape, sagittal length, and depth of the anterior border furrow, with larger specimens, generally, showing the more extreme differences in this area than do smaller and mid-sized specimens. In small holaspid cranidia of *S. pepinensis* the frontal area is definitively divided into a preglabellar field, at least in front of the lateral shoulders of the glabella. In these smaller cranidia, the posterior margin of the anterior border is clearly defined by a very steeply downsloping area immediately adjacent to the border furrow; there is also a preglabellar furrow that can be traced anteriorly, at least partially, past the glabellar shoulders into the frontal area. Thus, these small specimens possess a true, albeit reduced, preglabellar field in addition to a confluent condition of the anterior border and preglabellar furrows for the axial one-third of the glabellar anterior. The sagittal length of the combined furrow anterior to the glabella is always rather short, but through ontogeny, as the specimens grow larger, the sagittal length of the confluent furrows appears to shorten. In some larger individuals, the shape of the anterior border furrow develops an embayment to accommodate the glabella as it impinges upon the anterior border. Thus, *S. pepinensis* displays significant interspecific variability that is manifested most significantly in the morphology of the frontal area in a similar manner to *S. junia*, already discussed, which occurs stratigraphically above *S. pepinensis*. It remains to be seen whether these differences in morphology show systematic variation with stratigraphic occurrence as has been demonstrated in *S. junia*, but this may not be possible as many of Ulrich and Resser's specimens lack stratigraphic information.

SAUKIELLA PYRENE (Walcott 1914)

Figures 31.4–31.7; Text-figure 39

Saukia pyrene WALCOTT, 1914, p. 382, pl. 67, figs. 18–20.

Saukiella pyrene (Walcott) ULRICH AND RESSER, 1933, p. 204, pl. 34, pl. 35, figs. 1–8; RAASCH, 1951, p. 145; NELSON, 1951, p. 783, pl. 110, figs. 4, 7; LONGACRE, 1970, p. 51, pl. 5, figs. 4–8.

Saukiella cf. *pyrene* Ulrich and Resser, 1933, p. 204, pl. 35, figs. 9, 11 (not 10).

Saukiella pyrene limbata Ulrich and Resser, 1933, p. 206, pl. 35, figs. 12–14.

Saukiella frontalis Ulrich and Resser, 1933, p. 207, pl. 35, fig. 22.

Saukiella indenta Ulrich and Resser, 1933, p. 208, pl. 35, figs. 23–30; pl. 36, figs. 1–3.

Saukiella indenta intermedia Ulrich and Resser, 1933, p. 208, pl. 36, fig. 4.

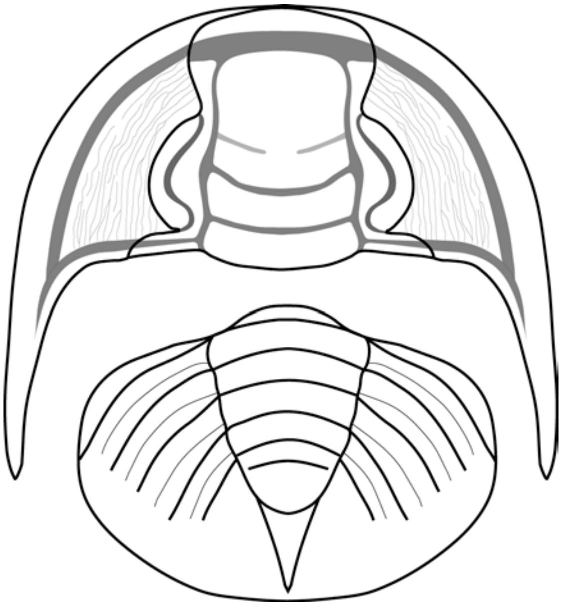
Saukiella signata Ulrich and Resser, 1933, p. 206, pl. 35, figs. 15–21.

not *Saukiella norwalkensis* Ulrich and Resser, Winston and Nicholls, 1967, p. 82, pl. 11, figs. 6–8, 12 (= *S. pyrene*).

Type material.—USNM 58644 (holotype)

Other material examined.—USNM 58645–58646, 84620; 85196, box with 7 specimens; 85197; 85200, box with 7 specimens; 187922, 192258–192261; 3 boxes of un-numbered material including 31 cranidia, 3 librigena, and 3 pygidia.

Diagnosis.—A species of *Prosaukia* distinguished by a relatively narrow (transversely) frontal area. S2 interrupted, posteriorly directed; S3 very faint, anteriorly-directed. Cranidial posterior limbs relatively narrow. Librigena with raised, anastomosing, subparallel ridges; lateral and posterior furrows confluent. Genal spines not advanced. Pygidium with 4 axial rings; a faint indication of a fifth axial ring is sometimes present; triangular postaxial ridge extends to posterior pygidial margin.



Text-figure 279. Reconstruction of *Saukiella pyrene*, based on specimens USNM 58466–58646, 192258–192261.

Discussion.—Adrain and Westrop (2004) placed this taxon into *Prosaukia* based on the presence of an approximately equally divided frontal area separated into a distinctly raised, convex anterior border, and possession of a true preglabellar field. The holotype cranidium (preserved in rather coarse sandstone) has an evenly curved anterior border, a preglabellar field that is largely concave and of approximately the same length as the anterior border, a distinctly raised anterior border, a rounded glabellar anterior, and well-define SO and S1 furrows. Additional material recovered from Texas by Winston and Nicholls (1967) and Longacre (1970) and from Oklahoma by Stitt (1971) added significantly to our understanding of the cranidial morphology of this species. These authors' cranidia are preserved in limestone rather than sandstone, possess a posteriorly-directed, discontinuous S2 furrow that is shallower than the S1 furrow, and a very shallow and short S3 furrow that is slightly anteriorly-directed (Longacre, 1970; Stitt, 1971). Additionally, Longacre's (1970) cranidia possess a slightly convex preglabellar field bounded at the front by a raised anterior border and at the rear by a distinct preglabellar furrow; this material confirms that *Saukiella pyrene* possesses a true preglabellar field and should thus be transferred to *Prosaukia* as suggested by Adrain and Westrop (2004).

Longacre (1970) assigned Winston and Nicholls' (1967) material to *P. misa*, but made no comment on her reasons for doing so. Winston and Nicholls' cranidia have a much shorter preglabellar field than does *P. misa*, the glabellar anterior is much more rounded, the glabellae much less anteriorly-tapering, and the associated librigena has a definitively advanced genal spine (Winston and Nicholls, 1967, see pl. 11, figs. 6-8). In these respects, Winston and Nicholls (1967) specimens are much more similar to *Saukiella norwalkensis*, to which they are herein referred.

Genus TAEBEKSAUKIA Lee and Choi 2011

Taebeksaukia LEE AND CHOI, 2011, p. 289.

Type species.—Taebaeksaukia spinata LEE AND CHOI, 2011, p. 289, from the Hwajeol and Dongjeom formations, Taebaek Group, Taebaeksan Basin, Korea (by original designation).

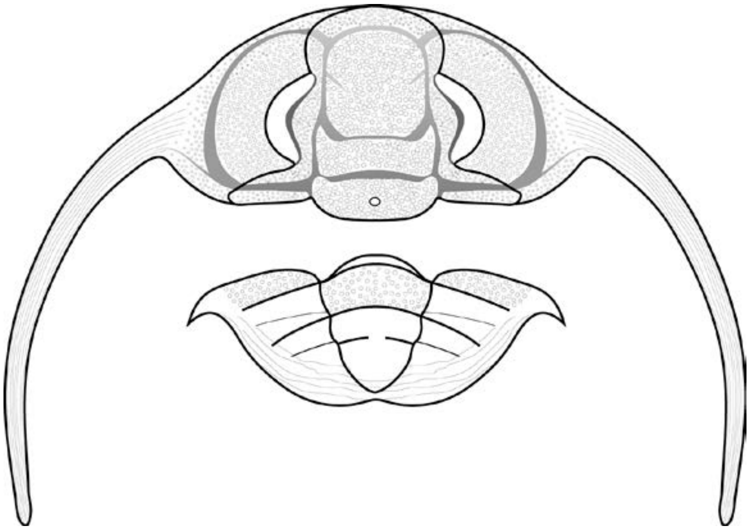
Diagnosis.—A genus of Saukiidae with very shallow anterior and lateral border furrows; anterior border furrow abaxially wide and obliquely bent forward; preglabellar area short, undifferentiated; palpebral lobes crescentic, large; genal spine long and slender; micropygous pygidium with paucisegmented axis and a pair of short marginal spines at anterolateral corners. (After Lee and Choi, 2011).

TAEBEKSAUKIA SPINATA Lee and Choi, 2011

Text-figure 40

Taebeksaukia spinata LEE AND CHOI, 2011, p. 289, figs. 3.5, 8.

Type material.—SNUP3159 (holotype).



Text-figure 40. Reconstruction of *Taebeksaukia spinata*, based on specimens in figure 8 of Lee and Choi (2011).

Diagnosis.—A species of *Taebaeksaukia* with densely tuberculate prosopon on cephalon; palpebral lobes anteriorly close to axial furrows; genal spine long and slender; pygidium with clearly-defined anteriormost axial ring; terminal piece parabolic in outline, constricted; straight ridges on posterior pleural bands. (Lee and Choi, 2011)

Discussion.—Currently this is a monospecific genera. *Taebeksaukia* consistently nests within or very close to the *Eosaukia* clade. Indeed, it is very similar to *Eosaukia bella*, but differs in having shallower confluent furrows of the librigena, lacking vincular structures on the ventral doublure of the librigena, and possessing a pair of curved pleural spines on the first pygidial segment (see Lee and Choi, 2011 for a full discussion).

Occurrence.—Units SCO1, 5, 11, 13, and 19 of Lee and Choi (2011); Hwajeol and Dongjeom Formations, Taebaek Group, Taebaeksan Basin, Korea.

Genus TELLERINA (Whitfield 1882)

Type species.—Dikelocephalus crassimarginatus, WHITFIELD, 1882, p. 344, pl. 27, fig. 14.

Diagnosis.—A genus of Saukiidae lacking a preglabellar field and differentiated by possession of an anteriorly-tapering glabella. Anterior border furrow interrupted, abaxial portions of anterior border furrow anterolaterally directed. Wide lateral borders of the librigenae (> 20% of cranidial length); lateral and posterior furrows of librigena confluent, posterior furrow continues into base of genal spine more strongly than lateral furrow. Subround to transversely subovate pygidium with unequally-divided pleurae.

Discussion.—Ulrich and Resser (1933) erected *Tellerina* to contain thirteen species and varieties of *Saukia*-like trilobites that were differentiated from *Saukia* by possessing wavy, anastomosing ridge ornament of the cranidia, a longer and more convex anterior cranidial border, more thickly-rimmed librigenae, more robust genal spines, differences in the glabellar furrows, and in possessing unequally divided pleurae of the pygidium. Raasch (1951) synonymized Ulrich and Resser's thirteen species to just four species: *T. crassimarginata*, *T. gothamensis, T. granistriata,* and *T. ? lucosia*; an additional species, *T. bigeneris* was assigned to *Saukia acuta*.

The genus *Tellerina* is very similar, morphologically, to the genus *Calvinella*. Both generally possess an anteriorly-tapering glabella, terrace ridge ornament of the cranidia (except in *C. ozarkensis*) and librigena, an interrupted cranidial anterior border furrow (no preglabellar field), and both possess a transversely ovate to subrounded pygidium. Ulrich and Resser (1933) noted that *Calvinella* differed from *Tellerina*, "... in little else than the possession of an occipital spine," (p. 219). However, in addition to the possession of an occipital spine, *Tellerina* also possesses a very wide lateral librigenal border (> 20% of the length of the cranidium), confluent librigenal border furrows that are distinctly directed posterolaterally after their point of confluence, and very wide genal spine bases with robust genal spines.

Raasch (1951) recognized *T. gothamensis* as a valid species, based, presumably, on its occurrence in a different stratigraphic interval; all of the taxa that Raasch assigned to *T. crassimarginata* occur in his *Saukia sublonga* Zonal Unit, while he placed *T. gothamensis* into his *Saukia subrecta* Zonal Unit [Ulrich and Resser (1933) list the locality for *T. gothamensis* as the Lodi Shale (Loc. x5.18), but all other specimens assignable to *T. crassimarginata* originate from other localities]. Based solely on morphology, the single cranidium assigned to *T. gothamensis* is indistinguishable from *T. crassimarginata*. The pygidium that Ulrich and Resser (1933) assigned to *T. gothamensis* may be a different genus because the axis is longer than is typical in *T. crassimarginata*. Because of the lack of any significant morphological criteria with which to distinguish it, we refer *T. gothamensis* to *Tellerina crassimarginata*; this leaves only two of Ulrich and Resser's (1933) original thirteen species, *T. crassimarginata*, *T. ? leucosia*.

Interestingly, Ulrich and Resser (1933) seemed to be at a loss as to where the specimens that they assigned to *T. ? leucosia* should be placed taxonomically. These specimens all occur in the Norwalk Sandstone at Ulrich and Resser's (1933) Locality 78, Osceola, Wisconsin. Morphologically, many of these specimens very strongly resemble *Saukiella*. Indeed, *Saukiella norwalkensis* occurs within the same outcrop (Loc. 87, Ulrich and Resser, 1933) as *T. ? leucosia*. Considering the apparent desire of Ulrich and Resser (1933) to sort material from the same outcrops based on size and/or very minor morphological differences, and then to associate cranidia, librigena, and pygidia that often do not co-occur on single slabs (we do not know if they occurred on single bedding planes, as there appears to be no stratigraphic information accompanying their material in many cases), and then to name new species based on these assortments, it is certainly possible that the material comprising *T. ? leucosia* represents *Saukiella* species that have been sorted based on the palpebral lobes being spaced slightly further apart than in *Saukiella norwalkensis*, for example. Alternatively, they could represent small individuals of *Tellerina crassimarginata*. Larger specimens would likely be more affected by flattening during taphonomy than smaller ones; thus the apparent greater degree of inflation in the cranidia of *T. ? leucosia* could simply be due to their much smaller size than *T. crassimarginata.*

Tellerina granistriata possesses strong pustulation of the cranidium, and aligned pustulation of the librigenal field and lateral and anterior librigenal border. It has the long anterior cranidial border, anteriorly-tapering glabella with four firmly-incised glabellar furrows (SO, S1-S3), and the wide librigenal lateral border that helps define *Tellerina*, but the cranidium is much more convex than is the cranidium of *T. crassimarginata*. The pygidium assigned by Ulrich and Resser to this species is hard to assess because it is damaged, but it is transversely ovate and appears to have more equally divided pleurae than *T. crassimarginata*. Due to the presence of these characters, we retain *T. granistriata* as a valid species.

Raasch (1951) referred *Tellerina bigeneris* to *confer Saukia acuta*. This is a puzzling assignment because the prosopon of *T. bigeneris* is definitively different than that of *Saukia acuta*; *T bigeneris* has raised, subparallel, anastomosing fingerprint-like ornament on the glabella and librigena, *Saukia acuta* has pustulated prosopon. Librigena of the single, articulated specimen assigned to *T. bigeneris* has wide librigenal borders with the posterior border furrow extending into very wide genal spine bases. The pygidium of *T. bigeneris* is also much more similar to *Tellerina* than to *Saukia*. It has 4 axial rings and a short, rounded terminal piece that lies far from the pygidial margin; *S. acuta* has a longer terminal piece that is located much more proximally to the pygidial posterior margin. For these reasons, we prefer to retain *T. bigeneris* within *Tellerina*, but place into synonymy with *T. crassimarginata* (see discussion under *T. crassimarginata* below for specific reasons for this).

Tellerina scotlandensis Resser, 1942 was erected based on a single pygidium that Walcott (1914) assigned as possibly representing *Saukia* (now *Prosaukia*) *stosei*. Because pygidia are often quite similar from saukiid species to species, and indeed, from genera to genera (compare pygidia of *Saukiella* with those of *Prosaukia*, for example) there is no significant material on which a meaningful diagnosis can be made, and we consider *Tellerina scotlandensis* to be *nomen dubium.*

Likewise, *Tellerina artigena* Howell 1945 was named based on tiny fragments of a "*Tellerina* type" glabella, and a partial librigena; *Tellerina regia* Howell 1945 was named based on a damaged and incomplete (no posterior margin, no axis) pygidium with unequally divided pleurae, and a small fragment of a single librigena. Because these taxa are exceptionally fragmentary and cannot be assessed in a meaningful comparative taxonomic way, they are necessarily of dubious taxonomic affinity, and should also be considered *nomen dubia*.

A number of Gondwanan species have been attributed to this genus as well. *Tellerina orientalis* (Resser and Endo 1937) possesses librigena with deeply impressed confluent lateral and posterior border furrows without either continuing into the base of the genal spine and has been referred to *Mictosaukia* by Lee and Choi (2011). These authors also assigned *Tellerina coreanica* (Kobayashi 1935) and *Tellerina callisto* (originally described by Walcott 1905 as *Ptychaspis callisto*) to *Eosaukia* (Lee and Choi, 2011). *Tellerina qingshuiheensis* Nan 1976 from North China and inner Mongolia is difficult to assess from the Nan's published material (three poorly-preserved cranidia). Nowhere in Nan's (1976) description are either librigena or pygidia mentioned; without librigena in particular, an assessment of the taxonomic affinity of these specimens is limited. Cranidia assigned to *T. qingshuiheensis* appear to be generally more convex than are specimens of *T. crassimarginata*, and also appear to have more deeply incised S1 furrows that are more strongly posteriorly-directed. These general characters agree with specimens of *Mictosaukia luanhensis,* which also occurs in North China. *Tellerina paichiaensis* Sun 1933 is similarly difficult to assess. *Tellerina chinshiensis* (Sun 1924) is a well-represented taxon that occurs in largely monospecific trilobite cocquinas or biomicrites from North China and which has confluent librigenal border furrows connecting in a C-shaped corner confluence, and no furrow extending into the genal spine; it is referred to *Mictosaukia*. *Tellerina sulcatifera* Resser in Endo 1937 has pygidia with a lower length to width ratio than is typical for *Tellerina*, have only 3 or 4 axial rings, a terminal piece that extends close to the posterior pygidial margin and a distinct, triangular postaxial ridge - all features much more similar to *Mictosaukia* pygidia. *Tellerina suni* (Kobayashi 1931) is not possible to assess based on the poorly preserved nature of the specimens. Based on these assignments, and on the few remaining valid species, it is apparent that *Tellerina* is a genus currently restricted to Laurentia and is of very limited taxonomic diversity with only four well-defined species currently recognized: *T. crassimarginata*, *T. granistriata*, *T. ? leucosia*, and *T. wardi*.

TELLERINA CRASSIMARGINATA (Whitfield 1882)

Figure 32.1–32.2; Text-figure 41

Dikelocephalus crassimarginatus, WHITFIELD, 1882, p. 344, pl. 27, fig. 14.

Saukia crassimarginata, Walcott, 1914, p. 377, pl. 61, fig. 8; pl. 65, figs. 3, 10; pl. 66, figs. 2–5, 5a.

Tellerina crassimarginata ULRICH AND RESSER, 1933, p. 244, pl. 41; pl. 42, fig. 1; SHIMER AND SHROCK, 1944, p. 633, pl. 261, figs. 5, 6; TWENHOFEL, 1945, p. 635, pl. 88, fig. 2.

Tellerina bigeneris ULRICH AND RESSER, 1933, p. 259, pl. 42, fig. 6.

Tellerina convexa ULRICH AND RESSER, 1933, p. 254, pl. 45, figs. 17–21.

Tellerina curta ULRICH AND RESSER, 1933, p. 249, pl. 42, figs. 2–3.

Tellerina gothamensis (in part) ULRICH AND RESSER, 1933, p. 260, pl. 42, fig. 4.

Tellerina lata ULRICH AND RESSER, 1933, p. 251, pl. 43, fig. 6.

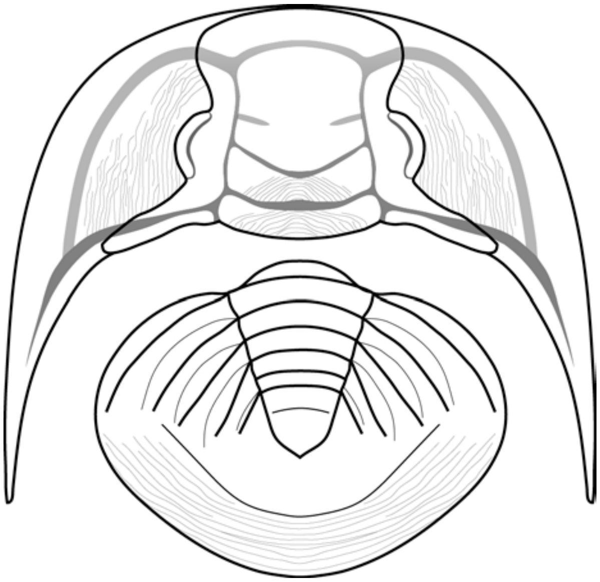
Tellerina norwalkensis ULRICH AND RESSER, 1933, p. 253, pl. 45, figs. 11–16.

Tellerina strigosa ULRICH AND RESSER, 1933, p. 249, pl. 43, figs. 1–5.

Tellerina recurva ULRICH AND RESSER, 1933, p. 252, pl. 43, fig. 7.

Type material.—USNM 58613 (holotype).

Other material examined.—USNM 14506, 58613–58615, 58620, 82517, 85215–85216, 85283–85285, and three un-numbered boxes with 7 cranidia, 3 librigena, 1 pygidium, and 1 articulated, but incomplete dorsal exoskeleton; UWGM 1099–1100, 1120–1122, 1164, 1207, 1209, 1374–1375, 1381, 1283–1384.



Text-figure 28. Reconstruction of *Tellerina crassimarginata*, based on USNM 58613 and many other specimens.

Diagnosis.—A species of *Tellerina* with raised, fingerprint-like anastomosing ornament of the cephalon. Glabella strongly narrows anteriorly; S2 weakly impressed, S3 absent. Genal spine bases very wide; genal spine stout. Pygidium with 5 axial rings (a 6th, weakly expressed ring may be present); terminal piece rounded, lacks well-developed postaxial ridge. Long (sagittally) ventral posterior pygidial doublure and dorsal postaxial area.

Discussion.—Raasch (1951) treated most of the species erected by Ulrich and Resser (1933) as representing junior synonyms of *Tellerina crassimarginata* Whitfield 1882. He assigned a fully-articulated specimen of *Tellerina bigeneris* Ulrich and Resser 1933 to *cf. Saukia acuta* even though it has clear morphological differences to that taxon; yet he offered no rationale to support this assignment (Raasch, 1951). A re-examination of Ulrich and Resser's type material reveals that the specimen assigned to *T. bigeneris* (USNM 58620, holotype) possesses a very wide (yet partially damaged) lateral librigenal border with the posterior border furrow continuing into the very wide base of the genal spine. Indeed, this specimen is very similar to *Tellerina crassimarginata*, but there are minor morphological differences that appear to separate *T. bigeneris* from *T. crassimarginata*. The cranidium of the only specimen known (which is articulated), is damaged on one side, the right free cheek is overturned and lies partially beneath the cephalon, and the pygidium is very slightly displaced from the trunk, and so this specimen likely represents a molt. *Tellerina bigeneris* appears to have only four pygidial axial rings, as opposed to five in *T. crassimarginata*. However, considering that this specimen likely represents a molt, overlapping of the tagma, or telescoping of the exoskeleton may have occurred. Close inspection of the slightly offset pygidium reveals that the anterior margin of the pygidium continues significantly beneath the trunk. On the left side of the cranidium, there are an interpleural and a pleural furrow that are both located in front of the anteriormost exposed axial ring. This indicates that a fifth pygidial axial ring lies beneath the twelfth trunk segment. Considering this revelation, there are no significant morphological disparities between these taxa, and *T. bigeneris* is assigned to *T. crassimarginata*.

TELLERINA WARDI (Walcott 1914)

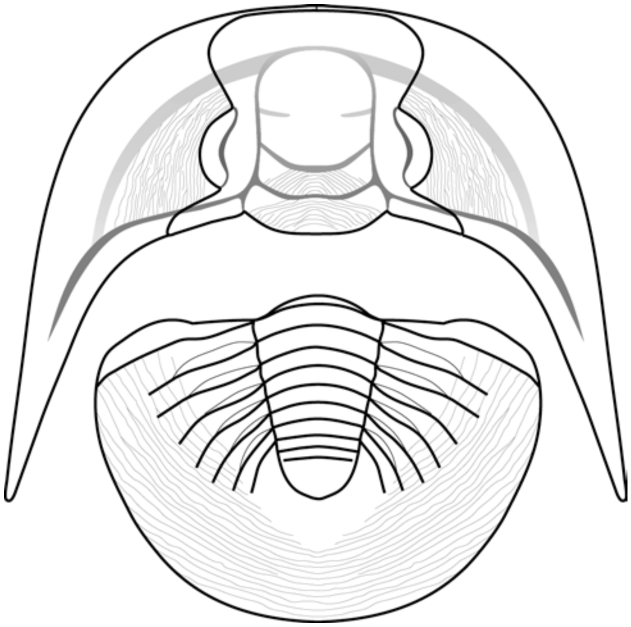
Figure 32.3–32.5; Text-figure 42

Saukia wardi WALCOTT, 1914, p. 384, pl. 69, figs. 1, 2.

Tellerina wardi, RESSER (in part), 1938a, p. 101, pl. 16, figs. 1–4 only.

Type material.—YPM 24759, 27987 (syntypes)

Other material examined.—YPM 8182, multiple un-numbered specimens; USNM 94998 (3 specimens), 94995 (5 specimens), additional un-numbered material.



Text-figure 29. Reconstruction of *Tellerina wardi* based on specimens YPM 24759, 27987 and others.

Diagnosis.—Librigena with very wide lateral borders. Pygidium very long (sagittally), subround; pygidial length to width ratio approximately 0.72; 9 axial rings present; axis relatively narrow. Very wide, flat, long (sagittally) pygidial border with terrace ridges.

Discussion.—This is another species that is difficult to assess, not because it is underrepresented in the fossil record, but because most examples, including the types, are severely flattened, limiting the morphological data that can be accurately collected (see Figure 31.3–31.5). In most cranidial specimens, wrinkles or cracks in the specimens indicate that the cuticle cracked in order to relieve stresses experienced during postdepositional compression. In these flattened cranidia (including the holotype slabs), the glabellae are generally sub-parallel to parallel sided. However, in many saukiid cranidia, the anterior lobe of the glabella is either more convex than the occipital ring, or extends more ventrally than does the occipital ring. The implication of this morphology is that, when flattened, the anterior lobes elongate transversely leading to a glabellar shape that is distorted, and much more parallel-sided than the original, convex structure. Many of these flattened cranidia show a medial constriction of the glabellae adjacent to the palpebral lobes and the point where the S1 and axial furrows join. In a glabella that is either more convex anteriorly, or has anterior lobes that continue more ventrally, this condition would be expected during flattening, and is thus not likely due to original morphology. A single cranidium was figured by Resser (1938a) from a different outcrop than the type material (Winchester, VA; approximately 130 miles northeast of the type locality, Natural Bridge, VA), and co-occurs with two pygidia (one is figured in Resser, 1938a, pl. 16, fig. 5) that he assigned to *T. wardi*. However, Resser (1938a) offered no justification for that assignment. These pygidia are both much shorter and transversely much more elliptical than pygidia from the type locality. More importantly, they are complete, and possess only five or six axial rings, while pygidia from the type locality have nine axial rings. These Winchester, VA pygidia are much closer in general morphology to *T. crassimarginata*, to which they are referred. The cranidium from Winchester (USNM 94995) is distinctly tellerinid; it lacks a preglabellar field, has a relatively long anterior border, anterolaterally-directed abaxial portions of the preglabellar furrow, and has only a well-defined SO and S1; in these characters it is similar to a small specimen of *T. crassimarginata*, to which this specimen is referred.

Because most of the convexity in trilobite cranidia occurs oriented transversely to the axis, most of the elongation due to flattening will also be oriented in this direction. The one major exception to this is the anterior of the glabella. In *T. crassimarginata*, the anterior of the glabella is not significantly convex. In nearly all specimens of *T. wardi*, there are cracks in the areas that would have had the greatest original convexity: the glabella, the axial lobe of the trunk, and the pygidial axis (see Figure 3.13). Glabellar furrows will be more elongate in flattened specimens and the degree of rounding will also be stretched over a longer run, leading to more evenly rounded shapes than in the original, un-flattened cranidium.

The glabella of *T. wardi* is relatively parallel-sided, but as previously discussed, this is likely due to flattening; thus this character cannot be used for phylogenetic analyses. The anterior margin of the cranidium is transversely flat, with slight puckers, or ripples in the anterior margin; these are also likely due to material with limited pliability being flattened. The anterior limb of the facial suture is divergent, and the abaxial part of the preglabellar field is slightly posterolaterally-directed. The palpebral lobes are located slightly further away from the glabella than in *T. crassimarginata*, and there is an indication in some cranidia of a very slightly posteriorly- or transversely-directed S2 furrow. There is no evidence of an S3 furrow, although this could be due to the relative tenuous nature of the S3 furrow in Saukiidae in combination with the taphonomic flattening of these specimens. Traces of raised ridge ornament can occasionally be observed on the occipital lobe of the glabella. These characters, especially those of the distinctive pygidium, are substantially different from all other species of the genus, and this species is retained as a valid species of *Tellerina*.

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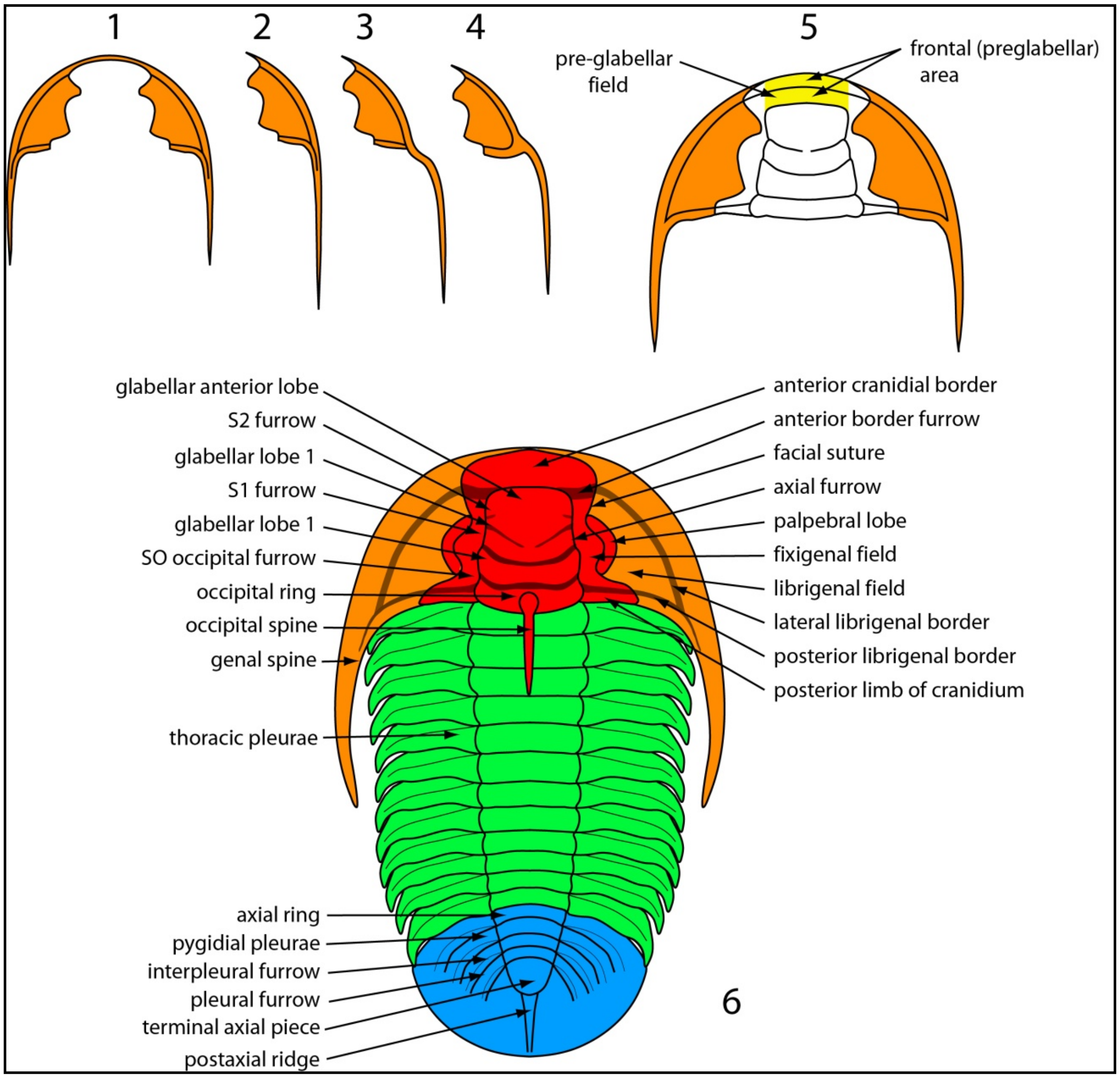
FIGURES

Figure 1. Generalized saukiid trilobite morphology. 1-4: Different morphological style found in saukiid librigenae, or free cheeks. 1) Yoked free cheeks. In this kind of librigena, an anterior brace connects the left and right free cheeks together into a single unit. 2) Smoothly continuous lateral margin grading into free cheek - this style of librigena typifies Laurentian saukiids. 3) Inflected lateral margin at base of free cheek. 4) Inflected lateral margin with advanced genal spine (genal spine base is moved slightly anterior to genal angle. 5) Morphology of the saukiid frontal area when a preglabellar field is present. A preglabellar field represents a distinct area immediately anterior to the glabella that is divided into a flat or gently convex area bounded anteriorly by an anterior border defined by a distinct furrow or a break in slope. Saukiids that lack a preglabellar field do not have the posterior flat, or slightly convex area (see Fig 1.6 as an example of a saukiid lacking a preglabellar field). 6) General morphology of saukiid trilobites. Orange = librigenae (free cheeks); Red = cranidium (librigenae + crandium together is termed cephalon); Green = thorax; Blue = pygidium.



1
2
3
4
5
pre-glabellar field
frontal (preglabellar) area
glabellar anterior lobe
S2 furrow
glabellar lobe 1
S1 furrow
glabellar lobe 1
SO occipital furrow
occipital ring
occipital spine
genal spine
thoracic pleurae
axial ring
pygidial pleurae
interpleural furrow
pleural furrow
terminal axial piece
postaxial ridge
anterior cranidial border
anterior border furrow
facial suture
axial furrow
palpebral lobe
fixigenal field
librigenal field
lateral librigenal border
posterior librigenal border
posterior limb of cranidium
6

Figure 2. Cladograms of previous studies that include the Saukiidae. The areas in gray represent general agreement among the trees presented here. See text for discussion.

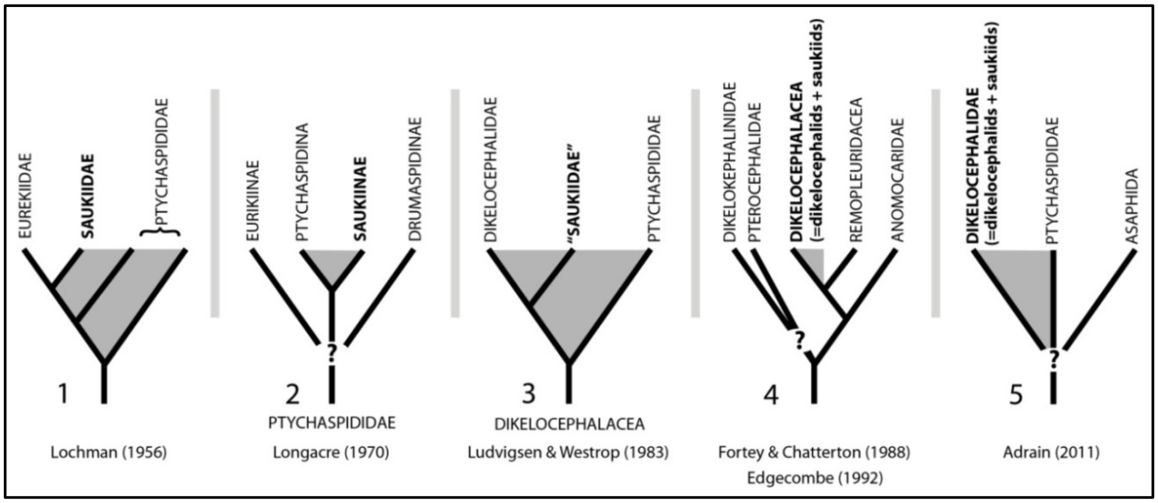

EUREKIIDAE
SAUKIIDAE
PTYCHASPIDIDAE
1
Lochman (1956)
EURIKIINAE
PTYCHASPIDINA
SAUKIINAE
DRUMASPIDINAE
?
2
PTYCHASPIDIDAE
Longacre (1970)
DIKELOCEPHALIDAE
"SAUKIIDAE"
PTYCHASPIDIDAE
3
DIKELOCEPHALACEA
Ludvigsen & Westrop (1983)
DIKELOKEPHALINIDAE
PTEROCEPHALIDAE
DIKELOCEPHALACEA (=dikelocephalids + saukiids)
REMOPLEURIDACEA
ANOMOCARIDAE
?
4
Fortey & Chatterton (1988)
Edgecombe (1992)
DIKELOCEPHALIDAE (=dikelocephalids + saukiids)
PTYCHASPIDIDAE
ASAPHIDA
?
5
Adrain (2011)

Figure 3. Inferred evolution of preglabellar field. The pre-glabellar field is the area between the preglabellar furrow at the anterior of the glabella) and the anterior border furrow (see text for details).

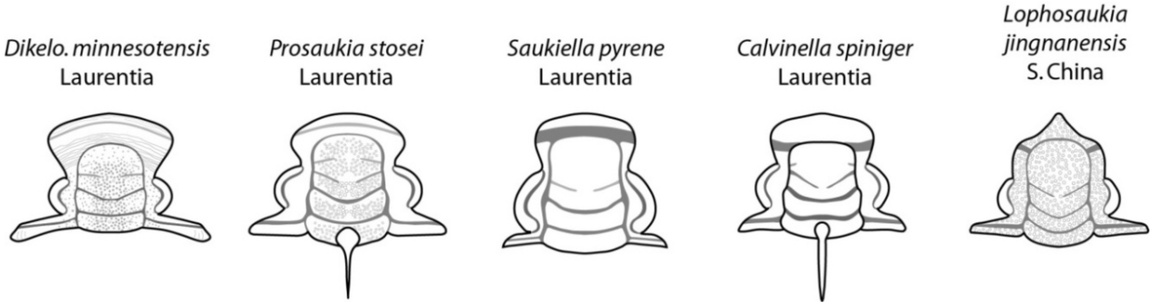

Dikelo. minnesotensis
Laurentia
Prosaukia stosei
Laurentia
Saukiella pyrene
Laurentia
Calvinella spiniger
Laurentia
Lophosaukia jingnanensis
S. China

Figure 4. Landmarks used in geometric morphometric analyses. For taxa with a preglabellar field (the space between the anterior cranidial border furrow (point 2, above), and the glabellar anterior (point 3, above), points 2 and 3 are separate. For taxa that lack a preglabellar field, points 2 and 3 are both overlain in the same position - the glabellar anterior.

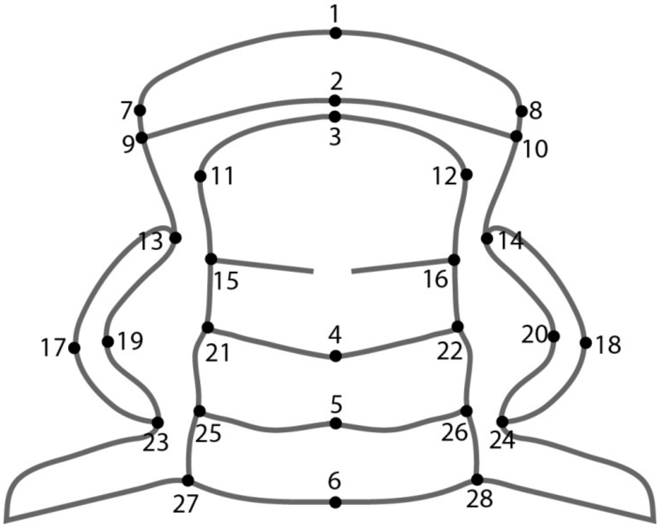

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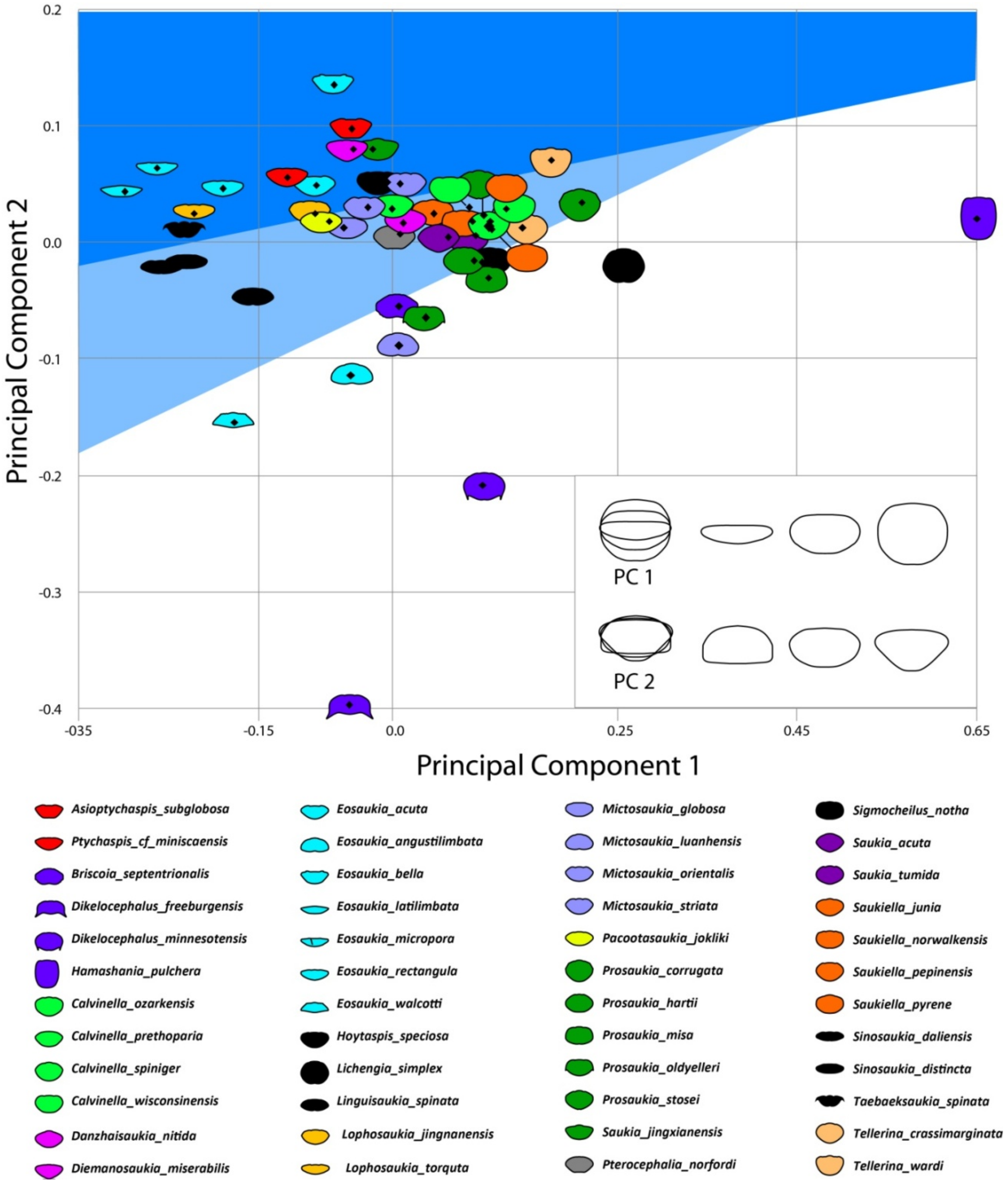
Figure 5. Principal component analysis of the pygidial shape of saukiid and outgroup taxa. The x-axis represents PC1, the component contributing most to the observed variation in shape, in this case it is a component contributing both to the length to width of the pygidia (see inset visual representation of principal component, lower right of graph). The y-axis represents PC2, or the shape and extent of the pygidial taper, and varies from flat to triangular. This graph can be used to both assess pygidial length to width, and overall shape.



0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
Principal Component 2
-035
-0.15
0.0
0.25
0.45
0.65
Principal Component 1
PC 1
PC 2
Asioptychaspis_subglobosa
Ptychaspis_cf_miniscaensis
Briscoia_septentrionalis
Dikelocephalus_freeburgensis
Dikelocephalus_minnesotensis
Hamashania_pulchera
Calvinella_ozarkensis
Calvinella_prethoparia
Calvinella_spiniger
Calvinella_wisconsinensis
Danzhaisaukia_nitida
Diemanosaukia_miserabilis
Eosaukia_acuta
Eosaukia_angustilimbata
Eosaukia_bella
Eosaukia_latilimbata
Eosaukia_micropora
Eosaukia_rectangula
Eosaukia_walcotti
Hoytaspis_speciosa
Lichengia_simplex
Linguisaukia_spinata
Lophosaukia_jingnanensis
Lophosaukia_torquta
Mictosaukia_globosa
Mictosaukia_luanhensis
Mictosaukia_orientalis
Mictosaukia_striata
Pacootasaukia_jokliki
Prosaukia_corrugata
Prosaukia_hartii
Prosaukia_misa
Prosaukia_oldyelleri
Prosaukia_stosei
Saukia_jingxianensis
Pterocephalia_norfordi
Sigmocheilus_notha
Saukia_acuta
Saukia_tumida
Saukiella_junia
Saukiella_norwalkensis
Saukiella_pepinensis
Saukiella_pyrene
Sinosaukia_daliensis
Sinosaukia_distincta
Taebaeksaukia_spinata
Tellerina_crassimarginata
Tellerina_wardi

Figure 6. Consensus tree computed from a set of most parsimonious trees generated from analysis of qualitative data matrix only, and including all 50 taxa (Analysis 1 from Table 2). Italicized numbers give bootstrap support values at the nodes directly above them. See text for discussion.

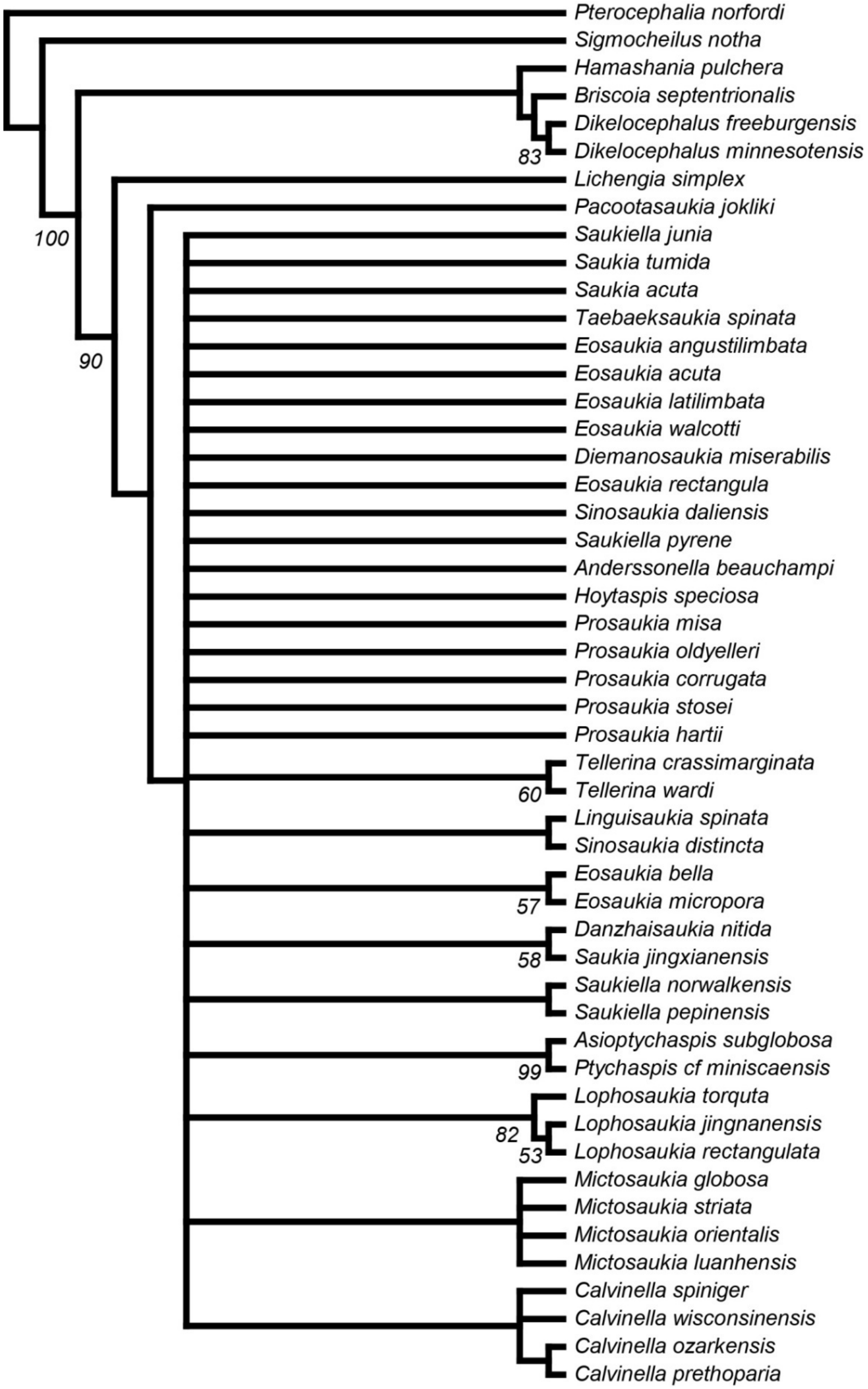
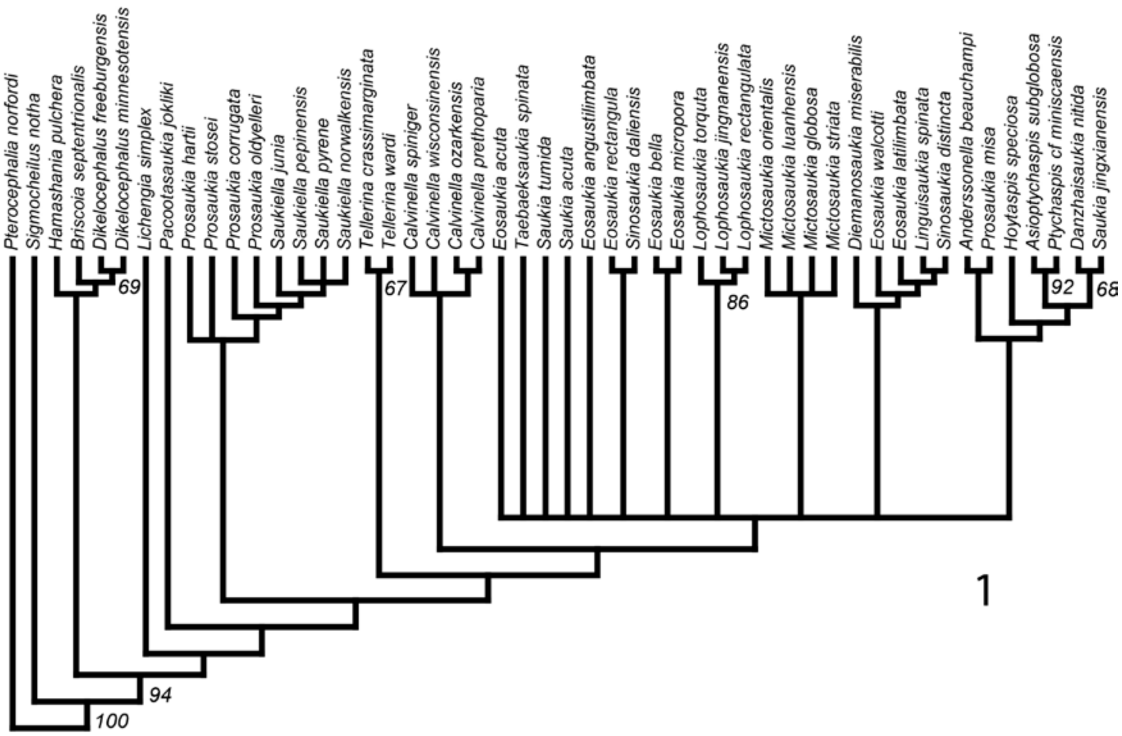
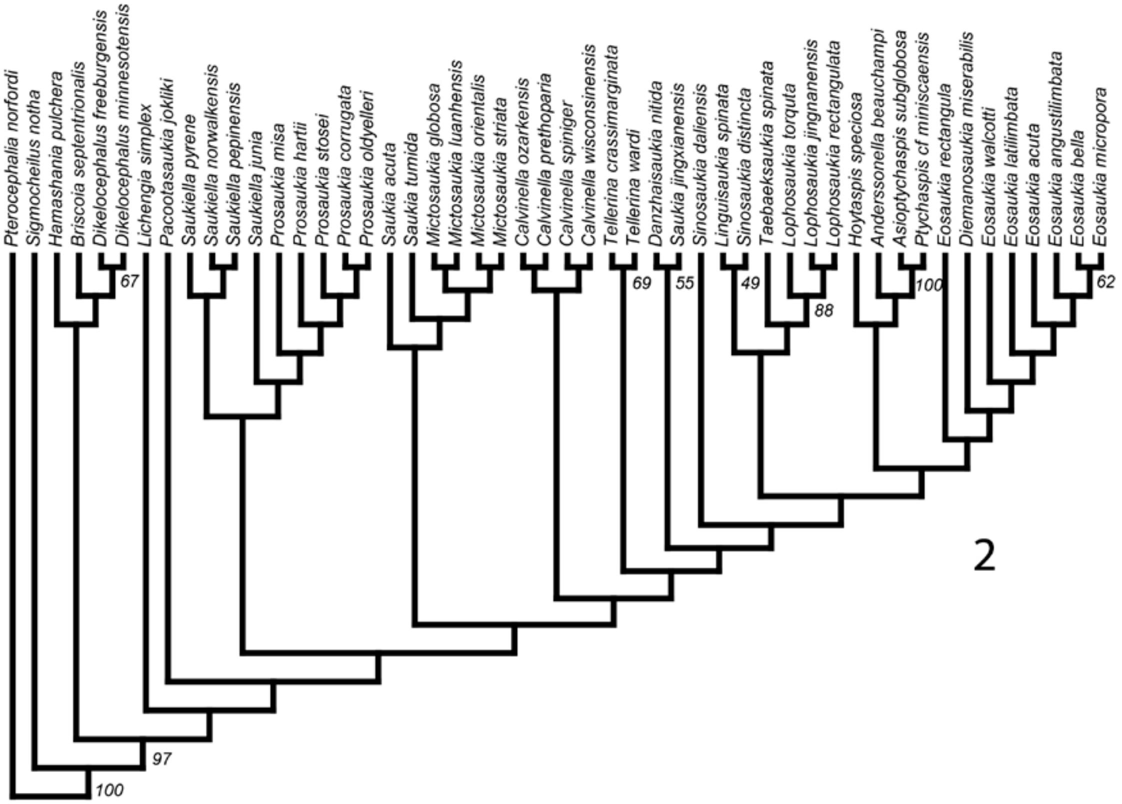

Pterocephalia norfordi
Sigmocheilus notha
Hamashania pulchera
Briscoia septentrionalis
Dikelocephalus freeburgensis
Dikelocephalus minnesotensis
83
Lichengia simplex
Pacootasaukia jokliki
100
Saukiella junia
Saukia tumida
Saukia acuta
Taebaeksaukia spinata
Eosaukia angustilimbata
90
Eosaukia acuta
Eosaukia latilimbata
Eosaukia walcotti
Diemanosaukia miserabilis
Eosaukia rectangula
Sinosaukia daliensis
Saukiella pyrene
Anderssonella beauchampi
Hoytaspis speciosa
Prosaukia misa
Prosaukia oldyelleri
Prosaukia corrugata
Prosaukia stosei
Prosaukia hartii
Tellerina crassimarginata
Tellerina wardi
60
Linguisaukia spinata
Sinosaukia distincta
Eosaukia bella
Eosaukia micropora
57
Danzhaisaukia nitida
Saukia jingxianensis
58
Saukiella norwalkensis
Saukiella pepinensis
Asioptychaspis subglobosa
Ptychaspis cf miniscaensis
99
Lophosaukia torquta
Lophosaukia jingnanensis
82
Lophosaukia rectangulata
53
Mictosaukia globosa
Mictosaukia striata
Mictosaukia orientalis
Mictosaukia luanhensis
Calvinella spiniger
Calvinella wisconsinensis
Calvinella ozarkensis
Calvinella prethoparia

Figure 7. Consensus trees computed from sets of most parsimonious trees generated from analysis of qualitative+ binned morphometric data and qualitative + gap-weighted matrices that include all 50 taxa. 1) consensus tree generated from analysis of qualitative+ binned morphometric characters that includes all 50 taxa (Analysis 4 from Table 2). 2) consensus tree generated from analysis of qualitative + gap-weighted characters of all 50 taxa (Analysis 7 from Table 2). Italicized numbers give bootstrap support values at the nodes directly to the left of them. See text for discussion.


Pterocephalia norfordi
Sigmocheilus notha
Hamashania pulchera
Briscoia septentrionalis
Dikelocephalus freeburgensis
Dikelocephalus minnesotensis
Lichengia simplex
Pacootasaukia jokliki
Prosaukia hartii
Prosaukia stosei
Prosaukia corrugata
Prosaukia oldyelleri
Saukiella junia
Saukiella pepinensis
Saukiella pyrene
Saukiella norwalkensis
Tellerina crassimarginata
Tellerina wardi
Calvinella spiniger
Calvinella wisconsinensis
Calvinella ozarkensis
Calvinella prethoparia
Eosaukia acuta
Taebaeksaukia spinata
Saukia tumida
Saukia acuta
Eosaukia angustilimbata
Eosaukia rectangula
Sinosaukia daliensis
Eosaukia bella
Eosaukia micropora
Lophosaukia torquta
Lophosaukia jingnanensis
Lophosaukia rectangulata
Mictosaukia orientalis
Mictosaukia luanhensis
Mictosaukia globosa
Mictosaukia striata
Diemanosaukia miserabilis
Eosaukia walcotti
Eosaukia latilimbata
Linguisaukia spinata
Sinosaukia distincta
Anderssonella beauchampi
Prosaukia misa
Hoytaspis speciosa
Asioptychaspis subglobosa
Ptychaspis cf miniscaensis
Danzhaisaukia nitida
Saukia jingxianensis
69
67
86
92
68
94
100
1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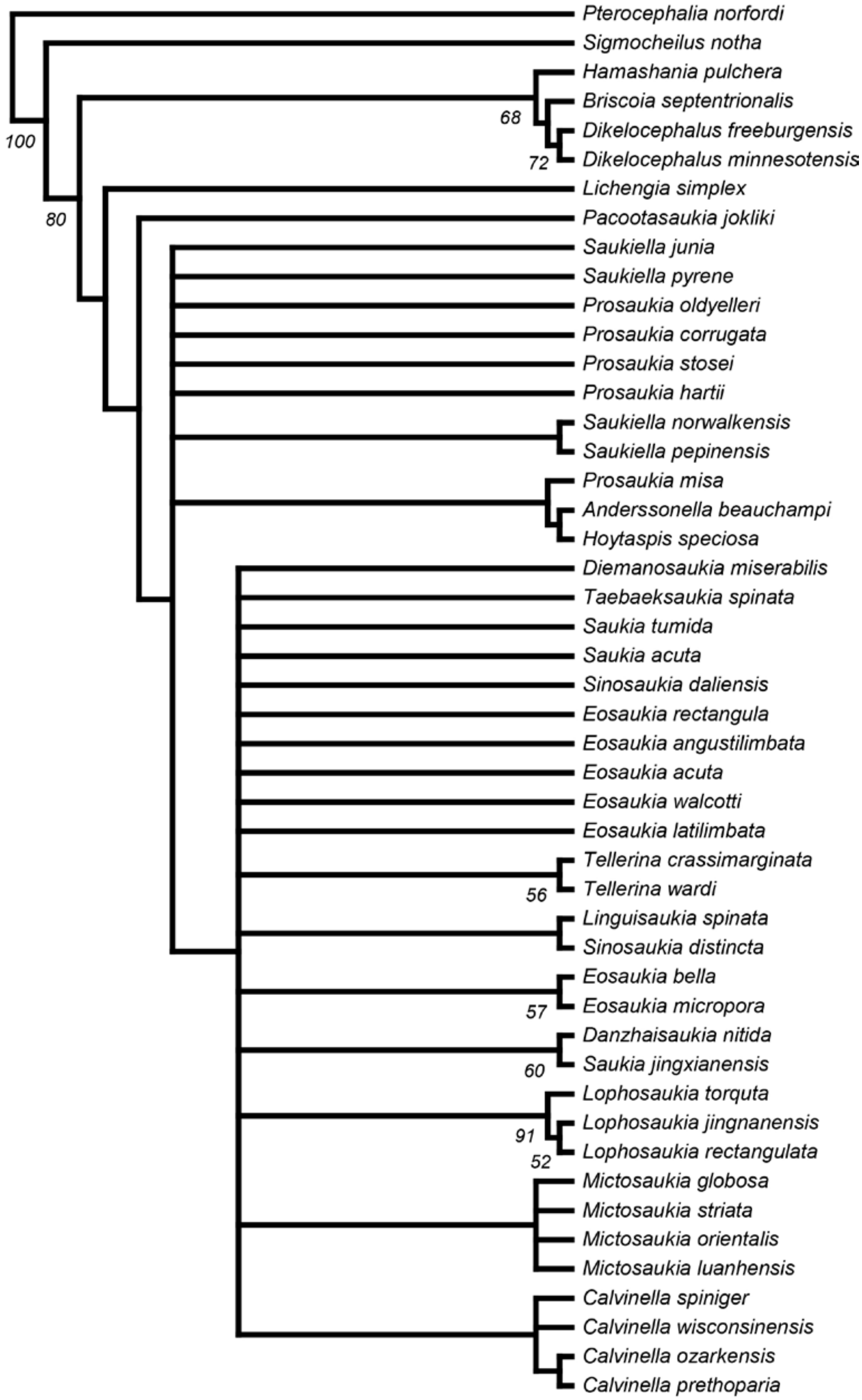
Dikelocephalus minnesotensis
Lichengia simplex
Pacootasaukia jokliki
Saukiella pyrene
Saukiella norwalkensis
Saukiella pepinensis
Saukiella junia
Prosaukia misa
Prosaukia hartii
Prosaukia stosei
Prosaukia corrugata
Prosaukia oldyelleri
Saukia acuta
Saukia tumida
Mictosaukia globosa
Mictosaukia luanhensis
Mictosaukia orientalis
Mictosaukia striata
Calvinella ozarkensis
Calvinella prethoparia
Calvinella spiniger
Calvinella wisconsinensis
Tellerina crassimarginata
Tellerina wardi
Danzhaisaukia nitida
Saukia jingxianensis
Sinosaukia daliensis
Linguisaukia spinata
Sinosaukia distincta
Taebaeksaukia spinata
Lophosaukia torquta
Lophosaukia jingnanensis
Lophosaukia rectangulata
Hoytaspis speciosa
Anderssonella beauchampi
Asioptychaspis subglobosa
Ptychaspis cf miniscaensis
Eosaukia rectangula
Diemanosaukia miserabilis
Eosaukia walcotti
Eosaukia latilimbata
Eosaukia acuta
Eosaukia angustilimbata
Eosaukia bella
Eosaukia micropora
67
69
55
49
88
100
62
97
100
2

Figure 8. Consensus tree computed from a set of most parsimonious trees generated from analysis of qualitative only data matrix, and including Saukiidae, Dikelocephaliidae, and Pterocephaliidae taxa only (Analysis 2 from Table 2). Italicized numbers give bootstrap support values at the nodes directly above them. See text for discussion.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Sigmocheilus notha
Hamashania pulchera
Briscoia septentrionalis
68
Dikelocephalus freeburgensis
100
72
Dikelocephalus minnesotensis
Lichengia simplex
80
Pacootasaukia jokliki
Saukiella junia
Saukiella pyrene
Prosaukia oldyelleri
Prosaukia corrugata
Prosaukia stosei
Prosaukia hartii
Saukiella norwalkensis
Saukiella pepinensis
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Hoytaspis speciosa
Diemanosaukia miserabilis
Taebaeksaukia spinata
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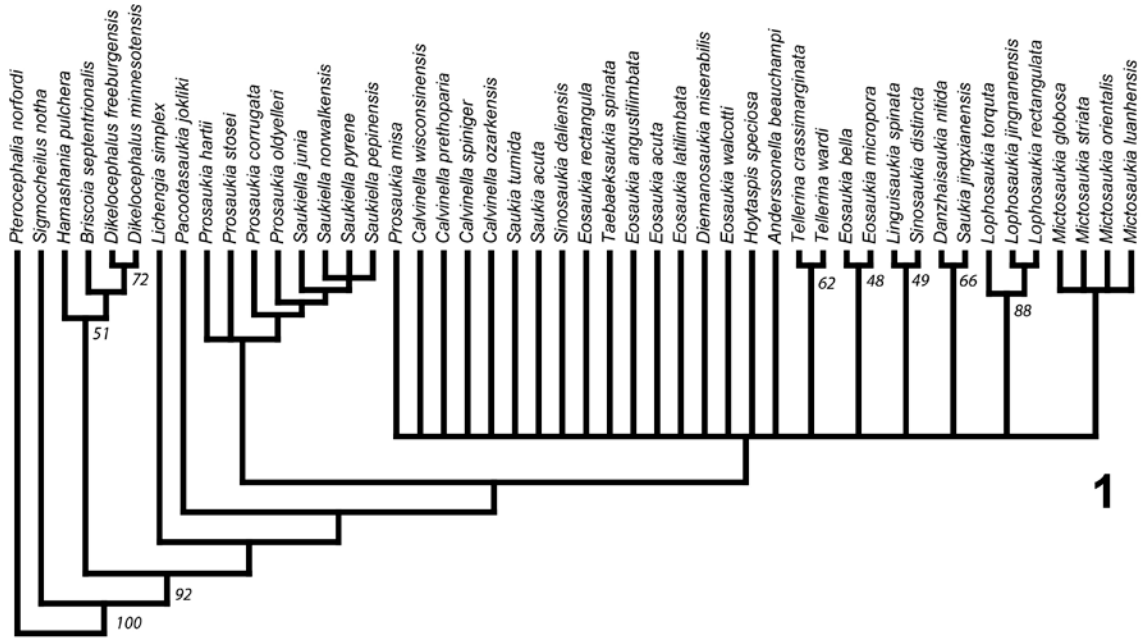
Saukia acuta
Sinosaukia daliensis
Eosaukia rectangula
Eosaukia angustilimbata
Eosaukia acuta
Eosaukia walcotti
Eosaukia latilimbata
Tellerina crassimarginata
56
Tellerina wardi
Linguisaukia spinata
Sinosaukia distincta
Eosaukia bella
57
Eosaukia micropora
Danzhaisaukia nitida
60
Saukia jingxianensis
Lophosaukia torquta
Lophosaukia jingnanensis
91
52
Lophosaukia rectangulata
Mictosaukia globosa
Mictosaukia striata
Mictosaukia orientalis
Mictosaukia luanhensis
Calvinella spiniger
Calvinella wisconsinensis
Calvinella ozarkensis
Calvinella prethoparia

Figure 9. Consensus trees computed from sets of most parsimonious trees generated from analysis of qualitative + binned morphometric data and qualitative + gap-weighted matrices that include Saukiidae, Dikelocephaliidae, and Pterocephaliidae taxa. 1) consensus tree generated from analysis of qualitative+ binned morphometric characters (Analysis 5 from Table 2). 2) consensus tree generated from analysis of qualitative + gap-weighted characters (Analysis 8 from Table 2). Italicized numbers give bootstrap support values at the nodes directly to the left of them. See text for discussion.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Sigmocheilus notha
Hamashania pulchera
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Dikelocephalus freeburgensis
Dikelocephalus minnesotensis
Lichengia simplex
Pacootasaukia jokliki
Prosaukia hartii
Prosaukia stosei
Prosaukia corrugata
Prosaukia oldyelleri
Saukiella junia
Saukiella norwalkensis
Saukiella pyrene
Saukiella pepinensis
Prosaukia misa
Calvinella wisconsinensis
Calvinella prethoparia
Calvinella spiniger
Calvinella ozarkensis
Saukia tumida
Saukia acuta
Sinosaukia daliensis
Eosaukia rectangula
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Diemanosaukia miserabilis
Eosaukia walcotti
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Tellerina crassimarginata
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Eosaukia bella
Eosaukia micropora
Linguisaukia spinata
Sinosaukia distincta
Danzhaisaukia nitida
Saukia jingxianensis
Lophosaukia torquta
Lophosaukia jingnanensis
Lophosaukia rectangulata
Mictosaukia globosa
Mictosaukia striata
Mictosaukia orientalis
Mictosaukia luanhensis
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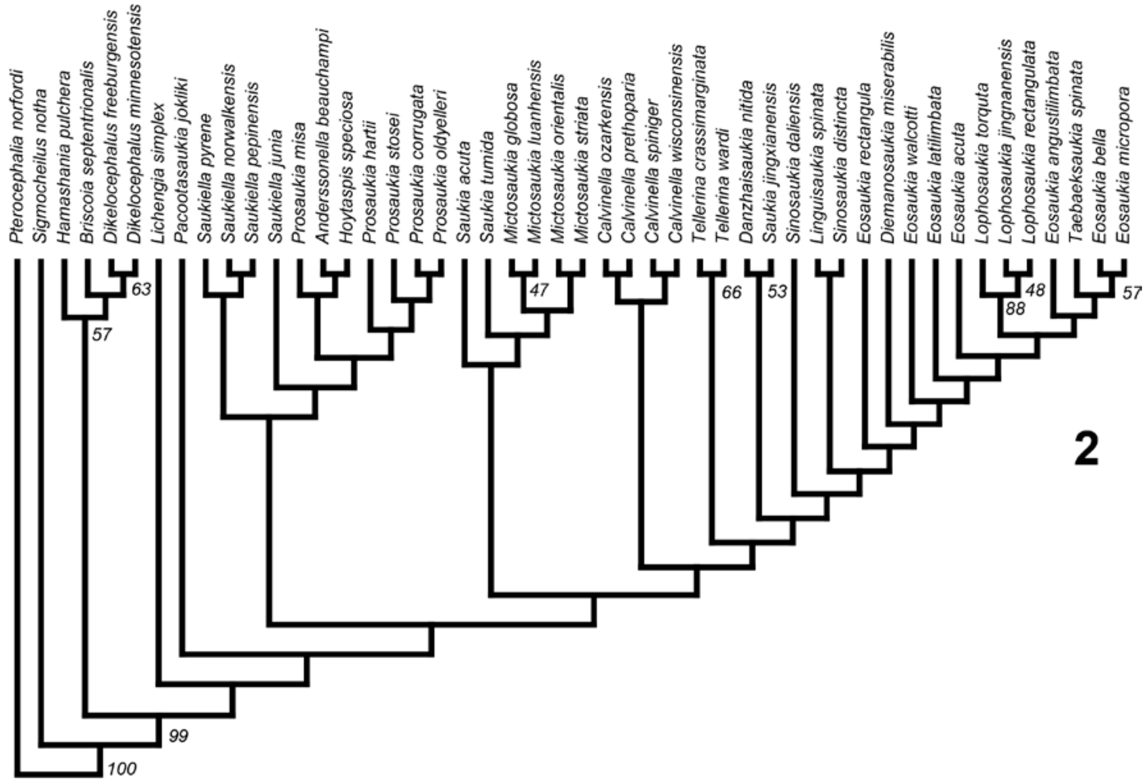
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Sigmocheilus notha
Hamashania pulchera
Briscoia septentrionalis
Dikelocephalus freeburgensis
Dikelocephalus minnesotensis
Lichengia simplex
Pacootasaukia jokliki
Saukiella pyrene
Saukiella norwalkensis
Saukiella pepinensis
Saukiella junia
Prosaukia misa
Anderssonella beauchampi
Hoytaspis speciosa
Prosaukia hartii
Prosaukia stosei
Prosaukia corrugata
Prosaukia oldyelleri
Saukia acuta
Saukia tumida
Mictosaukia globosa
Mictosaukia luanhensis
Mictosaukia orientalis
Mictosaukia striata
Calvinella ozarkensis
Calvinella prethoparia
Calvinella spiniger
Calvinella wisconsinensis
Tellerina crassimarginata
Tellerina wardi
Danzhaisaukia nitida
Saukia jingxianensis
Sinosaukia daliensis
Linguisaukia spinata
Sinosaukia distincta
Eosaukia rectangula
Diemanosaukia miserabilis
Eosaukia walcotti
Eosaukia latilimbata
Eosaukia acuta
Lophosaukia torquta
Lophosaukia jingnanensis
Lophosaukia rectangulata
Eosaukia angustilimbata
Taebaeksaukia spinata
Eosaukia bella
Eosaukia micropora
63
57
47
66
53
48
88
57
99
100

2

Figure 10. Consensus tree computed from a set of most parsimonious trees generated from analysis of qualitative only data matrix, and including Saukiidae, Dikelocephaliidae, and Ptychaspididae taxa only (Analysis 3 from Table 2). Italicized numbers give bootstrap support values at the nodes directly above them. See text for discussion.

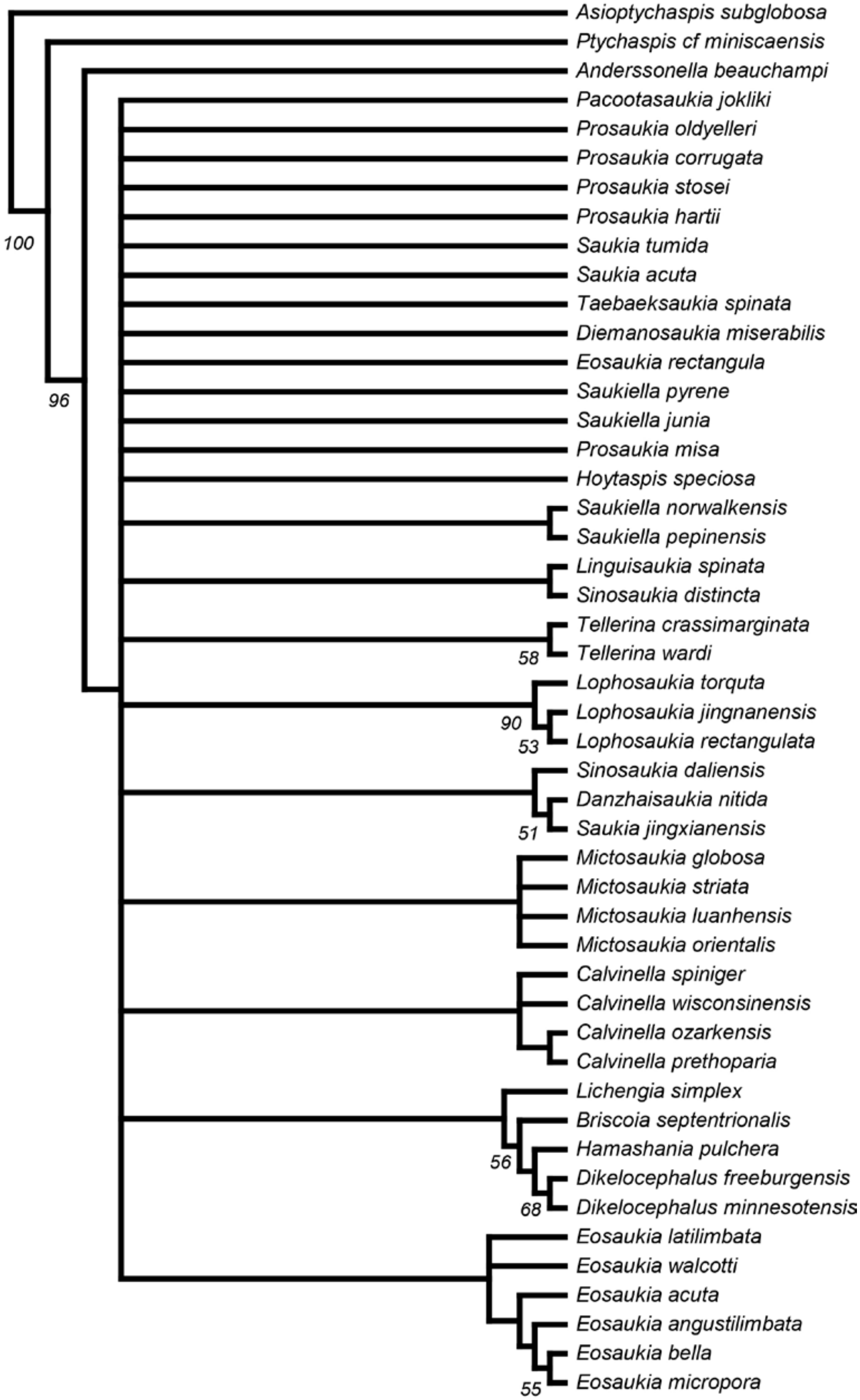
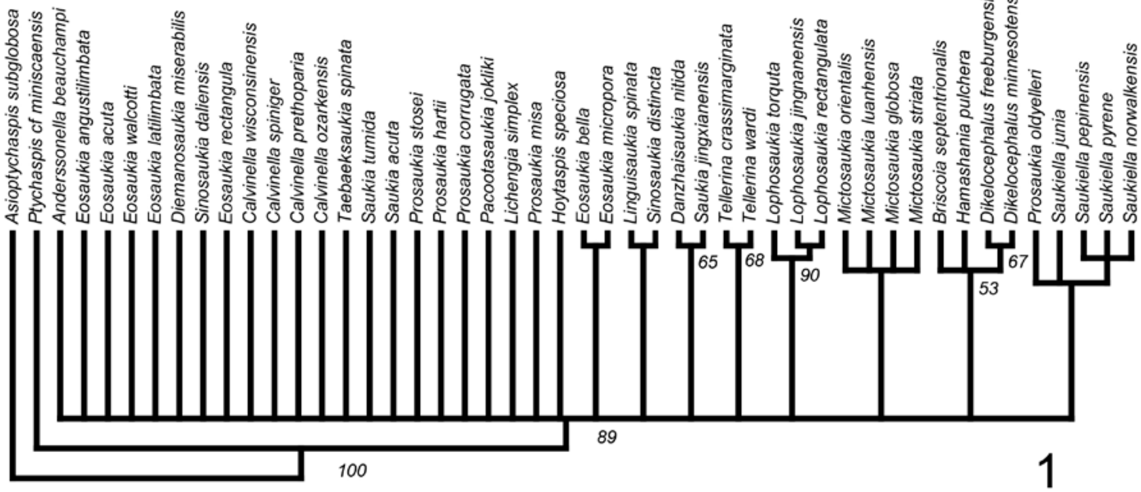

Asioptychaspis subglobosa
Ptychaspis cf miniscaensis
Anderssonella beauchampi
Pacootasaukia jokliki
Prosaukia oldyelleri
Prosaukia corrugata
Prosaukia stosei
Prosaukia hartii
Saukia tumida
Saukia acuta
Taebaeksaukia spinata
Diemanosaukia miserabilis
Eosaukia rectangula
Saukiella pyrene
Saukiella junia
Prosaukia misa
Hoytaspis speciosa
Saukiella norwalkensis
Saukiella pepinensis
Linguisaukia spinata
Sinosaukia distincta
Tellerina crassimarginata
Tellerina wardi
Lophosaukia torquta
Lophosaukia jingnanensis
Lophosaukia rectangulata
Sinosaukia daliensis
Danzhaisaukia nitida
Saukia jingxianensis
Mictosaukia globosa
Mictosaukia striata
Mictosaukia luanhensis
Mictosaukia orientalis
Calvinella spiniger
Calvinella wisconsinensis
Calvinella ozarkensis
Calvinella prethoparia
Lichengia simplex
Briscoia septentrionalis
Hamashania pulchera
Dikelocephalus freeburgensis
Dikelocephalus minnesotensis
Eosaukia latilimbata
Eosaukia walcotti
Eosaukia acuta
Eosaukia angustilimbata
Eosaukia bella
Eosaukia micropora
100
96
58
90
53
51
56
68
55

Figure 11. Consensus trees computed from sets of most parsimonious trees generated from analysis of qualitative + binned morphometric data and qualitative + gap-weighted matrices that include Saukiidae, Dikelocephaliidae, and Ptychaspididae taxa. 1) consensus tree generated from analysis of qualitative+ binned morphometric characters (Analysis 6 from Table 2). 2) consensus tree generated from analysis of qualitative + gap-weighted characters (Analysis 9 from Table 2). Italicized numbers give bootstrap support values at the nodes directly to the left of them. See text for discussion.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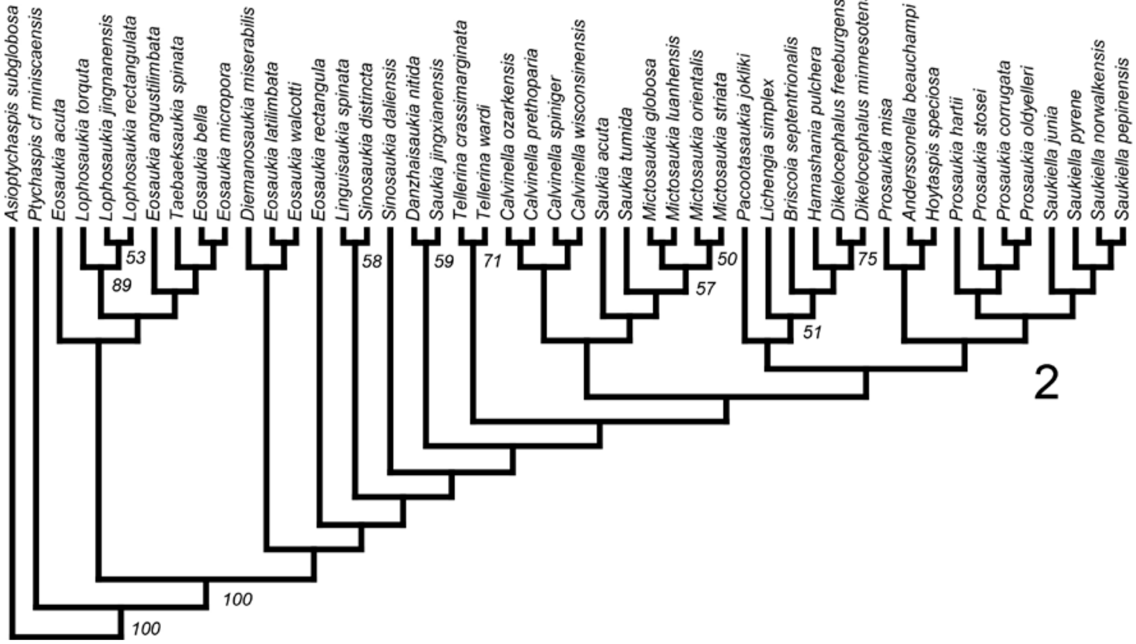
Ptychaspis cf miniscaensis
Anderssonella beauchampi
Eosaukia angustilimbata
Eosaukia acuta
Eosaukia walcotti
Eosaukia latilimbata
Diemanosaukia miserabilis
Sinosaukia daliensis
Eosaukia rectangula
Calvinella wisconsinensis
Calvinella spiniger
Calvinella prethoparia
Calvinella ozarkensis
Taebaeksaukia spinata
Saukia tumida
Saukia acuta
Prosaukia stosei
Prosaukia hartii
Prosaukia corrugata
Pacootasaukia jokliki
Lichengia simplex
Prosaukia misa
Hoytaspis speciosa
Eosaukia bella
Eosaukia micropora
Linguisaukia spinata
Sinosaukia distincta
Danzhaisaukia nitida
Saukia jingxianensis
Tellerina crassimarginata
Tellerina wardi
Lophosaukia torquta
Lophosaukia jingnanensis
Lophosaukia rectangulata
Mictosaukia orientalis
Mictosaukia luanhensis
Mictosaukia globosa
Mictosaukia striata
Briscoia septentrionalis
Hamashania pulchera
Dikelocephalus freeburgensis
Dikelocephalus minnesotensis
Prosaukia oldyelleri
Saukiella junia
Saukiella pepinensis
Saukiella pyrene
Saukiella norwalkensis
65
68
90
67
53
89
100

1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Ptychaspis cf miniscaensis
Eosaukia acuta
Lophosaukia torquta
Lophosaukia jingnanensis
Lophosaukia rectangulata
Eosaukia angustilimbata
Taebaeksaukia spinata
Eosaukia bella
Eosaukia micropora
Diemanosaukia miserabilis
Eosaukia latilimbata
Eosaukia walcotti
Eosaukia rectangula
Linguisaukia spinata
Sinosaukia distincta
Sinosaukia daliensis
Danzhaisaukia nitida
Saukia jingxianensis
Tellerina crassimarginata
Tellerina wardi
Calvinella ozarkensis
Calvinella prethoparia
Calvinella spiniger
Calvinella wisconsinensis
Saukia acuta
Saukia tumida
Mictosaukia globosa
Mictosaukia luanhensis
Mictosaukia orientalis
Mictosaukia striata
Pacootasaukia jokliki
Lichengia simplex
Briscoia septentrionalis
Hamashania pulchera
Dikelocephalus freeburgensis
Dikelocephalus minnesotensis
Prosaukia misa
Anderssonella beauchampi
Hoytaspis speciosa
Prosaukia hartii
Prosaukia stosei
Prosaukia corrugata
Prosaukia oldyelleri
Saukiella junia
Saukiella pyrene
Saukiella norwalkensis
Saukiella pepinensis
53
89
58
59
71
50
57
75
51
100
100

2

Figure 12. CONOP-computed composite section incorporating only those sections contributing locally-observed FAD and LAD from Laurentia (Canada, continental United states, and Mexico). Thin grey bars represent non-saukiid taxa used to establish taxa correlations, thicker blue bars indicate the ranges of saukiid and closely related taxa, and green bars represent conodont taxa correlated to stage boundaries. See text for discussion.

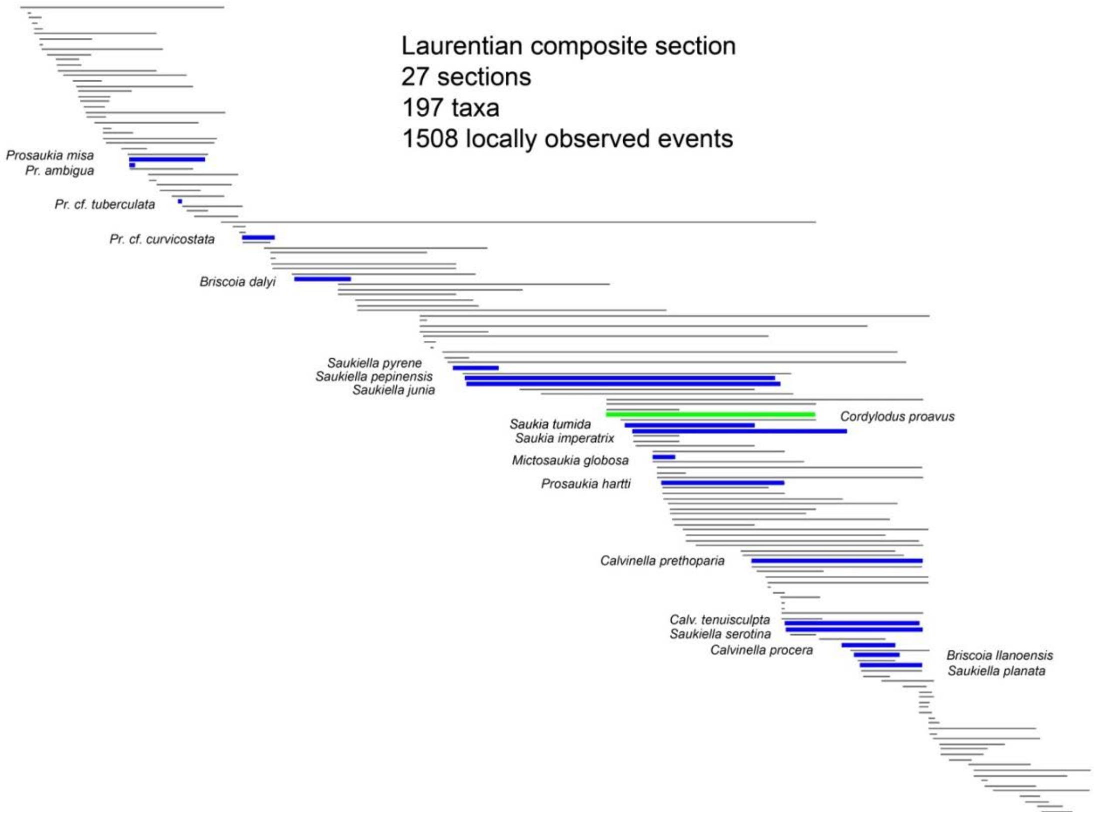

Laurentian composite section
27 sections
197 taxa
1508 locally observed events
Prosaukia misa
Pr. ambigua
Pr. cf. tuberculata
Pr. cf. curvicostata
Briscoia dalyi
Saukiella pyrene
Saukiella pepinensis
Saukiella junia
Cordylodus proavus
Saukia tumida
Saukia imperatrix
Mictosaukia globosa
Prosaukia hartti
Calvinella prethoparia
Calv. tenuisculpta
Saukiella serotina
Calvinella procera
Briscoia llanoensis
Saukiella planata

Figure 13. CONOP-computed composite section incorporating all 54 sections globally. Thin grey bars represent non-saukiid taxa used to establish taxa correlations, thicker blue bars indicate the ranges of saukiid and closely related taxa, and green bars represent conodont taxa correlated to stage boundaries. See text for discussion.

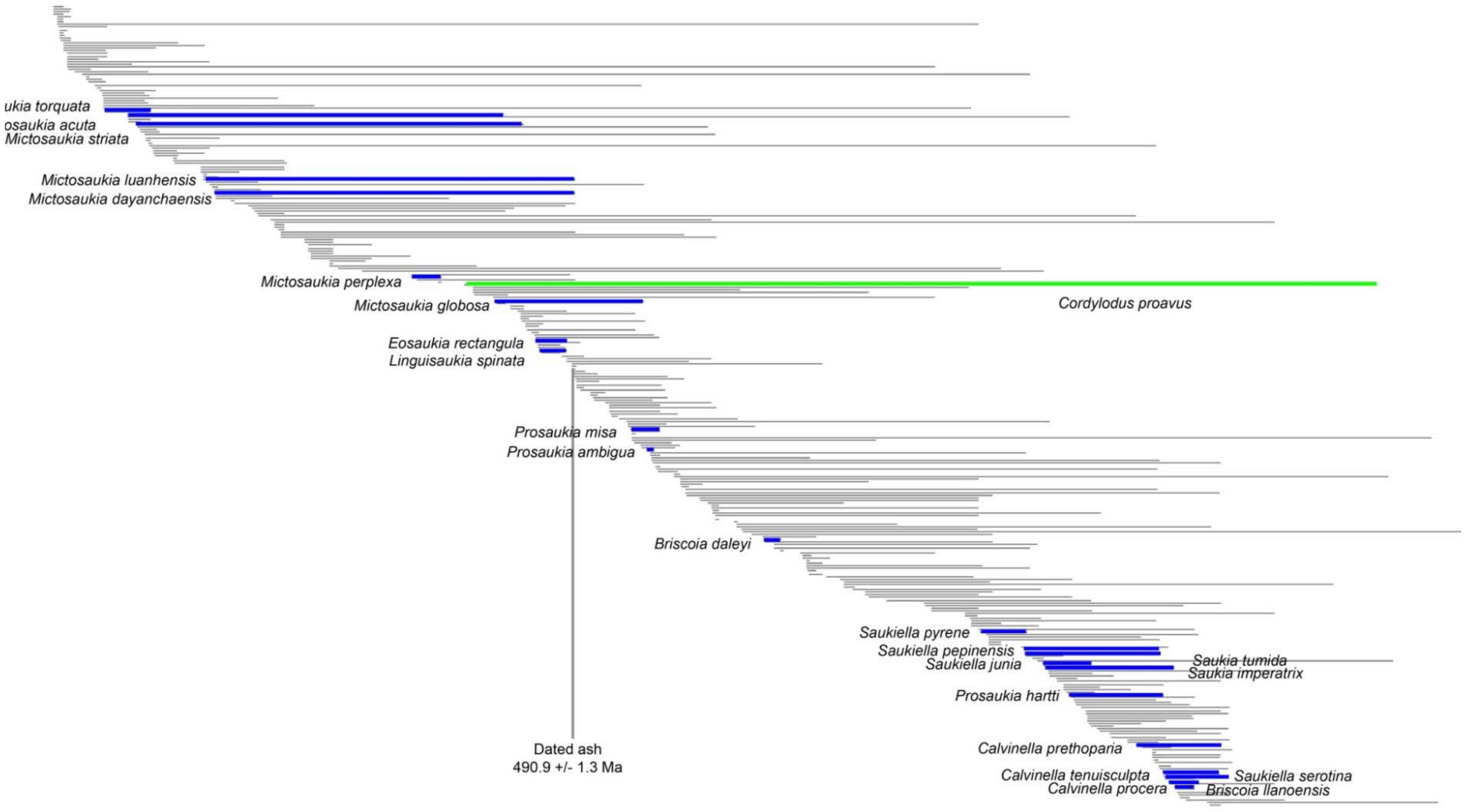

ukia torquata
osaukia acuta
Mictosaukia striata
Mictosaukia luanhensis
Mictosaukia dayanchaensis
Mictosaukia perplexa
Cordylodus proavus
Mictosaukia globosa
Eosaukia rectangula
Linguisaukia spinata
Prosaukia misa
Prosaukia ambigua
Briscoia daleyi
Saukiella pyrene
Saukiella pepinensis
Saukiella junia
Saukia tumida
Saukia imperatrix
Prosaukia hartti
Calvinella prethoparia
Calvinella tenuisculpta
Saukiella serotina
Calvinella procera
Briscoia llanoensis
Dated ash
490.9 +/- 1.3 Ma

Figure 14. Modified Fitch Parsimony optimization of the cladogram presented in Figure 4.2 (Pterocephaliidae outgroup, qualitative and gap-weighted character data included). The branches in this tree are color-coded to one of the seven area-states used in paleobiogeographic analyses (see Table 3). Nodes (colored circles) represent the last common ancestor of terminal taxa, or of the next higher node along a branch. The colored circles at each node represent the paleobiogeographic regions that a particular common ancestor is hypothesized to have occupied based on Fitch optimization. Arrows represent migration events; the color of the arrow represents the paleobiogeographic region to which the descendant taxon is moving. Arrows represent migration events; the color of the arrow represents the paleobiogeographic region to which the descendant taxon is moving. For this Fitch optimization of the pterocephaliid outgroup analysis, a minimum of 11 migration events are required to explain the paleogeographic distribution of the terminal taxa. Of these migrations, three are interpreted to represent 'geodispersal' events sensu Lieberman and Eldredge 1996. See text for discussion.

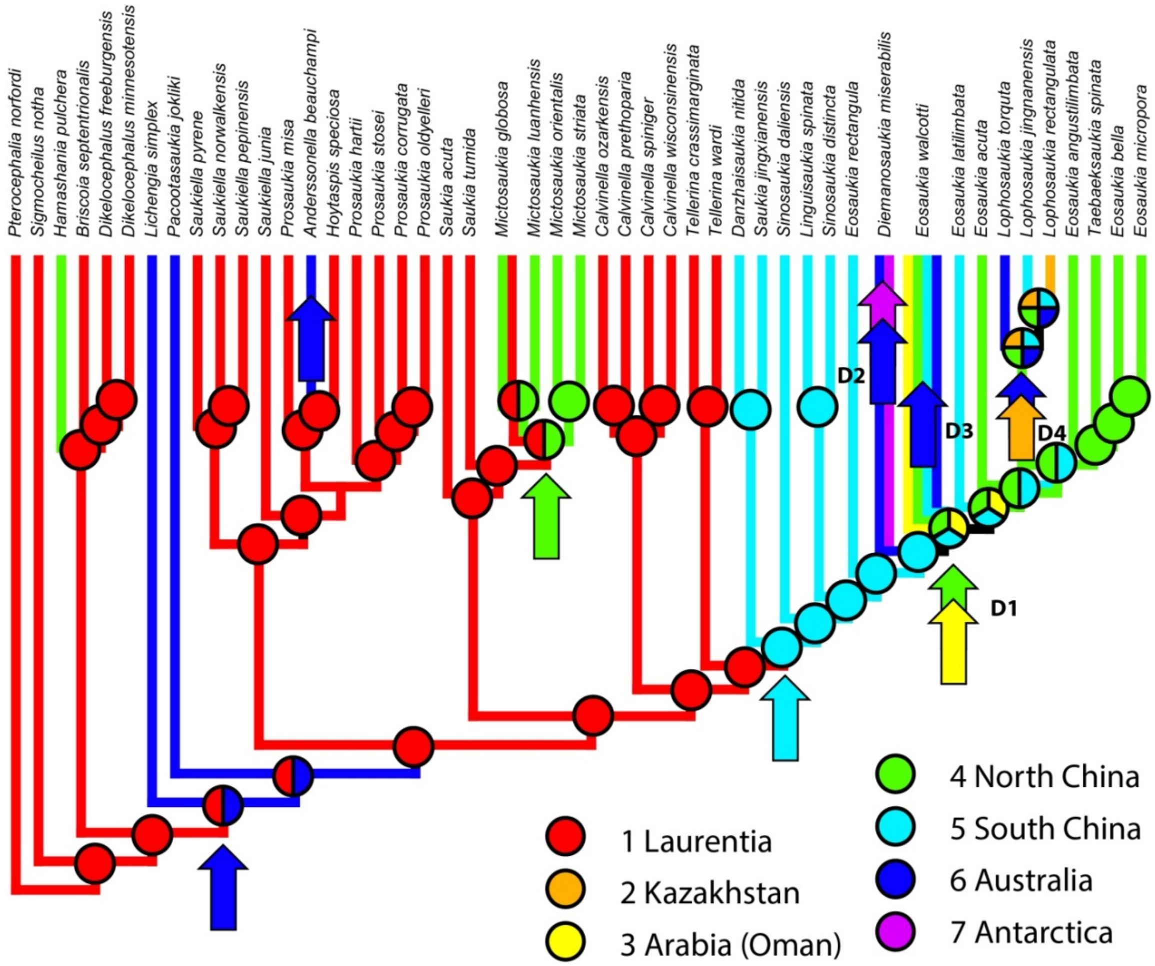

Pterocephalia norfordi
Sigmocheilus notha
Hamashania pulchera
Briscoia septentrionalis
Dikelocephalus freeburgensis
Dikelocephalus minnesotensis
Lichengia simplex
Pacootasaukia jokliki
Saukiella pyrene
Saukiella norwalkensis
Saukiella pepinensis
Saukiella junia
Prosaukia misa
Anderssonella beauchampi
Hoytaspis speciosa
Prosaukia hartii
Prosaukia stosei
Prosaukia corrugata
Prosaukia oldyelleri
Saukia acuta
Saukia tumida
Mictosaukia globosa
Mictosaukia luanhensis
Mictosaukia orientalis
Mictosaukia striata
Calvinella ozarkensis
Calvinella prethoparia
Calvinella spiniger
Calvinella wisconsinensis
Tellerina crassimarginata
Tellerina wardi
Danzhaisaukia nitida
Saukia jingxianensis
Sinosaukia daliensis
Linguisaukia spinata
Sinosaukia distincta
Eosaukia rectangula
Diemanosaukia miserabilis
Eosaukia walcotti
Eosaukia latilimbata
Eosaukia acuta
Lophosaukia torquta
Lophosaukia jingnanensis
Lophosaukia rectangulata
Eosaukia angustilimbata
Taebaeksaukia spinata
Eosaukia bella
Eosaukia micropora
D2
D3
D4
D1
1 Laurentia
2 Kazakhstan
3 Arabia (Oman)
4 North China
5 South China
6 Australia
7 Antarctica

Figure 15. Modified Fitch Parsimony optimization of the cladogram presented in Figure 6.2 (Ptychaspididae outgroup, qualitative and gap-weighted character data included). The branches in this tree are color-coded to one of the seven area-states used in paleobiogeographic analyses (see Table 3). Nodes (colored circles) represent the last common ancestor of terminal taxa, or of the next higher node along a branch. The colored circles at each node represent the paleobiogeographic regions that a particular common ancestor is hypothesized to have occupied based on Fitch optimization. Arrows represent migration events; the color of the arrow represents the paleobiogeographic region to which the descendant taxon is moving. For this Fitch optimization of the ptychaspidid outgroup analysis, a minimum of 14 migration events are required to explain the paleogeographic distribution of the terminal taxa. Of these migrations, three are interpreted to represent 'geodispersal' events sensu Lieberman and Eldredge 1996. See text for discussion.

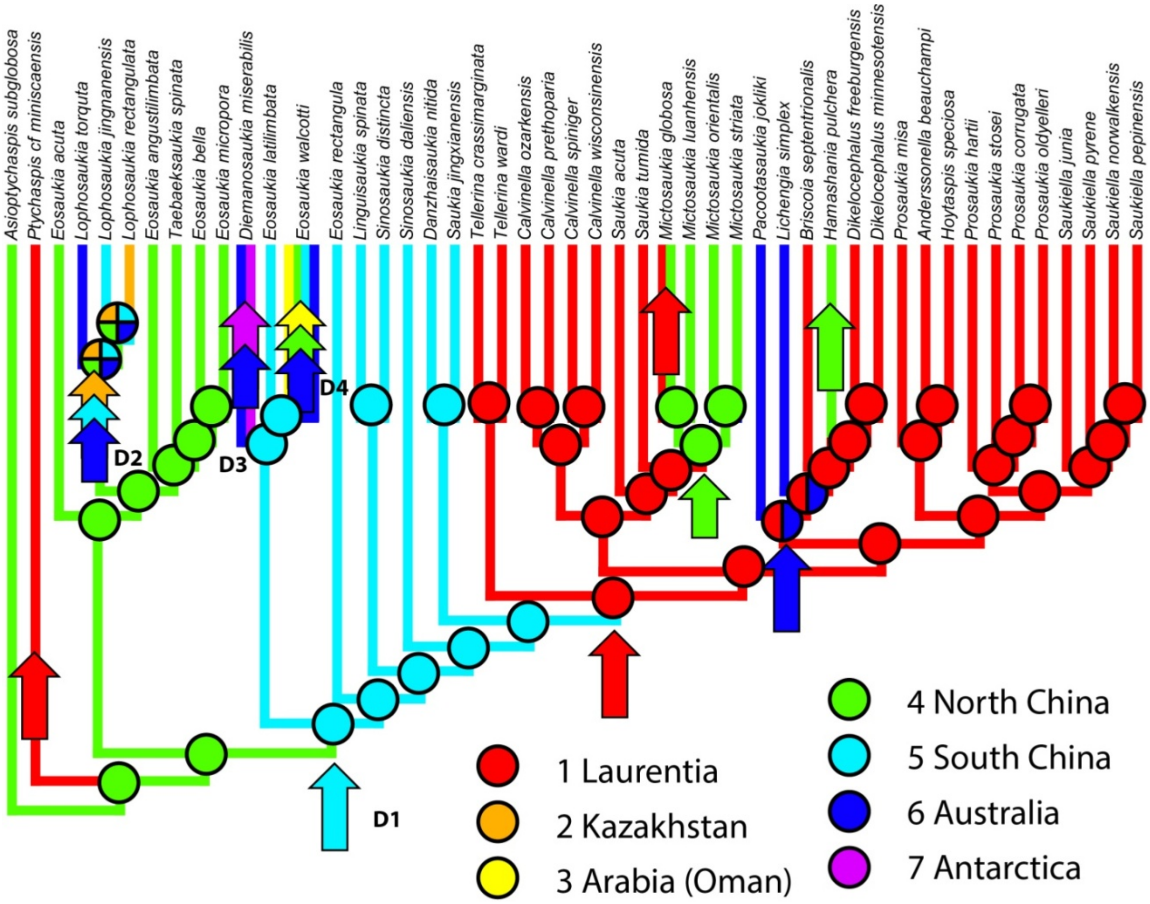

Asioptychaspis subglobosa
Ptychaspis cf miniscaensis
Eosaukia acuta
Lophosaukia torquta
Lophosaukia jingnanensis
Lophosaukia rectangulata
Eosaukia angustilimbata
Taebaeksaukia spinata
Eosaukia bella
Eosaukia micropora
Diemanosaukia miserabilis
Eosaukia latilimbata
Eosaukia walcotti
Eosaukia rectangula
Linguisaukia spinata
Sinosaukia distincta
Sinosaukia daliensis
Danzhaisaukia nitida
Saukia jingxianensis
Tellerina crassimarginata
Tellerina wardi
Calvinella ozarkensis
Calvinella prethoparia
Calvinella spiniger
Calvinella wisconsinensis
Saukia acuta
Saukia tumida
Mictosaukia globosa
Mictosaukia luanhensis
Mictosaukia orientalis
Mictosaukia striata
Pacootasaukia jokliki
Lichengia simplex
Briscoia septentrionalis
Hamashania pulchera
Dikelocephalus freeburgensis
Dikelocephalus minnesotensis
Prosaukia misa
Anderssonella beauchampi
Hoytaspis speciosa
Prosaukia hartii
Prosaukia stosei
Prosaukia corrugata
Prosaukia oldyelleri
Saukiella junia
Saukiella pyrene
Saukiella norwalkensis
Saukiella pepinensis
D1
D2
D3
D4
1 Laurentia
2 Kazakhstan
3 Arabia (Oman)
4 North China
5 South China
6 Australia
7 Antarctica

Figure 16. Modified Brooks Parsimony Analyses of the cladogram presented in Figure 4.2, Pterocephaliidae outgroup, qualitative and gap-weighted character data. 1) Vicariance tree. 2) Geo-dispersal tree. See text for details.

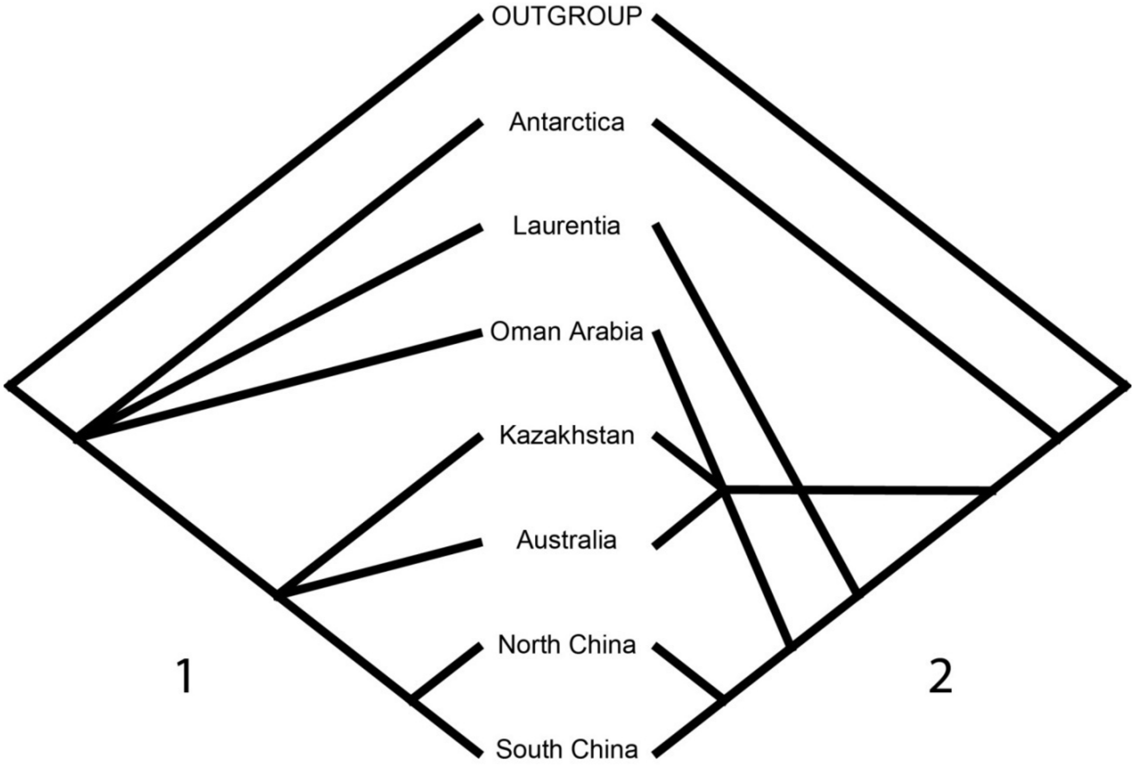

OUTGROUP
Antarctica
Laurentia
Oman Arabia
Kazakhstan
Australia
North China
South China
1
2

Figure 17. Modified Brooks Parsimony Analyses of the cladogram presented in Figure 6.2, Pterocephaliidae outgroup, qualitative and gap-weighted character data. 1) Vicariance tree. 2) Geo-dispersal tree. See text for details.

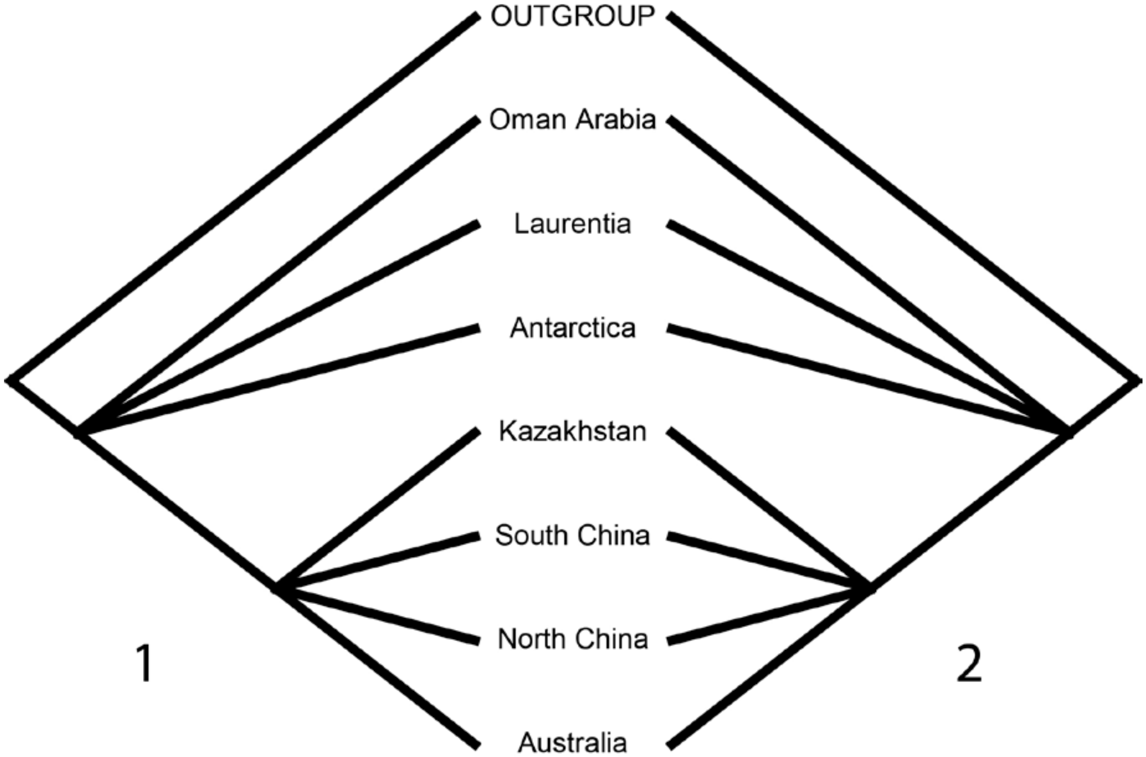

OUTGROUP
Oman Arabia
Laurentia
Antarctica
Kazakhstan
South China
North China
Australia
1
2

Figure 18. Principal component analysis of well-preserved cranidia of *Dikelocephalus minnesotensis* (blue triangles) and *D. freeburgensis* (red squares). The morphospace represented shows a strong separation between these species, indicating that *D. freeburgensis* is a distinct species from *D. minnesotensis* (see text for additional discussion).

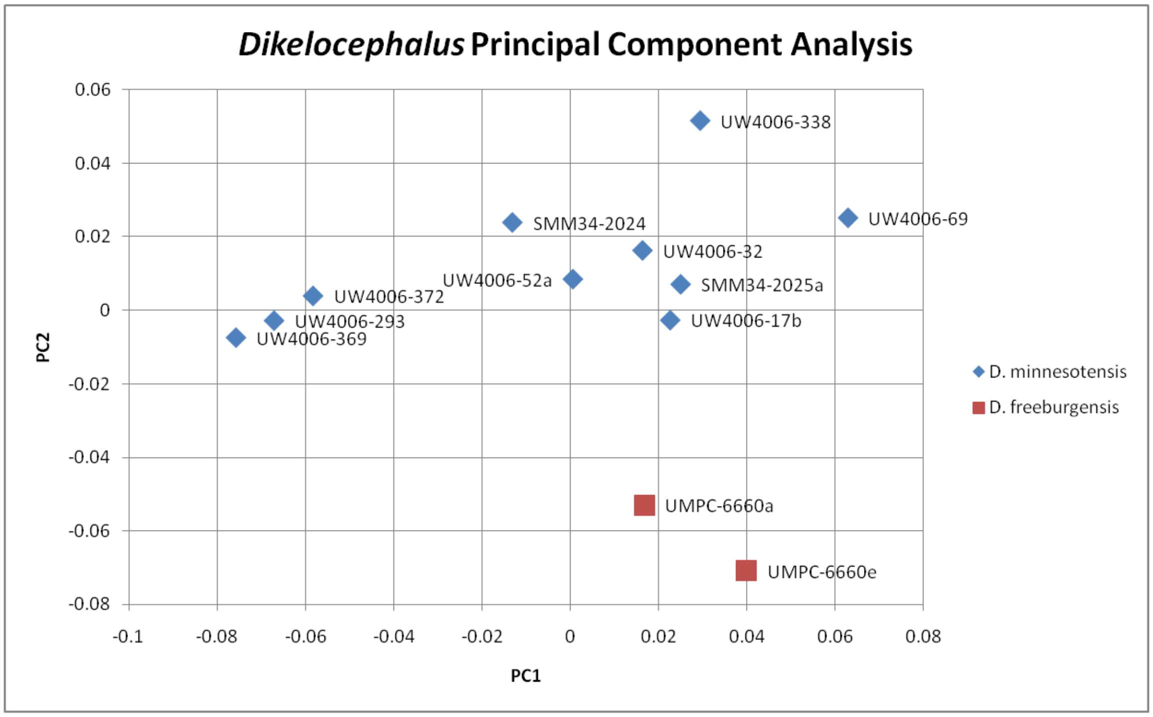
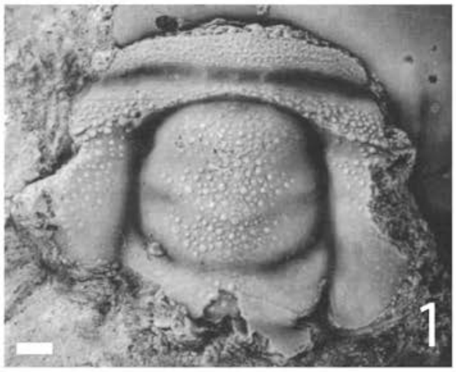
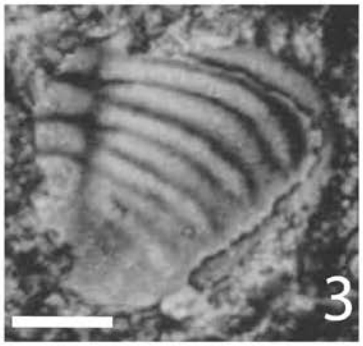

Dikelocephalus Principal Component Analysis
0.06
0.04
0.02
0
-0.02
-0.04
-0.06
-0.08
PC2
-0.1
-0.08
-0.06
-0.04
-0.02
0
0.02
0.04
0.06
0.08
PC1
UW4006-338
UW4006-69
SMM34-2024
UW4006-32
UW4006-52a
SMM34-2025a
UW4006-372
UW4006-293
UW4006-17b
UW4006-369
UMPC-6660a
UMPC-6660e
◆ D. minnesotensis
■ D. freeburgensis

Figure 19. *Anderssonella beauchampi*, *Calvinella ozarkensis*, *Calvinella prethoparia*. 1-3: *Anderssonella beauchampi*. 1) cranidium showing characteristic ornament and raised ocular ridge composed of large pustules, CPC 11749, holotype (refigured from pl. 20, fig. 1, Shergold, 1975). 2) librigena showing raised ridge parallel to distinct furrow (refigured from pl. 21, fig. 1, Shergold, 1975). 3) partial pygidium with 3 axial rings, CPC 11754 (refigured from pl. 20, fig. 5, Shergold, 1975). 4-5: *Calvinella ozarkensis*. 4) Cranidium showing characteristic prosopon and long occipital spine. Note the greater length (sag.) of the anterior border furrow where it meets the cranidial margins and the shorter length (sag.) immediately anterior to the glabella. 5) Pygidium showing 4 axial rings and long postaxial ridge. 6-9: *Calvinella prethoparia*. 6) cranidium showing position of palpebral lobes, and arrangement of glabellar furrows. 7) cranidium showing exceptionally long occipital spine. 8) librigena showing confluence of lateral and posterior librigenal furrows. 9) pygidium showing at least 4 axial rings, long postaxial ridge, subequally divided pleurae, and pustulate prosopon. Scale bars: 1-3 = 1 mm; 4-5, 8-9 = 1 cm; 6-7 = 5 mm.


1


2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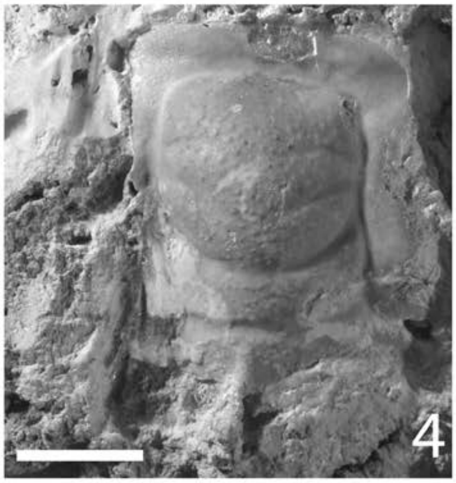
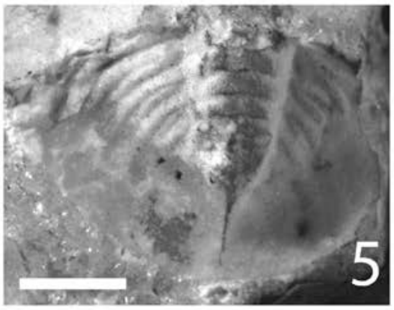

4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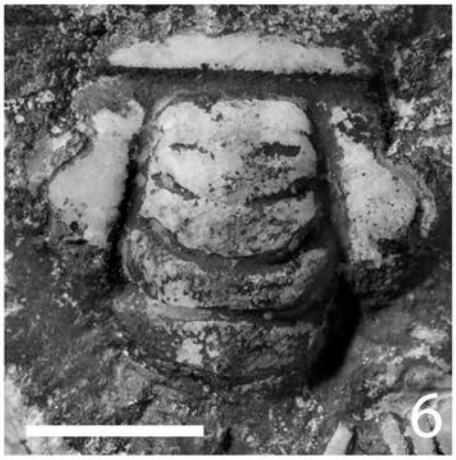
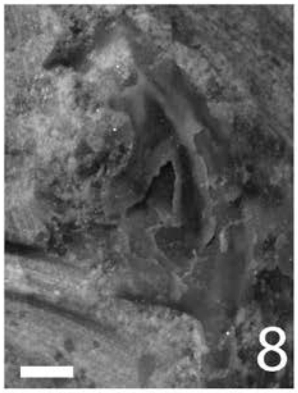
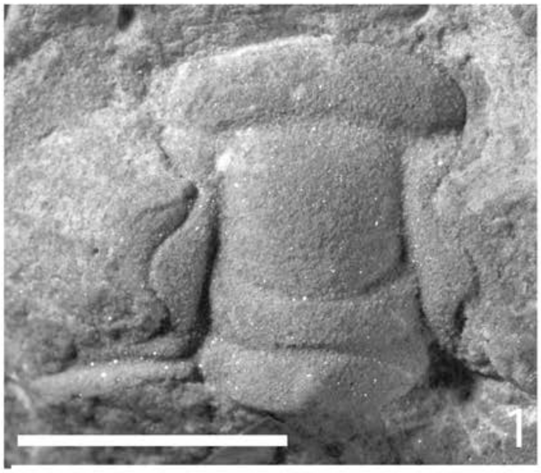

6


7


8


9

Figure 20. *Calvinella spiniger*, *Calvinella wisconsinensis*, and *Diemanosaukia misirabilis.* 1-3: *Calvinella spiniger*. 1) Cranidium showing the low-angle abaxial portion of the anterior border furrow, USNM 58659 . 2) Pygidium showing pygidial shape, long postaxial ridge, distinctly unequally divided pleurae, USNM 58660. 3) librigena showing the relatively wide lateral border, and the confluent lateral and posterior border furrows, un-numbered USNM plaster cast. 4-6: *Calvinella wisconsinensis*. 4) Cranidium. 5) pygidium. 6) Librigena with raised, wavy, subconcentric ornamentation of librigenal field, un-numbered USNM specimen. 7: *Diemanosaukia miserabilis*. 7) cranidium showing the wide spacing of the palpebral lobes from the axial furrows, the strongly pustulated prosopon, and the arrangement of glabellar furrows, UT 123925. Scale bars: 1-3 = 1 cm; 4-6 = 5 mm.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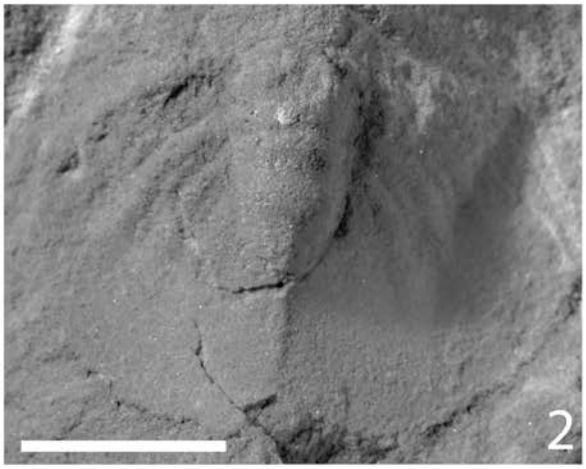
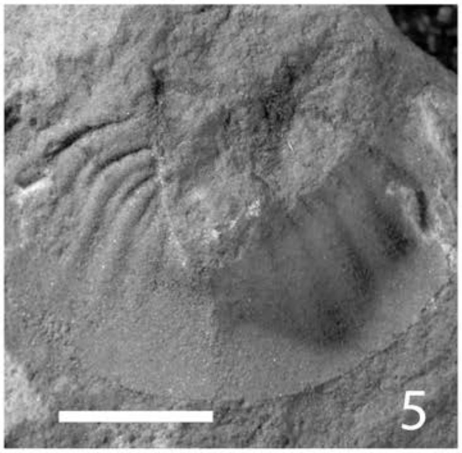

2


4

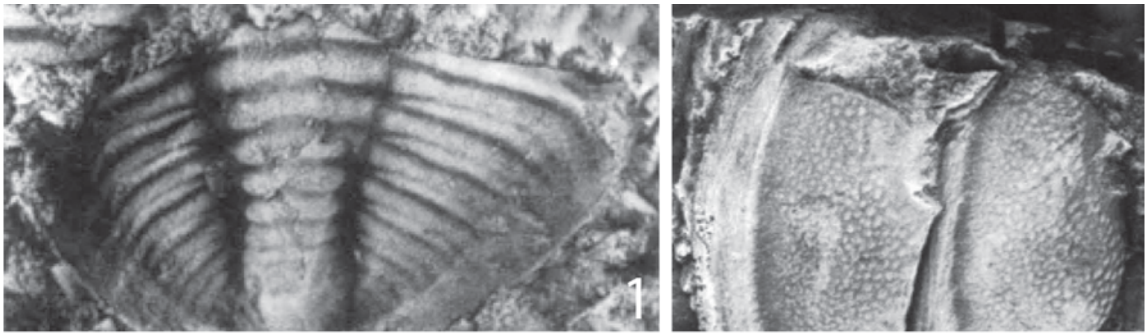

5


3


6


7

Figure 21. *Diemanosaukia miserabilis* and *Eosaukia latilimbata*. 1-2: *Diemanosaukia miserabilis.* 1) Pygidium, showing seven axial rings, terminal piece extending to posterior margin, and equally divided pleurae, UT 123929 (refigured from Jago and Corbett, 1990). 2) Librigenae, showing very wide genal spine bases, posterior furrow continuing into base of spine, and pustulated prosopon. Note the wide lateral margin, UT 123931 (refigured from Jago and Corbett, 1990). 3-6: *Eosaukia latilimbata*. 3) cranidium, showing pustulation, and the limited nature of S2 and S3 furrows. Note the semi-circular notch anterior to S2 on the left side - this is the only indication of S3 furrow, NIGPAS 98774. 4) librigena showing the dorsal surface. Note the ornament consisting of irregular rows of connected tubercles, the confluent lateral and posterior border furrows, and the low ridge near the genal angle. It is hypothesized that this is where the genal spine would have attached. All known librigena are without their genal spines, NIGPAS 98767. 5) librigena showing ventral aspect. Note at least nine prominent vincular notches in the posterolateral doublure, NIGPAS 98771. 6) associated pygidium. Three axial rings are present. Note terminal piece extends all the way to the posterior margin, NIGPAS 98775. Scale bars: 1, 3 = 5 mm; 2, 4, 5 = 1 cm; 6 = 1 mm.


1

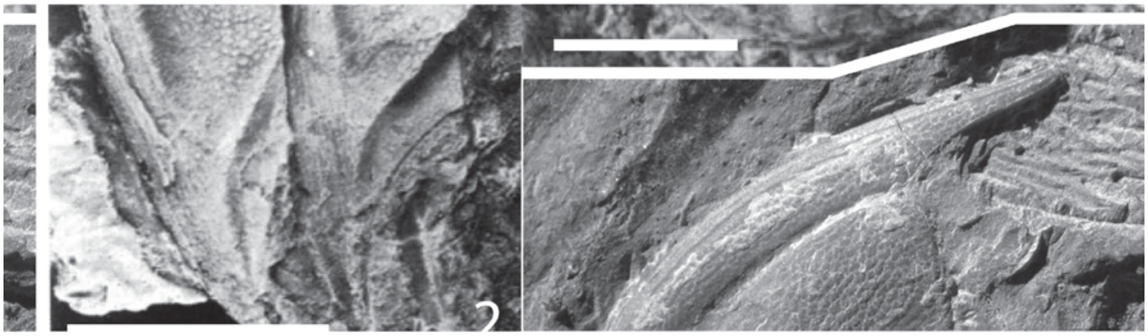

2


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Figure 22. *Eosaukia bella*, *E. latilimbata*, and *E. walcotti*. 1: *Eosaukia bella*, holotype cranidium showing characteristic prosopon on anterior border and fixigenal field; glabella largely exfoliated, USNM 58124 (holotype). 2-3: *Eosaukia latilimbata*. 2) articulated holotype with 11 thoracic segments. Note the foreshortening of the thorax, NIGPAS 7226. 3) Anterior view of NIGPAS 7226, showing the degree of inflation of the cephalon and damage to frontal area, NIGPAS 7226. 4-6: *Eosaukia walcotti*, un-reposited material from southwestern Guangxi Province, South China, refigured from Zhu (20XX).4) partially articulated exoskeleton showing the arrangement of the librigenal furrows, the prosopon of the cephalon, and the long, slender axial spine on thoracic segment five, refigured from pl. 13, fig. 4 (Zhu, 20XX). 5) well-preserved cranidium showing the nature of the cranidial prosopon, and also illustrating the arrangement of the pre-occipital glabellar furrows. Note the prominent occipital spine, refigured from pl. 15, fig. 10 (Zhu, 20XX). 6. Pygidium showing characteristic acutely angled sides and transversely ovate shape of pygidium. Note the 2 prominent axial rings and the 2 triangular spines on the terminal piece. Scale bars: 1-3, 5 = 5 mm; 4, 6 = 1 mm.

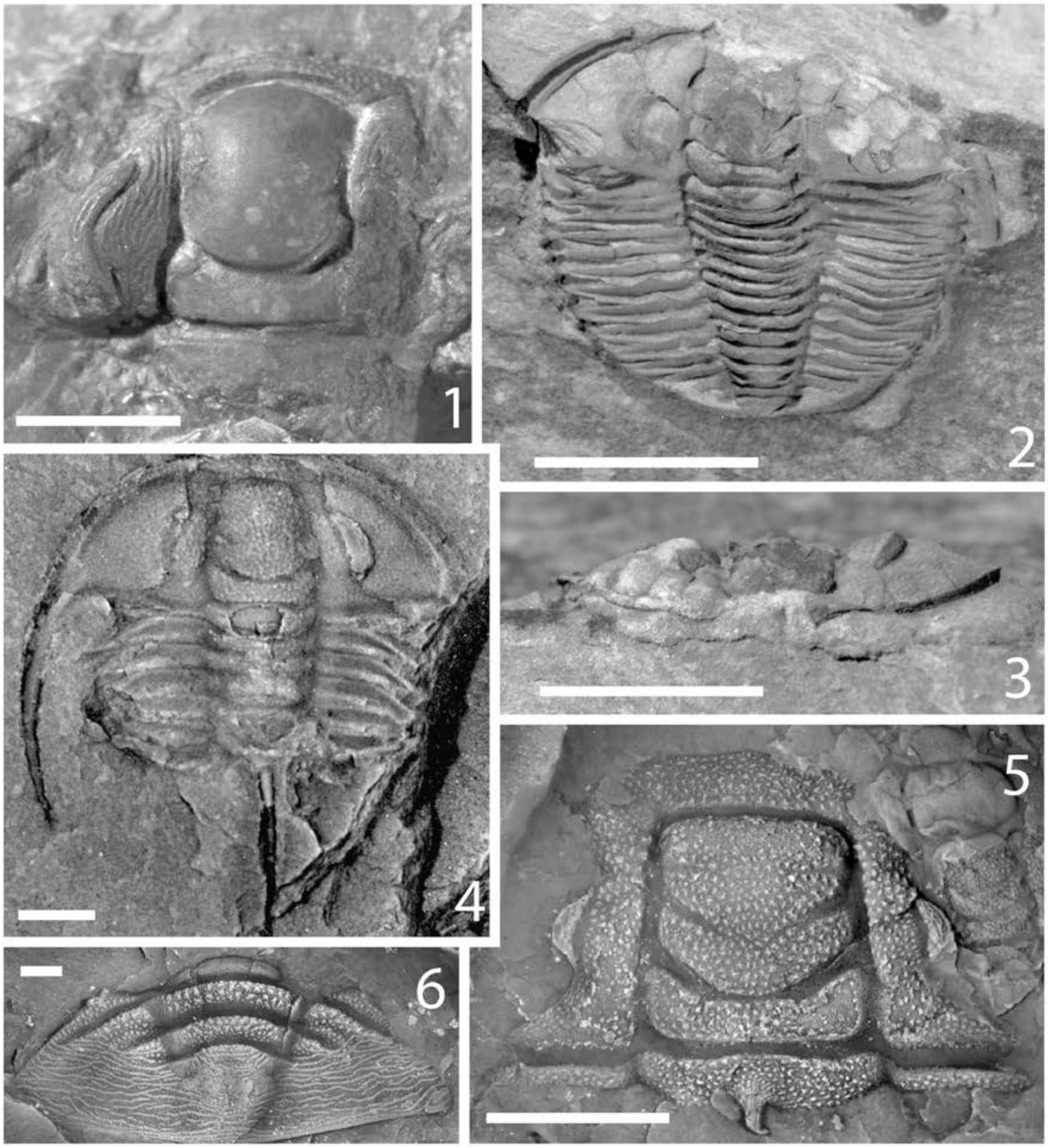
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Figure 23. *Lichengia simplex*, and *Linguisaukia spinata*. 1-3: *Lichengia simplex*. 1) holotype cranidium showing interrupted pre-occipital glabellar furrows, posteriorly-located palpebral lobes, and prosopon, CPC 26771 (holotype). 2) yoked librigena. This character is considered derived in dikelocephaliids, although given the position of Lichengia as basal to the included members of the Dikelocephaliidae, this character may represent a less-derived condition in the Saukiidae, CPC 26779. 3) pygidium showing prosopon and at least four axial rings, CPC 26788. 4-5: *Linguisaukia spinata*. 4) holotype cranidium of Linguisaukia spinata showing long occipital spine, pustulated prosopon, anteriorly-tapering, anteriorly-rounded glabella, and S1 and S2 furrows (S3 absent), NIGPAS 83078a (holotype). 5) holotype crandium of *Linguisaukia affinis* (Peng), referred herein to *L. spinata*. Note the much more inflated nature of the crandium compared with figure 11.4. See text for discussion of synonymy reasoning, NIGPAS 83088 (holotype). Scale bars: 1, 2, 5 = 1 cm; 3, 4 = 5 mm.

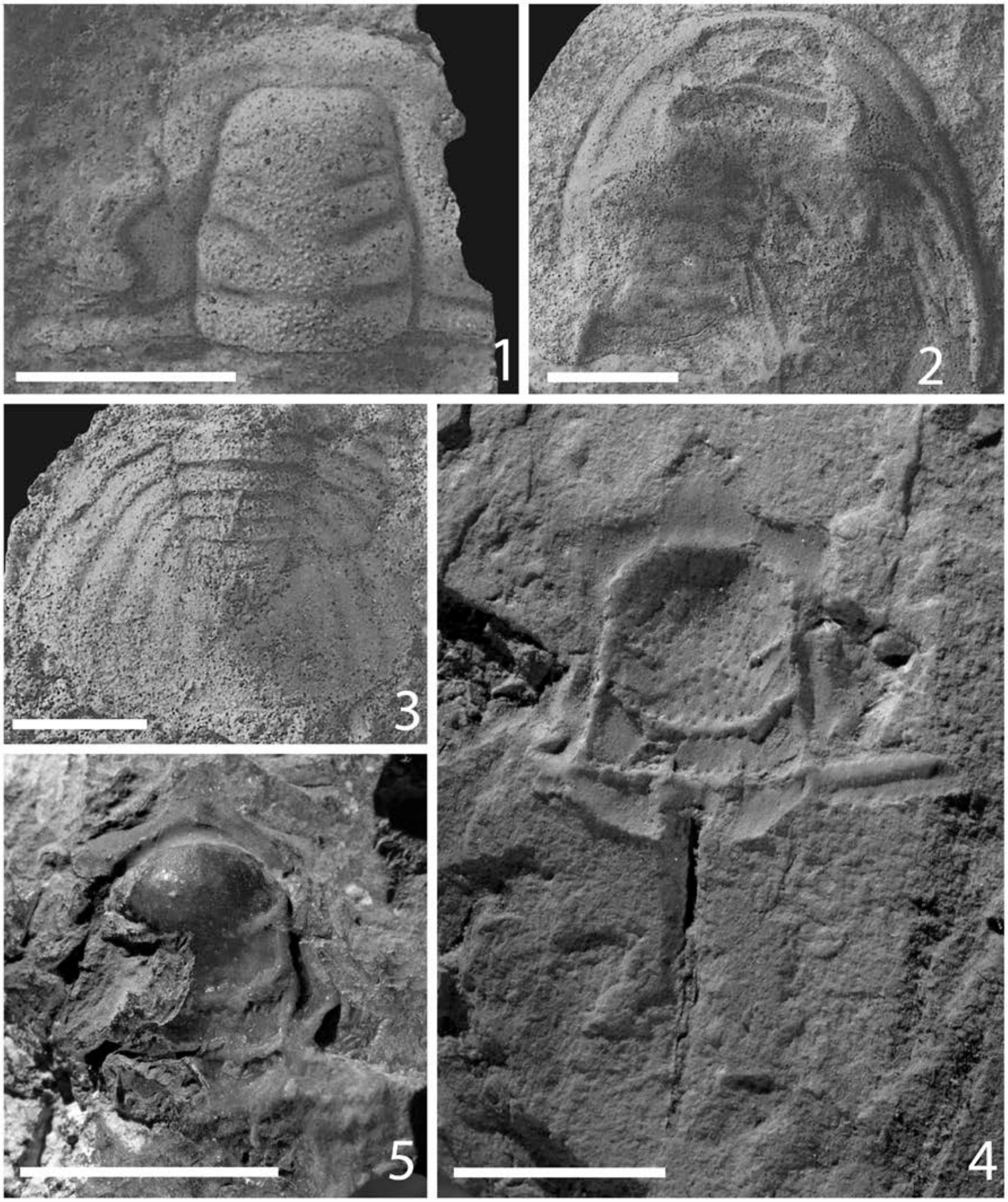
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Figure 24. *Linguisaukia spinata*, *Lophosaukia torquata*, *Lophosaukia jingxianensis*, and *Mictosaukia globosa*. 1-2: *Linguisaukia spinata* librigenae. 1) librigena with long, but broken genal spine, the characteristic strong pustulation adjacent to the cutout for the palpebral lobe, and the slightly advanced genal spine. In this taxon, unbroken genal spines can be well over four times the cranidial length. Note the transverse terrace ridges on the genal spine (these are on the ventral doublure). 2) librigena assigned to *L. affinis* and transferred herein to *L. spinata*. Note the large tubercles adjacent to the cutout for the palpebral lobe, and slight advancement of genal spine as in figure 12.1. 3) *Lophosaukia torquata.* Cranidium showing robust pustulate ornament, CPC 9765 (holotype). 4-5: *Lophosaukia jingxianensis.* 4) cranidium showing long anterior projection (compare with *L. torquata* in Figure 12.3), NIGPAS 83542. 5) librigena showing very strong pustulation on librigenal field and border, but raised ridges at genal angle and on genal spine. Note also the inflection of the posterolateral librigenal border just anterior to the genal spine, and slight advancement of the genal spine, NIGPAS 83537. 6-7: *Mictosaukia globosa.* 6) Librigena showing the confluent lateral and posterior border furrows, an apomorphy for this genus. Note also the prominent line of tubercles adjacent to the cutout for the palpebral lobe and rather wide genal spine base. 7) partial pygidium four prominent axial rings and a prominent U-shaped 'flap' on the terminal piece. Scale bars: 1-6 = 5 mm; 7 = 1 cm.

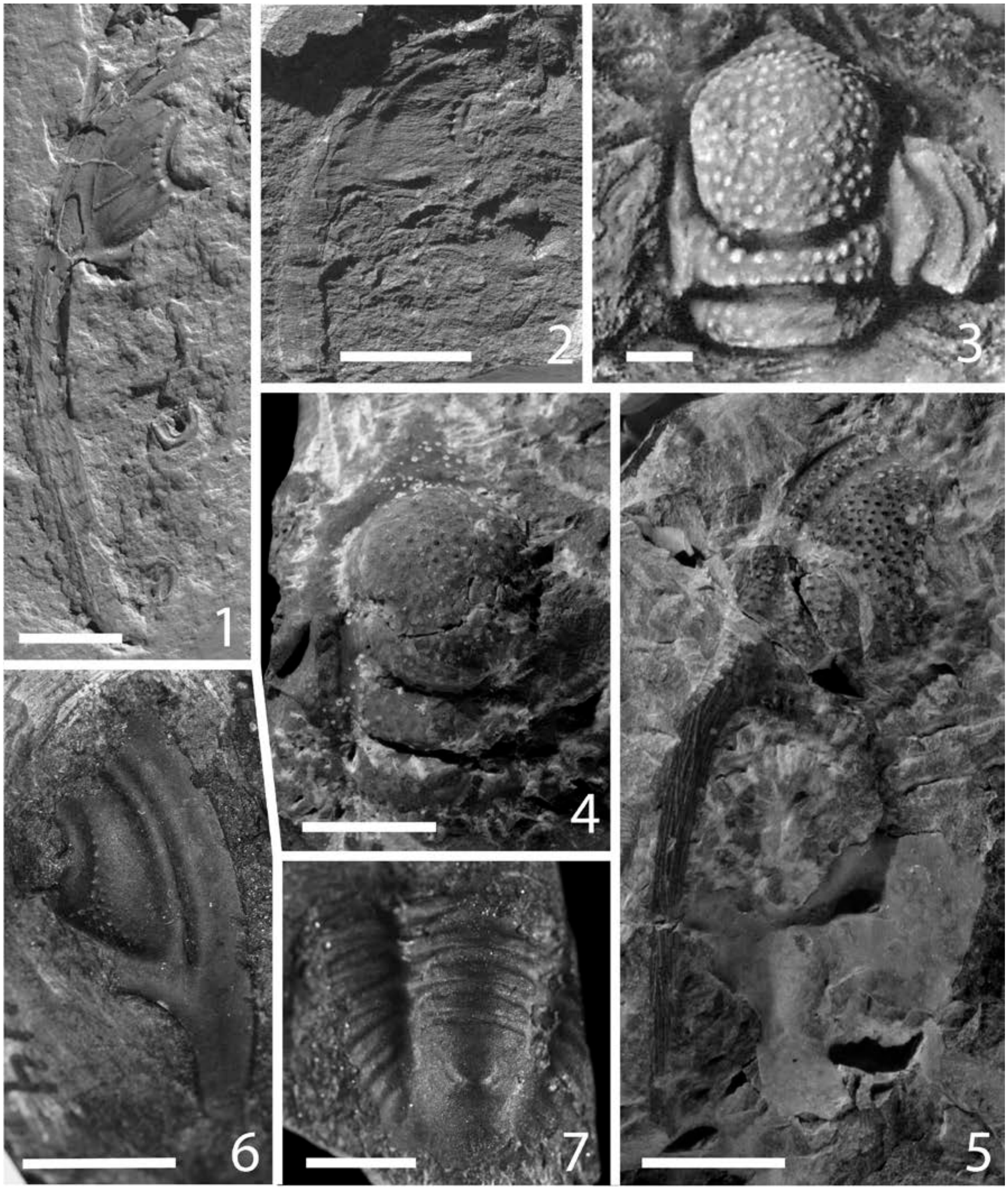
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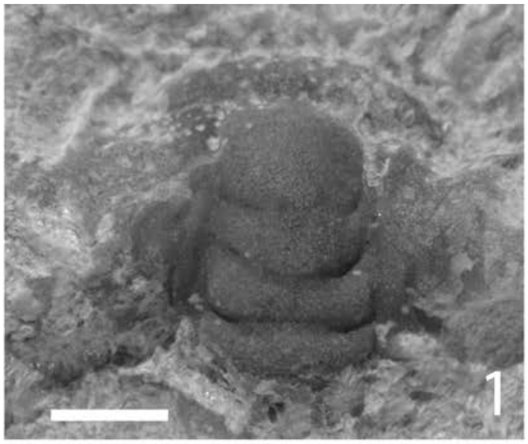
Figure 25. *Mictosaukia orientalis*, *M. luanhensis*, and *M. striata.* 1-3: *Mictosaukia orientalis.* 1) holotype cranidium showing very fine-scale pustulation and anteriorly-tapering glabella, NIGPAS 46578 (holotype). 2) pygidium with four axial rings (anteriormost damaged medially, visible near axial furrows) and a faint trace of a flap-like structure on the terminal piece, NIGPAS 78823. 3) largely exfoliated librigena showing faint pustulation of librigenal field. Note the terrace ridges of the lateral border continue into the base of the genal spine. 4-7: *Mictosaukia orientalis*. 4) exfoliated syntype cranidium. Note the strongly anteriorly-tapering glabella, the divergent anterior limb of the facial suture, and the curved, anterolaterally directed abaxial part of the anterior border furrow, USNM 86927 (syntype). 5) smaller, slightly flattened cranidium showing much more linear abaxial anterior border furrows, NIGPAS 78740. 6) Librigena with the typical *Mictosaukia* arrangement of lateral and posterior border furrows confluent near the genal angle. Note the finely pustulated prosopon, and subparallel striations of the border, NIGPAS 7909X. 7) Pygidium with 4 axial rings, faint flap-like process on the terminal piece, subequally-divided pleurae (compare with pleurae of *M. luanhensis* in Figure 25.2), and a postaxial ridge continuing to posterior margin, NIGPAS 87996. 8-9: *Mictosaukia striata*. 8) holotype cranidium showing fine pustulation and anterior border with raised, subparallel ridges, USNM 86768 (holotype). 9) partial pygidium with four axial rings and faint flap like process of terminal piece, NIGPAS 83097. Scale bars: 1-5, 7-9 = 5 mm; 6 = 1 mm.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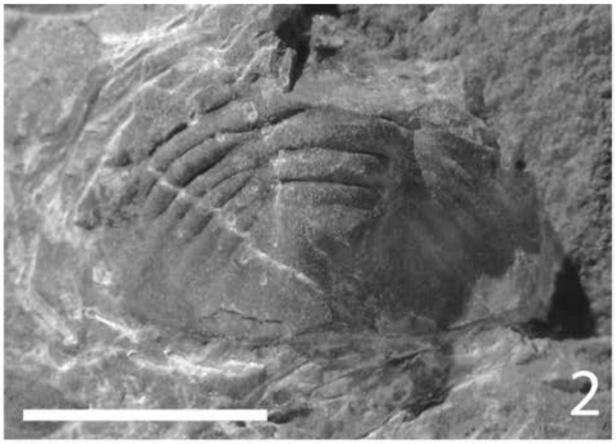
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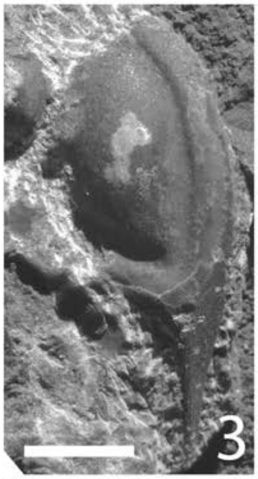
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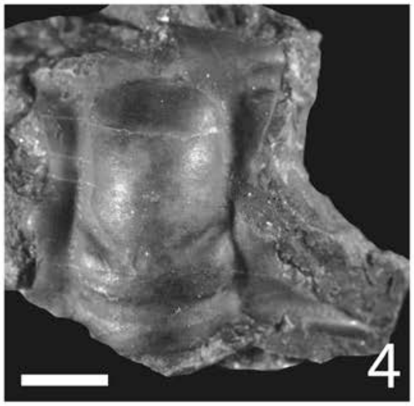
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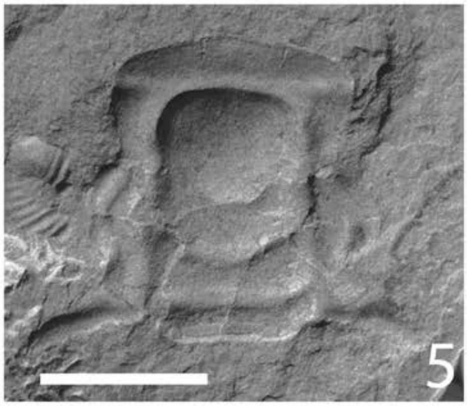
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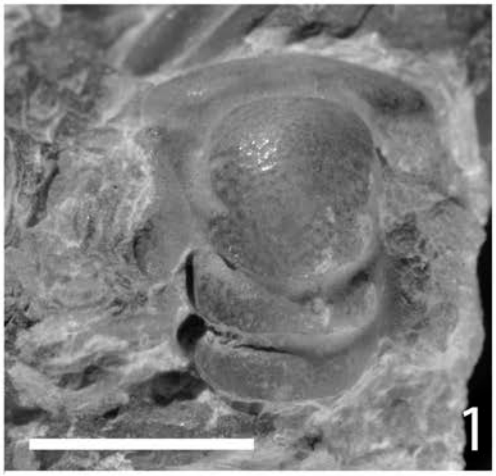
Figure 26. *Mictosaukia striata* and *Prosaukia corrugata*. 1-4: *Mictosaukia striata*. 1) cranidium previously assigned to M. luanhensis. Note pustulated prosopon, deep, continuous S1 furrow, and highly convex nature of cranidium, NIGPAS 100028. 2) same specimen in lateral view, showing terrace lines on the anterior border, NIGPAS 100028. 3) small librigena with pustulated librigenal field prosopon, and raised ridge ornament on anterior part of border. Note the slight lateral deflection of the genal spine, a possible ontogenetic condition (in larger holaspid librigena this condition is absent), NIGPAS 98758. 4) larger exfoliated librigena showing extent of genal spine and evenly curved lateral border smoothly transitioning into genal spine, NIGPAS 98764. 5-8: *Prosaukia corrugata*. 5) large exfoliated cranidium showing very faint terrace lines on glabella, and faint transverse S3 furrow. A possible very faint, anteriorly-directed S4 is anterior to this, USNM 136963 (syntype). 6) Small holaspid cranidium showing a preglabellar furrow, anterior border furrow, and a slightly convex preglabellar field lying between these furrows. S3 furrow is transverse, and the finger-print like terrace ridge ornament is well-preserved, USNM 136963 (syntype). 7) small librigena showing confluent lateral and posterior border furrows and terrace lines, USNM 136963 (syntype). 8) pygidium with at least 8 axial rings, distinctly unequally-divided lateral pleurae, and weakly-expressed postaxial ridge, USNM 136963 (syntype). Scale bars: 1-3, 8 = 5 mm; 4-5= 1 cm; 6-7 = 1 mm.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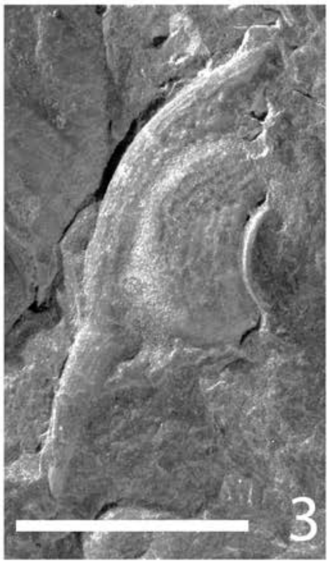
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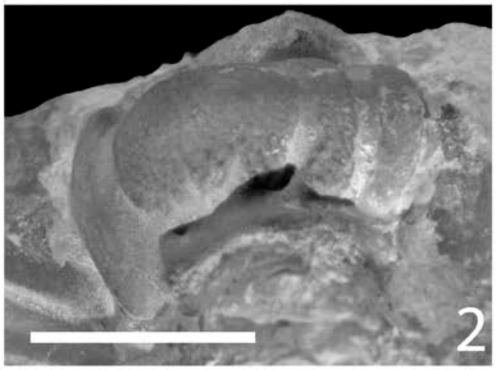
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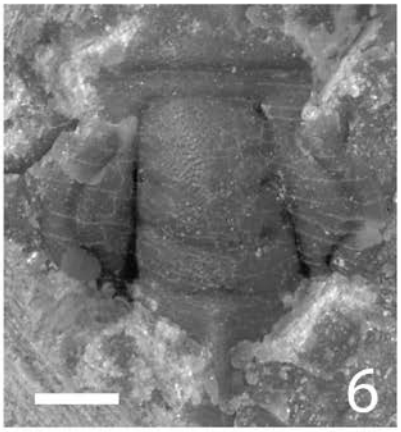
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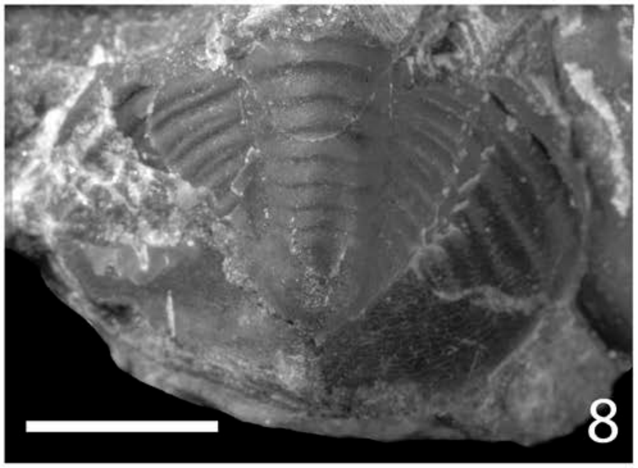
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Figure 27. *Prosaukia hartti* and *Prosaukia misa*. 1-4: *Prosaukia hartti*. 1) large, mostly exfoliated holotype cranidium showing pre-occipital glabellar furrows that do not strongly connect to the axial furrows, USNM 58571. 2) small holaspid cranidium showing the prosopon and glabellar furrows that more strongly connect to the axial furrows, USNM 32815. 3) large pygidium with five axial rings, unequally-divided pleurae, and a narrow postaxial ridge running to the posterior pygidial margin, USNM 58576. 4) librigena showing confluent border furrows and unusual prosopon of the librigenal field, USNM 25749. 5-8: *Prosaukia misa*. 5) Prosaukia misa with relatively long (sagittally), convex preglabellar field with separate and distinct preglabellar furrow, USNM 84540. 6) librigena with very long genal spine and non-confluent lateral and posterior border furrows, un-numbered USNM specimen. 7) librigena with broken genal spine showing the arrangement of the border furrows in more detail. Note the lateral border furrow shallows and terminates well before the genal angle, and the posterior border furrow strongly continues into the genal spine, USNM 84540. 8) pygidium with four axial rings, more equally divided pleurae, and a long, slender postaxial ridge extending to pygidial posterior margin, USNM 84540. Scale bars: 1, 3-6, 8 = 1 cm; 4 = 1 mm; 7 = 5 mm.

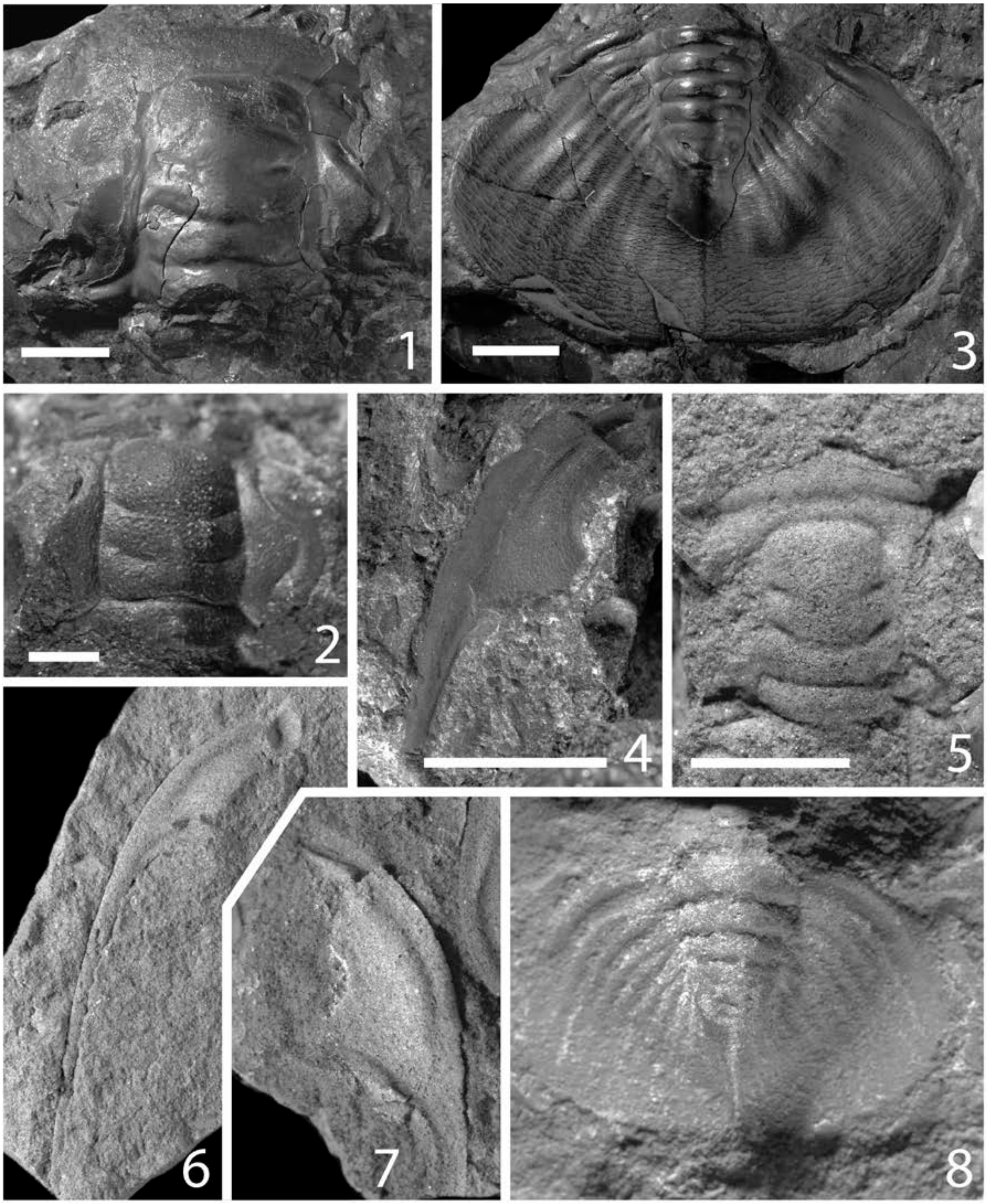
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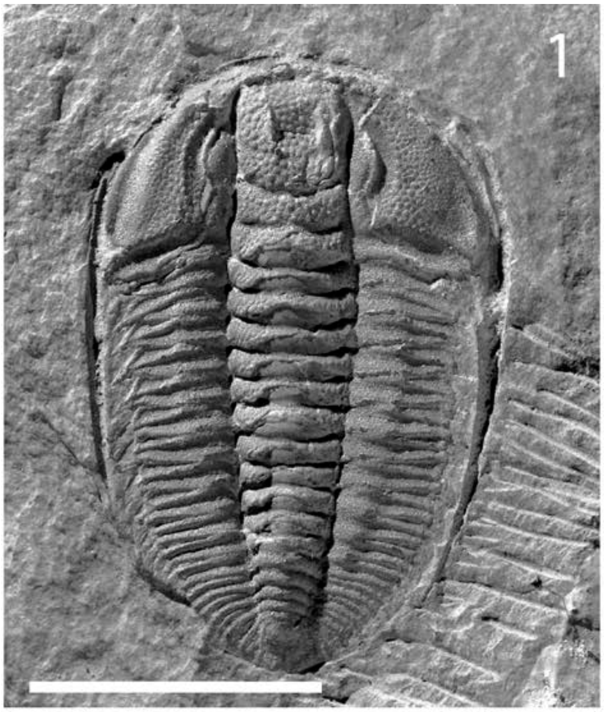
Figure 28. 1-5: all taxa assigned herein to *"Prosaukia" jingxianensis*. 1) fully articulated dorsal exoskeleton originally assigned to Saukia jingxianensis based on the apparent lack of a preglabellar field due to slight damage to the frontal area and the anterior margin of the cranidium. Note the prosopon of the cranidium and the row of tubercles adjacent to the eye on the librigenae, NIGPAS 23743 (holotype). 2) cranidium originally assigned to *Saukia jingxianensis* photographed under low angle lighting. Note the row of tubercles anterior to the preglabellar furrow and the low relief anterior border furrow, NIGPAS 79343. 3) partial dorsal exoskeleton originally assigned to *Prosaukia diversa*. Note the continuation of the librigenal lateral border furrow anteriorly as it transitions into an anterior border furrow of the cranidium, NIGPAS 79360. 4) partial dorsal exoskeleton originally assigned to *Prosaukia diversa deformata*. This specimen is not as well-preserved as the example in Figure 28.3, but a an anterior border furrow is still evident as are tubercles immediately anterior of the preglabellar furrow, NIGPAS 79350. 5) pygidium originally assigned to *Prosaukia diversa deformata*, with six axial rings and a small, triangular terminal piece that extends nearly to the posterior pygidial margin, NIGPAS 79349. Scale bars: 1, 5 = 1 cm; 2 = 1mm; 3, 4 = 5 mm.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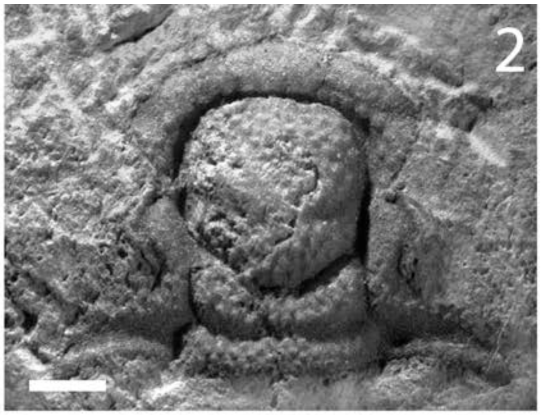
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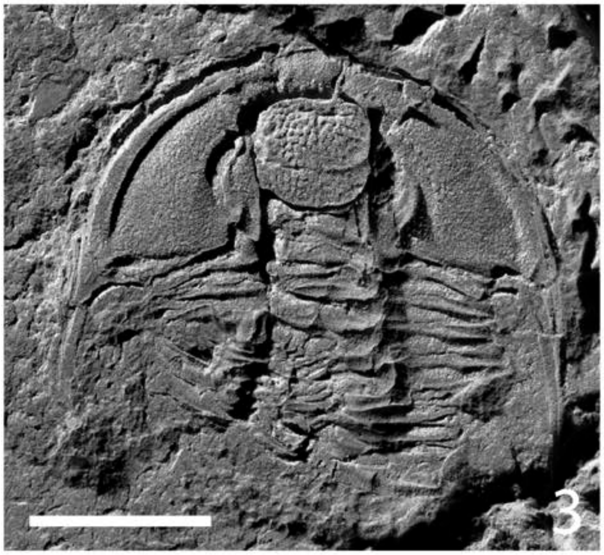
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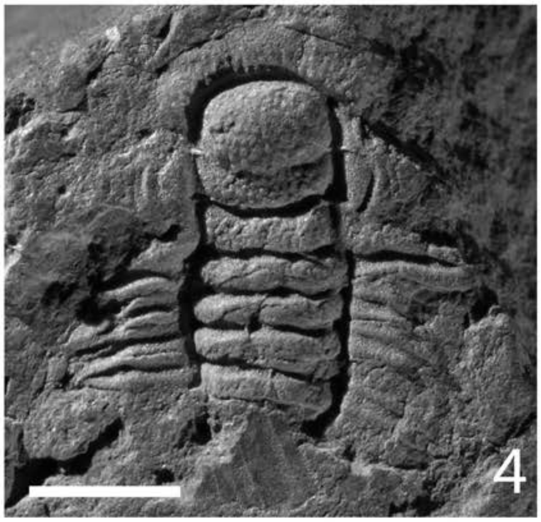
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Figure 29. *Prosaukia oldyelleri*, *Prosaukia stosei*, *Saukia acuta* and *Saukia tumida*. 1-3: *Prosaukia oldyelleri*. 1) well-preserved holaspid cranidium showing characteristic ridge prosopon, and the very short occipital spine, SUI 99055. 2) pygidium showing postaxial ridge, lateral spines, and five axial rings, SUI 99065. 3) librigena with ridge prosopon and confluent border furrows, SUI 99080. 4-6 : *Prosaukia stosei*. 4) Cranidium showing the pustulated prosopon, USNM 136960. 5) pygidium with 6 pustulated axial rings and unequally-divided pleurae, USNM 136960. 6) librigena with long, straight genal spine, confluent lateral and posterior margins, and terrace ridge ornament, USNM 137115. 7: *Saukia acuta*, fully articulated dorsal exoskeleton with eleven thoracic segments, USNM 58618 (holotype). 8-9: *Saukia tumida*. 8) inflated crandium with strong pustulation showing palpebral lobes located close to the axial furrow, USNM 185828. 9) cranidium in lateral view showing continuous transverse S2 furrow, the strongly downsloping glabellar anterior lobe and anterior border, and the preglabellar furrow that undercuts the anterior glabellar lobe, USNM 185828. Scale bars: 1, 2= 1 mm; 3, 5, 6 = 5mm; 4, 7-9 = 1 cm. Figs. 1-3 from Adrain and Westrop (2004).


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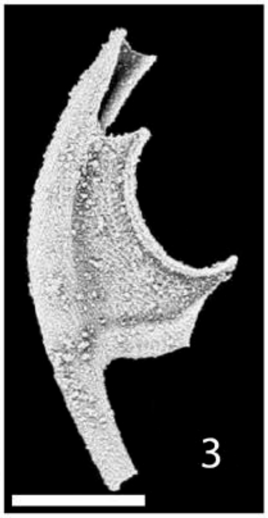
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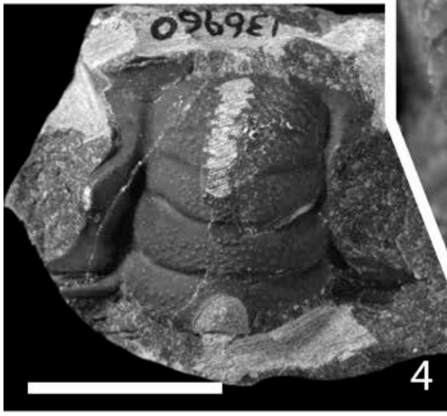
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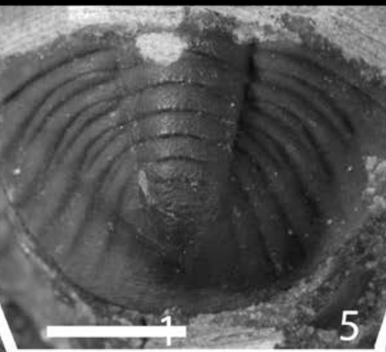
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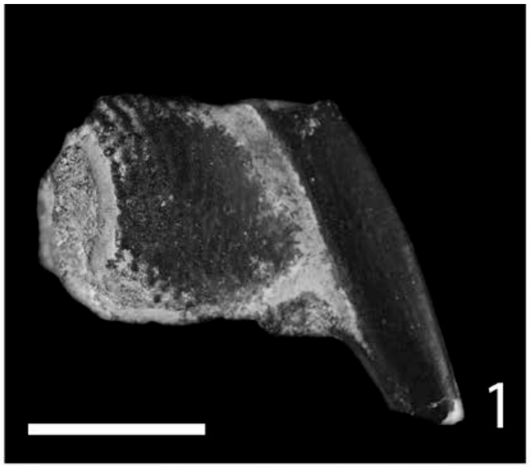
Figure 30. *Saukia tumida* and *Saukiella junia varieties A* and *B.* 1-2: *Saukia tumida.* 1) librigena showing the confluent nature of the lateral and posterior librigenal furrows. Note the strong pustulation that is arranged into rows in the librigenal field prosopon, USNM 192244. 2) partial pygidium with three well-defined axial rings, and relatively high length to width ratio. 3-4: *Saukiella junia species A.* 3) cranidium showing the anterior border furrow with a more strongly posteriorly-curved orientation and a short (sag.) combined preglabellar field composed of the preglabellar furrow and the anterior border furrow. Note also the slight dimpling of the anteromedial portion of the anterior glabellar lobe, USNM 192273. 4) pygidium showing a more strongly divided posteriormost axial ring, and more equally-divided lateral pleurae, USNM 192275. 5-6: *Saukiella junia species B*. 5) cranidium showing an arrangement of the lateral part of the anterior border furrow that is angled slightly more forward, typical of *Saukiella pepinensis*, which occurs stratigraphically below *S. junia sp B*; the distinctly longer anterior border distinguished it from *S. pepinensis*, USNM 192267. 6) pygidium with more unequally-divided lateral pleurae and a less well-defined posteriormost axial ring, USNM 192272. Scale bars: 1, 4, 5 = 1 cm; 2, 3, 6 = 5mm.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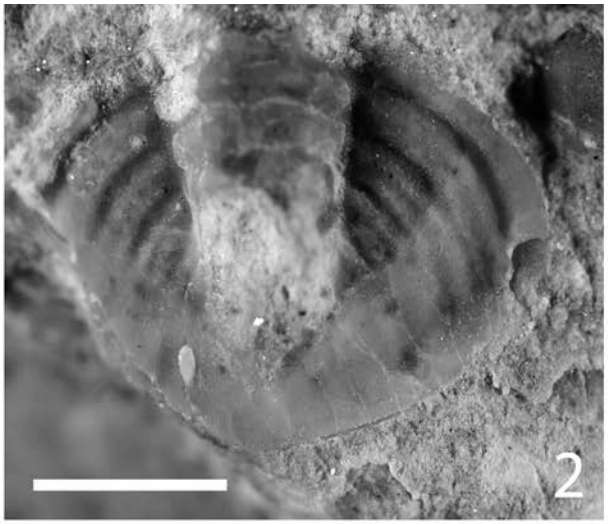
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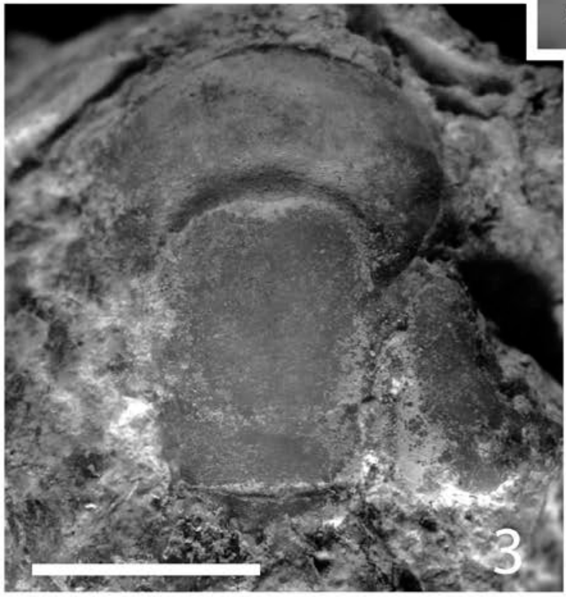
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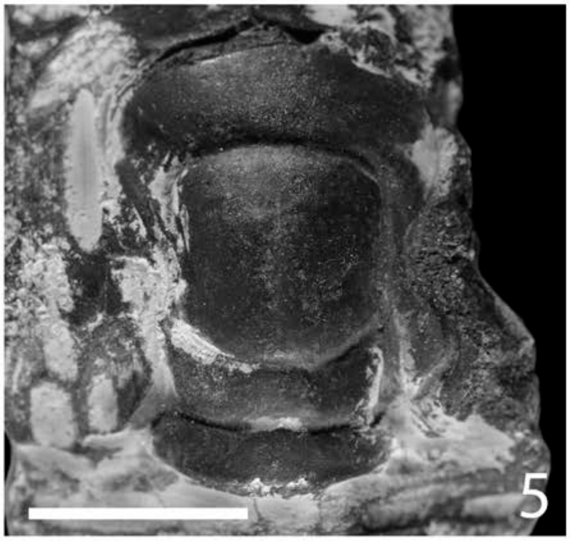
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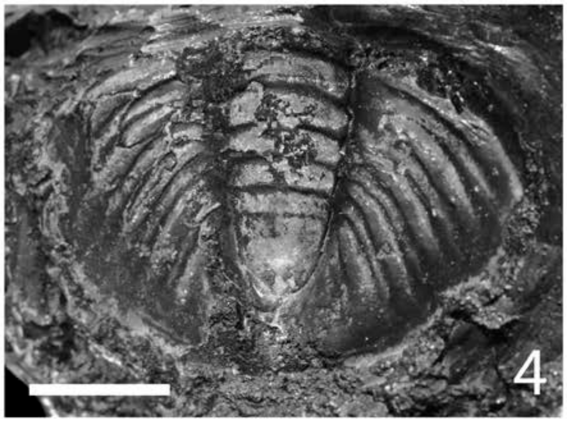
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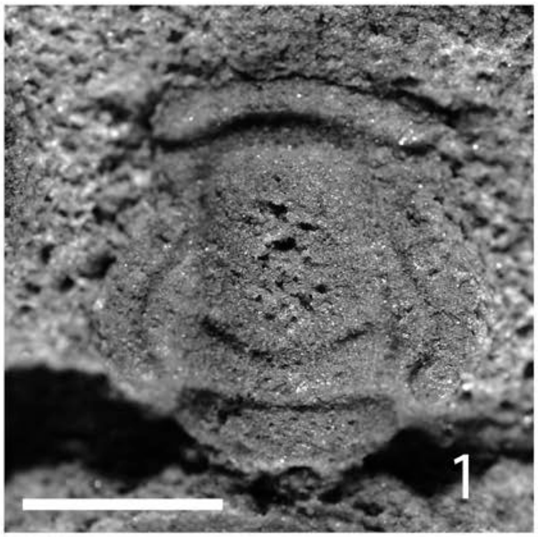
Figure 31. *Saukiella norwalkensis* and *Saukiella pyrene.* 1-3: *Saukiella norwalkensis*. 1) cranidium showing the slightly inflected, upturned lateral parts of the anterior border furrow, USNM 82509. 2) pygidium showing transversely ovate shape, 4 axial rings, and postaxial ridge, USNM 82507. 3) librigena, showing confluent lateral and posterior border furrows, and advance condition of the genal spine. Compare this free cheek with the free cheek of S. pyrene (in Figure 30.6) from the type locality which is not advanced. This is the primary taxabase separating these two taxa, USNM 82507. 4-7: *Saukiella pyrene.* 4) holotype cranidium. Note the slightly wider spacing of the palpebral lobes from the axial furrow compared to S. norwalkensis, and also the more even curvature along the entire anterior border furrow, USNM 58644. 5) cranidium from the Wilberns Formation of Texas preserving much greater detail of the details of the cranidial sutures. S2 can be distinctly seen to be discontinuous across the glabellar midpoint, and a pair of short S3 furrows extends diagonally anteromedially. S2 and S3 furrows are only very rarely preserved in material from sandy facies of the upper Mississippi valley, USNM 192259. 6) librigena from the type area. Note the lack of advancement of the genal spine (compare with *S. norwalkensis* in Figure 30.3, USNM 58645. Pygidium attributed to *S. norwalkensis.* This pygidium is typical of the genus *Saukiella*. Note the relatively evenly divided lateral pleurae. All scale bars 5mm.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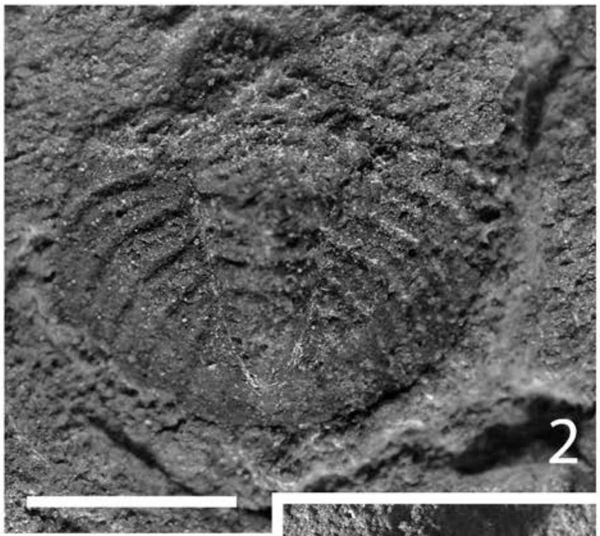
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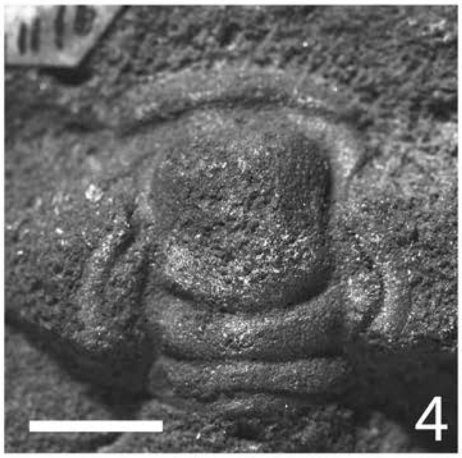
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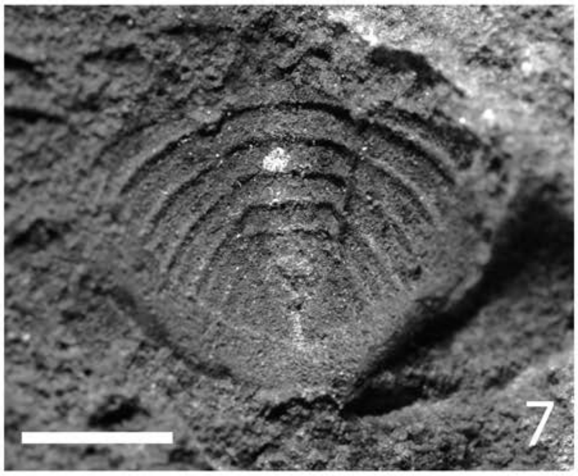
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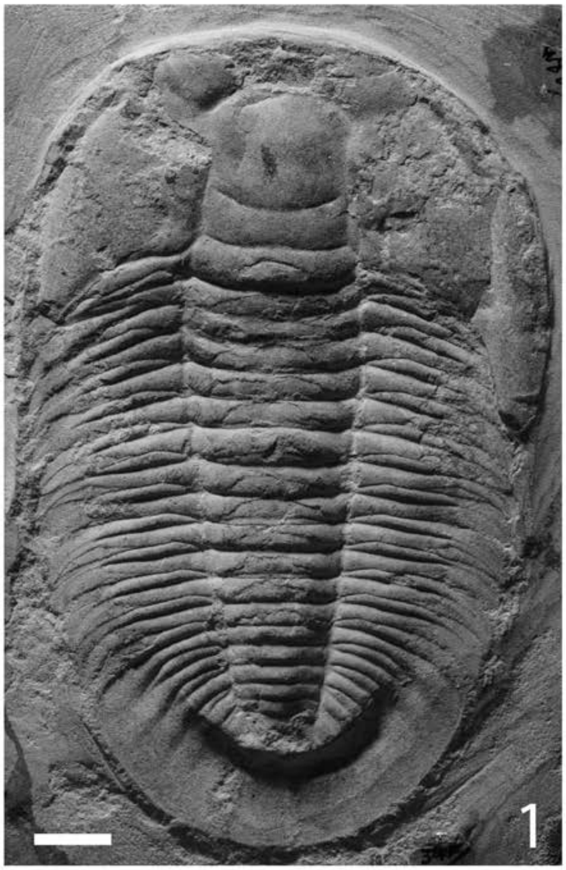
Figure 32. *Tellerina crassimarginata* and *Tellerina wardi.* 1-2: *Tellerina crassimarginata.* 1) fully articulated dorsal exoskeleton from the type locality (Prarie du-Sac, Wisconsin). There are 12 thoracic segments in this articulated specimen, the condition for all articulated saukiids (and dikelocephaliids) known from Laurentia, USNM 58613 (Ulrich and Resser's 1933 plesiotype). A second, fully articulated specimen from USNM (also labeled USNM 58613). This specimen more fully details the shape of the dorsal exoskeleton. Note the abaxial portions of the anterior border furrow more clearly extending anterolaterally. 3-5: *Tellerina wardi.* 3) dorsally flattened cranidium. Note the wrinkle-like structures. These are interpreted to be caused by post-depositional flattening and compression. Because all remains attributable to this species show some form of flattening, it is possible that this taxon may have had a comparatively thin cuticle, YPM 8182. 4) pygidium with at least 8 axial rings. Note the prominent ridge ornament or the posterior and lateral border area, and the fold extending down the axial pleurae. This is interpreted to have been caused by compaction, YPM 27987. 5) librigena showing the very wide lateral border typical of the genus Tellerina, and the fine scale terrace ridge ornament of the librigenal field, un-numbered YPM specimen. All scale bars 1 cm.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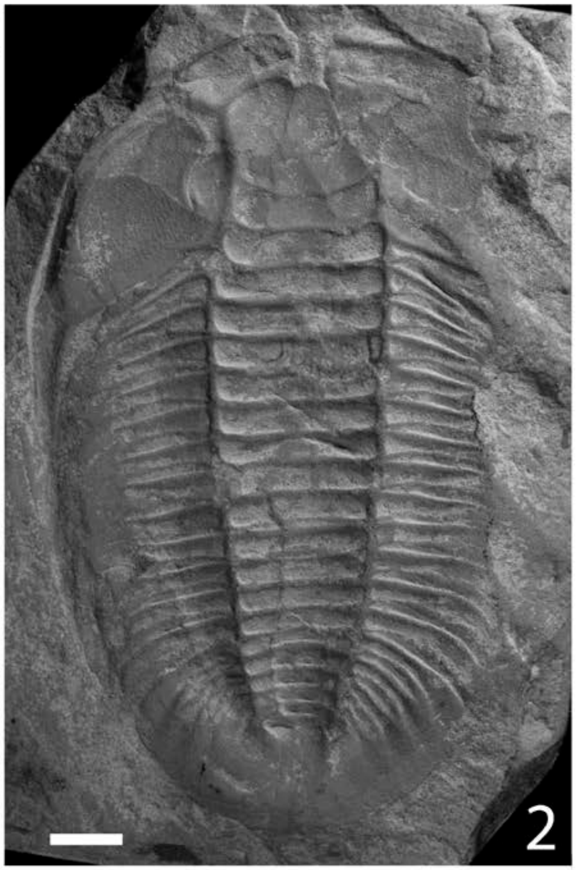
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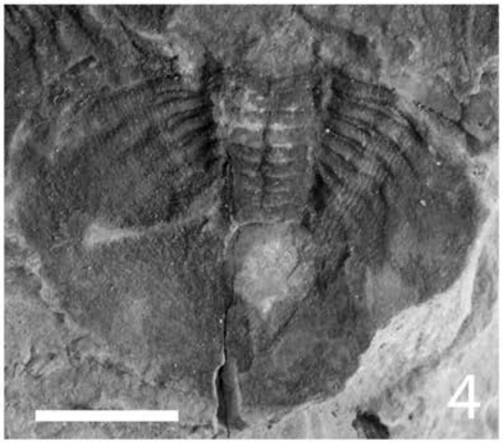
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TABLES

Table 1. Species included in phylogenetic analyses, and original author and date of first publication. **†** indicates Ptychaspididae outgroup species; * indicates Pterocephaliidae outgroup species; ‡ indicates species with close (hypothesized sister-group relationships to Saukiidae; names in bold indicate taxa coded entirely from literature. Numbers refer to taxon number in character matrices in Appendices 1 and 2.

taxon #	species name	original author, date
1	***Anderssonella beauchampi***	Shergold, 1975
2	**†*Asioptychaspis subglobosa***	(Sun, 1924)
3	‡*Briscoia septentrionalis*	Kobayashi, 1935
4	*Calvinella ozarkensis*	Walcott, 1914
5	*Calvinella prethoparia*	Longacre, 1970
6	*Calvinella spiniger*	(Hall, 1963)
7	*Calvinella wisconsinensis*	Ulrich and Resser, 1933
8	***Danzhaisaukia nitida***	Lu and Chien 1978
9	***Diemanosaukia miserabilis***	Jago and Corbett, 1990
10	‡*Dikelocephalus freeburgensis*	Feniak, 1948
11	‡*Dikelocephalus minnesotensis*	Owen, 1852
12	*Eosaukia acuta*	(Kuo and Duan in Kuo, Duan, and An, 1982)
13	*Eosaukia angustilimbata*	Qian, 1986
14	*Eosaukia bella*	(Walcott, 1906)
15	*Eosaukia latilimbata*	Lu, 1954
16	*Eosaukia micropora*	(Qian, 1985)
17	***Eosaukia rectangula***	Lu and Zhou, 1990
18	*Eosaukia walcotti*	(Mansuy, 1915)
19	**‡*Hamashania pulchera***	Kobayashi, 1942
20	***Hoytaspis speciosa***	(Walcott, 1879)
21	***Lichengia simplex***	Shergold, 1991
22	*Linguisaukia spinata*	Peng, 1984
23	*Lophosaukia jingnanensis*	Lu and Lin, 1984
24	***Lophosaukia rectangulata***	Ergaliev, 1980
25	***Lophosaukia torquta***	Shergold, 1972

26	*Mictosaukia globosa*	(Robison and Pantoja-Alor, 1968)
27	*Mictosaukia luanhensis*	Zhou and Zhang, 1978
28	*Mictosaukia orientalis*	(Resser and Endo in Endo, 1931)
29	*Mictosaukia striata*	(Resser and Endo, 1937)
30	***Pacootasaukia jokliki***	(Shergold, 1991)
31	*Prosaukia corrugata*	Rasetti, 1959
32	*Prosaukia hartii*	(Walcott, 1879)
33	*Prosaukia misa*	(Hall, 1963)
34	***Prosaukia oldyelleri***	Adrain and Westrop 2004
35	*Prosaukia stosei*	Rasetti, 1959
36	****Pterocephalia norfordi***	Chatterton and Ludvigsen, 1998
37	†*Ptychaspis miniscaensis*	(Owen, 1852)
38	*Saukia acuta*	Ulrich and Resser, 1933
39	*Saukia tumida*	Ulrich and Resser, 1933
40	*Saukia jingxianensis*	(Chien, 1974)
41	*Saukiella junia*	(Walcott, 1914)
42	*Saukiella norwalkensis*	Ulrich and Resser, 1933
43	*Saukiella pepinensis*	(Owen, 1852)
44	*Saukiella pyrene*	(Walcott, 1914)
45	**Sigmocheilus notha*	(Resser, 1942)
46	*Sinosaukia daliensis*	Zhu, 2011
47	*Sinosaukia distincta*	Zhou, 1977
48	***Taebaeksaukia spinata***	Lee and Choi, 2011
49	*Tellerina crassimarginata*	(Whitfield, 1882)
50	*Tellerina wardi*	(Walcott, 1914)

Table 2. Search results for analyses presented herein. GROUP 1Analyses all include the full matrix of all 50 taxa subjected to tree search. GROUP 2 Analysis all include a partial data matrix of 48 taxa [including saukiids, dikelocephaliids, and pterocephaliids (but no ptychaspidids)]. GROUP 3 Analyses all include a partial data matrix 48 taxa [including saukiids, dikelocephaliids, and ptychaspidids (but no pterocephaliids)]. GP = GROUP, analysis group number. Each GROUP includes 1 analysis each of qualitative only, qualitative and binned morphometric, and qualitative and gap-weighted morphometric data; Char = number of characters; MPT = number of most parsimonious trees; score = tree length; CI = consistency index; RI = retention index.

GP	analysis	data type	Chars	MPT	score	C.I.	R.I.
1	1	QU	53	160	219	0.32	0.672
	4	QU + BM	60	10	280	0.282	0.629
	7	QU + GW	60	1	244.796	0.31	0.653
2	2	QU	53	85	204	0.338	0.679
	5	QU + BM	60	90	264	0.295	0.632
	8	QU + GW	60	1	228.395	0.327	0.659
3	3	QU	53	40	205	0.322	0.675
	6	QU + BM	60	406	265	0.283	0.627
	9	QU + GW	60	1	229.495	0.31	0.654

Table 3. Area codes used in Fitch optimization and mBPA analyses.

Area code	paleogeographic region
1	Laurentia
2	Kazakhstan
3	Oman
4	North China
5	South China
6	Australia
7	Antarctica