CALMONIID TRILOBITES OF THE LOWER DEVONIAN *SCAPHIOCOELIA* ZONE OF BOLIVIA, WITH REMARKS ON RELATED SPECIES

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ABSTRACT

The calmoniid trilobites of the *Scaphiocoelia* assemblage zone (Lower Devonian) of Bolivia are described. The *Scaphiocoelia* Zone is the oldest Devonian unit in Bolivia and is recognized in the base of the Belén Formation, the Icla Formation, and the Gamoneda Formation, in northern, central, and southern Bolivia, respectively. Twenty-one trilobite and one eurypterid taxa are recognized from this zone, 17 of which are species of Calmoniidae. *Scaphiocoelia* Zone calmoniids herein described as new include one genus (*Deltacephalaspis*), and five subgenera [*Bainella* (*Belenops*), the nominate subgenus of *Deltacephalaspis*, *Deltacephalaspis* (*Prestalia*), *Schizostylus* (*Curuyella*), and *Kozlowskiaspis* (*Romanops*)]. Ten new *Scaphiocoelia* Zone species are described: *D.* (*Deltacephalaspis*) *comis*, *D.* (*D.*) *retrospina*, *D.* (*D.*) *magister*, *D.* (*Prestalia*) *tumida*, *Schizostylus* (*Curuyella*) *granulata*, ?*Acastoides gamonedensis*, *Phacopina convexa*, *Kozlowskiaspis* (*Romanops*) *borealis*, *K.* (*Romanops*) *australis*, and *Tarijactinoides tikanensis*. Additionally, two new species are characterized but not formally diagnosed, and two others are distinguished but remain unassigned to genera. Three previously described species from the *Scaphiocoelia* Zone are redescribed: *Bainella* (*Belenops*)

insolita (Wolfart), *Parabouleia calmonensis* Eldredge, and *Tarijactinoides jarcasensis* Suárez Soruco. The vicariant pattern within Bolivia, and the biogeographic affinities of Bolivia with other areas within the Malvino-Kaffric Province are briefly discussed. We also present a general discussion of calmoniid anatomy and taxic diversity.

Non-*Scaphiocoelia* Zone trilobites from Bolivia and elsewhere are also described, discussed or figured as a consequence of our study of the *Scaphiocoelia* Zone material. We describe the new genus *Andinacaste* from the Silurian of Bolivia. We describe as new *Andinacaste legrandi* and *Phacopina padilla*, the latter from the Icla Formation, above the *Scaphiocoelia* Zone, at Padilla, Bolivia. We present formal revisions for the following six genera: *Bainella*, *Schizostylus*, *Phacopina*, *Kozlowskiaspis*, *Parabouleia*, and *Tarijactinoides*. We discuss the status of three additional genera: *Probolops*, *Acastoides*, and *Scotiella*. We formally revise *Kozlowskiaspis* (*Kozlowskiaspis*) *superna* and *Andinacaste chojnacotensis*. Finally, we also discuss or figure an additional 15 calmoniid and acastid species in conjunction with our analysis of the composition of the calmoniid component of the *Scaphiocoelia* Zone fauna.

RESUMEN

Se describen los trilobites calmoniidos de la Zona de *Scaphiocoelia* (Devónico Inferior) de Boliva. La Zona de *Scaphiocoelia* es la unidad mas antigua del Devónico boliviano y se la reconoce en la base de la Formación Belén, de la Formación Icla y de la Formación Gamoneda en Bolivia septentrional, central y meridional respectivamente. Se han identificado veintiuna formas de trilobites y una de euriptéridos de esta zona, y de ellas dieciesiete pertenecen a la familia Calmoniidae. Los trilobites calmoniidos que se describen aquí como nuevos, incluyen un nuevo género (*Deltacephalaspis*) y cinco nuevos subgéneros [*Bainella* (*Belenops*), el subgénero nominante de *Deltacephalaspis*, *Deltacephalaspis* (*Prestalia*), *Schizostylus* (*Curuyella*) y *Kozlowskiaspis* (*Romanops*)]. Se describen diez nuevas especies de la Zona de *Scaphiocoelia*: *D.* (*Deltacephalaspis*) *comis*, *D.* (*D.*) *retrospina*, *D.* (*D.*) *magister*, *D.* (*Prestalia*) *tumida*, *Schizostylus* (*Curuyella*) *granulata*, ?*Acastoides gamonedensis*, *Phacopina convexa*, *Kozlowskiaspis* (*Romanops*) *australis*, *K.* (*Romanops*) *borealis*, y *Tarijactinoides tika-*

nensis. Además dos nuevas especies son caracterizadas, pero no se da un diagnóstico formal, y se individualizan otras dos formas pero no se asignan a ningún género. Se da una nueva descripción de tres especies descritas anteriormente de la Zona de *Scaphiocoelia*, es decir: *Bainella* (*Belenops*) *insolita* (Wolfart), *Parabouleia calmonensis* Eldredge y *Tarijactinoides jarcasensis* Suárez Soruco. Se discute brevemente el modelo de reemplazo (vicaría) en las faunas de Bolivia, igualmente que las afinidades biogeográficas de Bolivia con otras áreas de la Provincia Malvino-Kaffra. Presentamos además una discusión general de la anatomía de los trilobites calmoniidos y su diversidad taxonómica.

También se describen, discuten e ilustran algunos trilobites de Bolivia y de otras partes aunque no pertenecen a la Zona de *Scaphiocoelia*, como consecuencia de nuestro estudio del material de la Zona de *Scaphiocoelia*. Así describimos un nuevo género *Andinacaste* del Silúrico boliviano. Describimos como nuevas especies *Andinacaste legrandi* y *Phacopina padilla*, ésta última

de la Formación Icla, pero de un nivel superior, encima de la Zona de *Scaphiocoelia,* ejemplar proveniente de la localidad de Padilla (Bolivia). Presentamos además revisiones fòrmales de los seis géneros siguientes: *Bainella, Schizostylus, Phacopina, Kozlowskiaspis, Parabouleia* y *Tarijactinoides.* Discutimos también la posición de tres géneros adicionales: *Probolops, Acastoides* y *Scotiella.* Revisamos formalmente *Kozlowskiaspis (Kozlowskiaspis) superna* y *Andinacaste chojnacotensis.* Finalmente discutimos o ilustramos admeás quince especies de las familias de Calmoniidae y Acastidae en relación con nuestro análisis de la composición de los elementos calmoniidos dentro de la fauna de *Scaphiocoelia.*

INTRODUCTION

The Devonian faunas of the Southern Hemisphere have been studied sporadically since the mid-nineteenth century. The unique quality of the fauna was clear to most of its earliest students. The fauna is sufficiently well known to allow recognition of the Malvino-Kaffric faunal province and analysis of its affinities with other Devonian biogeographic areas. Eldredge and Ormiston (1979) have reviewed and summarized trilobite occurrences within the Malvino-Kaffric Province.

Yet, for all the descriptive and analytic work performed to date, it has become clear that the job of basic descriptive taxonomy of the elements of this fauna is far from complete. Nowhere within the Malvino-Kaffric Province is the section more continuously developed, and the fauna better known, than in Bolivia. Among the many works describing fossils from the Bolivian Devonian (see Eldredge and Ormiston, 1979, for a full bibliography of the trilobite literature), those of Kozlowski (1923), Braniša (1965), and Wolfart (1968) stand out as landmarks. Wolfart's (1968) carefully prepared monograph, in particular, reviewed nearly all previously described trilobites from the Bolivian Devonian, and added new taxa to the list. But with the acquistion of the Braniša Collection by the National Museum of Natural History, Smithsonian Institution (NMNH) in the early 1970s (a collection of over 10,000 specimens, many of them Devonian trilobites), it was immediately obvious that the job of describing the species in the fauna was far from complete.

In the summer of 1972, LeGrand Smith, then of La Paz, Bolivia, visited the American Museum of Natural History (AMNH), donating a specimen of the synziphosuran merostome later described (Eldredge, 1974) as *Legrandella lombardii.* Smith became a catalyst for the production of the present monograph by putting Braniša and Eldredge in contact with each other, and by making a large collection (over 3000 specimens, most of which are Devonian trilobites) available to the American Museum of Natural History. Braniša followed suit by adding many important specimens from his collections, making them available for study. Braniša pointed out that the most obviously unique undescribed taxa all came from approximately the same stratigraphic horizon in various places in Bolivia. This horizon, the *Scaphiocoelia* Zone, is a biostratigraphic assemblage zone discussed in further detail below.

The survey of Malvino-Kaffric trilobites reported by Eldredge and Ormiston (1979) occasioned a comparative study through the literature and all available specimens, of all previously described trilobites from the province. In many cases, examination of type specimens has proved impossible, although the National Museum and the New York State Museum (NYSM) each hold the type specimens for many of J. M. Clarke's species from the Amazon Basin, southern Brazil, and the Falkland Islands. The taxa newly recognized and described herein have been defined only after exhaustive comparison with faunal elements from all other areas within the province and from all known stratigraphic horizons. In the course of this study, moreover, we have found it necessary to revise several genera, and have described or revised some taxa not occurring in the *Scaphiocoelia* Zone. However, this study is not simply a chaotic melange of descriptions

and revisions of trilobites. All the trilobites treated here are either members of the family Calmoniidae, or are acastids either previously confused with Calmoniidae proper, or thought (by us) to be closely related to calmoniids. Furthermore, not all new genera and species of Calmoniidae known to us are described herein. These will be described in future studies. Rather, all new taxa described herein come from the *Scaphiocoelia* Zone or are congeneric with species from that zone. All revisions of non-*Scaphiocoelia* Zone taxa arise directly from our work on trilobites from that zone.

We recognize 17 species of calmoniid trilobites in the *Scaphiocoelia* Zone (table 1). Of these, only three had previously been described, and a fourth had been figured: Wolfart (1968) described *Acastoides insolitus*, new species, here redescribed as *Bainella* (*Belenops*) *insolita*. Eldredge (1972a) described *Parabouleia calmonensis*, new genus and species, not recognizing at the time that that taxon is restricted to the *Scaphiocoelia* Zone. Suárez Soruco (1971) described *Tarijactinoides jarcasensis*, new genus and species, and figured *Phacopina* sp., described herein as *Phacopina convexa*, new species. All 13 additional species (nine formally named, two recognized provisionally, and two others unassigned to genera) are new. We recognize eight calmoniid genera in the *Scaphiocoelia* Zone, three of which appear restricted to it, and one of which—*Deltacephalaspis*–is newly described. We recognize eight subgenera (two for each of four genera) among the eight *Scaphiocoelia* Zone genera. Among these eight subgenera, five occur only in the *Scaphiocoelia* Zone in Bolivia, though two are known from elsewhere within the Malvino-Kaffric Province.

The term *Scaphiocoelia* Zone has been used by Braniša to designate the basal beds of the Devonian sequence in the northern, central, and southern outcrop areas in Bolivia (fig. 1). Isaacson (1977, p. 141) used the expression "*Scaphiocoelia*-bearing beds" and the "*Scaphiocoelia* zone" (p. 145). According to Isaacson (1977, p. 139), the brachiopod genus *Scaphiocoelia* is restricted to

the "lower portion of the sequence," and the *Scaphiocoelia*-bearing beds of the Belén Formation in northern Bolivia are correlative with those of the Lower Icla Formation at Icla (central Bolivia—see fig. 1) as well as "the lower sandstone at Quilco, Pojo and Presto." Isaacson (1977, p. 141) furthermore correlated the Belén Formation and the Icla Formation with the Gamoneda Formation of southern Bolivia. However, the basal portion of the Gamoneda Formation so far has not yielded *Scaphiocoelia* (Isaacson, 1977, p. 145). Isaacson (1977, p. 141) interprets the *Scaphiocoelia*-bearing beds as intertidal, and their absence in the Gamoneda Formation to be simply a reflection of deeper water conditions. Whatever the merits of this environmental interpretation may be, trilobite distributional data, including stratigraphic position and geographic occurrence, indicate that the *Scaphiocoelia* Zone is a true biostratigraphic assemblage zone, correlative throughout Bolivia, even where *Scaphiocoelia* itself is absent.

The suite of trilobites which in part defines the *Scaphiocoelia* Zone is listed in table 1. All occur in the basal portion of the Belén, Icla or Gamoneda formations (B, I, and G, respectively in table 1) in direct association with *Scaphiocoelia* in northern and central Bolivia. Of the 20 trilobite species identified to date in the *Scaphiocoelia* Zone, all but one—*Otarion* (*Maurotarion*) *dereimsi*, are restricted to that unit. (The identities of the homalonotid species are insufficiently known at this point to be considered in this respect.) Only one species, *Bainella* (*Belenops*) *insolita*, occurs in all three areas. Its only close relative is *B.* (*Belenops*) *gamkaensis* from the Lower Devonian of South Africa.

All other species are either restricted to one of the three outcrop areas, or at most occur in two. The Icla Formation and the Gamoneda Formation tend to share species in common [*Deltacephalaspis* (*Prestalia*) *tumida, Kozlowskiaspis* (*Romanops*) *australis, Tarijactinoides jarcasensis*] not present in the north. Furthermore, there is a persistent pattern of vicariance whereby the sister species of a taxon occurring in the

FIG. 1.   Map of Bolivia showing position of collecting localities mentioned in the text.

north is to be found in the beds of the central and southern regions. Even *B. (Belenops) insolita,* which occurs in all three regions, shows a pattern of intraspecific variation mirroring the general pattern of vicariance. The *Scaphiocoelia* Zone is a well-integrated biogeographic area, as well as a true biostratigraphic unit, but it shows a pattern of geographic differentiation within it such that the Icla and Gamoneda areas are more closely related to each other (in terms of biogeographic history—speciation patterns) than

either is to the Belén area to the north. Further remarks on vicariant patterns and geographic variation are presented in relevant portions of the systematics section of this report.

The definition of the *Scaphiocoelia* Zone as a biostratigraphic assemblage zone is strengthened by the observation that three genera and four subgenera are entirely restricted to it. Most of the calmoniids in the zone belong to the informally designated "*Calmonia* group" (see Eldredge, 1979 and below for further characterization of this group). As such, their closest relatives outside Bolivia include species of *Calmonia*, *Bainella*, *Paracalmonia*, *Pennaia*, and *Schizostylus*, some of which are not yet known from Bolivia. The Devonian platform sequences of cratonal South America, the Falkland Islands, and South Africa are all much thinner than the Andean sequences of Peru, Bolivia, and Argentina. The pattern of occurrences of trilobites (see Eldredge and Ormiston, 1979) and their interrelationships suggest the possibility that the thinner sequences of the cratonal areas within the Malvino-Kaffric Province may correlate with the lower portion of the Devonian sequence in Bolivia.

TABLE 1

Trilobite and Eurypterid Occurrences in the *Scaphiocoelia* Zone of Bolivia

SPECIES	B	I	G
Bainella (*Belenops*) *insolita*	X	X	X
Deltacephalaspis (*Deltacephalaspis*) *comis*	—	—	X
D. (*Deltacephalaspis*) *retrospina*	—	—	X
D. (*Deltacephalaspis*) *magister*	X	—	—
Deltacephalaspis (*Prestalia*) *tumida*	—	X	X
D. (*Prestalia*) sp. A	X	—	—
Schizostylus (*Curuyella*) *granulata*	?	—	X
?Acastoides gamonedensis	—	—	X
Phacopina convexa	—	—	X
Phacopina cf. *P. convexa*	?	—	—
Kozlowskiaspis (*Romanops*) *borealis*	X	—	—
K. (*Romanops*) *australis*	—	X	X
Parabouleia calmonensis	X	—	—
Tarijactinoides jarcasensis	—	X	X
Tarijactinoides tikanensis	X	—	—
Calmoniid genus and species indet. A	—	X	—
Calmoniid genus and species indet. B	—	—	X
Gamonedaspis scutata	—	—	X
cf. *Francovichia* sp.	—	—	X
Otarion (*Maurotarion*) cf. *dereimsi*	—	X	—
Burmeisteria (s.l.) sp. or spp.	X	X	X
eurypterid	—	—	X

B—Lower Belén Formation, Belén-La Paz-Sicasica region, northern Bolivia; I—Lower Icla Formation, Icla-Padilla region, east-central Bolivia; G—Gamoneda Formation, Tarija region, southern Bolivia.

ACKNOWLEDGMENTS

TAXIC DIVERSITY AND ASPECTS OF THE
MORPHOLOGY OF CALMONIID TRILOBITES

The Calmoniidae as here understood comprise a distinctive portion of the "acastid" division of dalmanitid trilobites. By "dalmanitid" we loosely refer to a taxon of disputable hierarchical rank similar in scope to, e.g., the Dalmanitacea of *Treatise* (Harrington et al., 1959) usage. One of us (N.E.) is currently revising all valid genera and subgenera of calmoniids, diagnosing several new genera, and evaluating the relationships among these taxa. That study will define more precisely the limits of the Calmoniidae and the relationship this monophyletic taxon has with other trilobites. It is thus premature to present an emended diagnosis of the Calmoniidae; however, the present study has revealed so much new information on calmoniid diversity (taxic and morphologic) that a brief characterization of the calmoniids in these terms is appropriate here.

For the purposes of present discussion, we use the term "calmoniid" to embrace only the Malvino-Kaffric Lower and Lower Middle Devonian trilobites classified as Calmoniinae by Struve (1959), plus of course additional taxa described, *inter alia,* by Baldis (1967), Wolfart (1968), Suárez Soruco (1971), Eldredge (1972a), Braniša and Vaněk (1973), Baldis et al. (1976), and in the present paper. Assignment of such genera as *Acastoides* Delo, *Phacopina* Clarke, and *Andinacaste,* new genus, is moot and is discussed more fully in a later paper; we shall discuss these taxa and compare them with undoubted calmoniids freely throughout the remainder of this paper, ignoring for the moment the fact that these plesiomorphic taxa may ultimately best be allocated to the Acastidae.

Hammann (1974, p. 54) has pointed out many similarities between *Crozonaspis* and the Calmoniiidae and elsewhere (p. 30) claims a phylogenetic link between *Kloucekia* and other Ordovician genera (from Spain and Morocco) and the Calmoniidae, though he classifies these various genera into Dalmanitininae and Acastinae of the Dalmanitidae. The similarities are certainly striking, encompassing a host of general features, but also, on the specific level, there are some astonishing homeomorphies. Compare, e.g., *Deltacephalaspis* (*Deltacephalaspis*) *comis* or *D.* (*D.*) *retrospina* (figs. 11, 12 of this paper) with *Eodalmanitina destombesi* figured by Henry and Nion (1970, fig. 3G). Although a detailed discussion of the limits and relationships of the Calmoniidae is beyond the scope of this paper, one simply must consider the possibility of a direct relationship between these various Ordovician dalmanitids and the Devonian Malvino-Kaffric Calmoniidae, for if a direct sister-group relationship does appertain to these groups, it would color all further attempts to assess primitive and derived character states among the Malvino-Kaffric taxa, as well as directly affect any analysis of evolutionary and biogeographic patterns. For this reason we believe that it is crucial to present here what we consider to be the decisive piece of evidence which shows the Malvino-Kaffric calmoniids to be solely homeomorphs of, and only remotely related to, these Ordovician taxa, and which instead allies them with other Siluro-Devonian taxa. As Dr. Jean-Louis Henry has pointed out (personal commun.), and as far as we can determine from the examination of original material and from the literature, all Dalmanitininae, Zelliskellinae, and Ordovician so-called Acastinae (e.g., *Kloucekia*) possess a "lozenge" pattern of the auxiliary impression system on the anterior glabellar lobe. This lozenge or diamond-shaped pattern is only vaguely "triangular dalmanitid" (*contra* Eldredge, 1971) and consists of a poorly organized field of impressions with its widest portion well set off from the facial suture, preglabellar furrow, or anterior border furrow (whichever is more proximal), and with impressions covering the midline. There are at least two other kinds of "dalmanitid" pattern presently known to us: (1) the typically ill-defined (i.e., with relatively few impressions) pattern seen in Siluro-Devonian Dalmanitidae *sensu stric-*

to and Synphoriidae, and (2) the acastid pattern—a highly organized and distinctly triangular series of two major radiating rows of impressions (with accessory impressions in subsidiary rows), with the midline devoid of impressions, and with the widest portion of the field situated adjacent to the pre-glabellar furrow or facial suture. Figure 2 is a comparative diagram of the pattern of accessory impressions of most of the taxa discussed in this paper. This pattern is characteristic of all Siluro-Devonian Acastinae, Acastavinae, and Calmoniidae known to us (as pointed out in Eldredge, 1971) and, we add, further shared by all Asteropyginae in which the pattern is known. Inasmuch as earliest probable calmoniids (*Andinacaste,* Silurian of Bolivia; *Phacopina*) as well as many of the other "true" Calmoniidae considered to be relatively primitive on other grounds, share many other features with acastids, we conclude that the Malvino-Kaffric Calmoniidae are the sister-group of the Siluro-Devonian "acastids" (including Acastinae, Acastavinae, and Asteropyginae of various usages; see Eldredge, 1979) and that their resemblances with certain Ordovician taxa are not to be considered indicative of close phylogenetic affinity, or the retention of ancestral, primitive features, but rather an example of homeomorphy (parallelism). We can thus hypothesize that the calmoniid trilobites of the Malvino-Kaffric faunal province (or the Malvino-Kaffric Realm of Boucot, 1971, 1975) represent a *de novo* and *in situ* radiation from an acastid stock.

The radiation that produced the presently estimated 35 genera and subgenera of this monophyletic assemblage occurred very quickly (apparently within the interval Upper Emsian-Lower Eifelian) and is surely unusual for any group of post-Ordovician trilobites. In its array of conservative and unusual morphologies (some of which, in an earlier day, would have been considered downright bizarre) the Malvino-Kaffric calmoniids offer a unique opportunity to come to grips with a major radiation which can be analyzed in terms of component species. The stratigraphic record of these trilobite species, especially in the thick Andean sequences ex-

posed in southern Peru, throughout the length of Bolivia, and in northern Argentina, are unusually complete and have much to offer in terms of the analysis of within-species micro-evolutionary patterns. Similarly, the abundance of most taxa, and their generally excellent state of preservation, admit to detailed studies of functional morphology. Integration of these aspects of calmoniid paleobiology with a detailed analysis of intergeneric relationships, study of distributions of primitive vs. derived character states in all species (they are all "mosaics" in this respect), and with the community framework of Boucot (1971, 1975) and the intra- and interprovincial biogeographic patterns of the calmoniids (Eldredge and Ormiston, 1979), should result in a remarkably detailed picture of a major adaptive radiation useful in macroevolutionary theory (Eldredge and Cracraft, 1980).

While generalizations of this scope are beyond the immediate purview of this paper, the crucial role that calmoniids of the *Scaphiocoelia* Zone play in the analysis of the radiation must be emphasized. Paradoxically, the 17 species and eight genera are all very distinct yet all confusingly similar at the same time. Inasmuch as the fauna is not in as good a state of preservation as is the case in the younger, more classic and better known Bolivian faunas, a great deal of effort has gone into the initial segregation of the available fossils into discrete taxa. Understanding *why* these trilobites are all so very different, yet confusingly similar reveals much about calmoniid morphology in particular, and has further implications for trilobite comparative anatomy in general.

All the calmoniids of the *Scaphiocoelia* Zone have affinities with genera higher up in the section in Bolivia and with genera located elsewhere within the Malvino-Kaffric Province. Virtually all *Scaphiocoelia* Zone species possess unique morphological specializations that stamp them as unique and debar them from simple ancestry to their younger relatives. The most glaring example is *Parabouleia calmonensis,* described by Eldredge (1972a) as a primitive relative of *Bouleia.* The genus was described on the
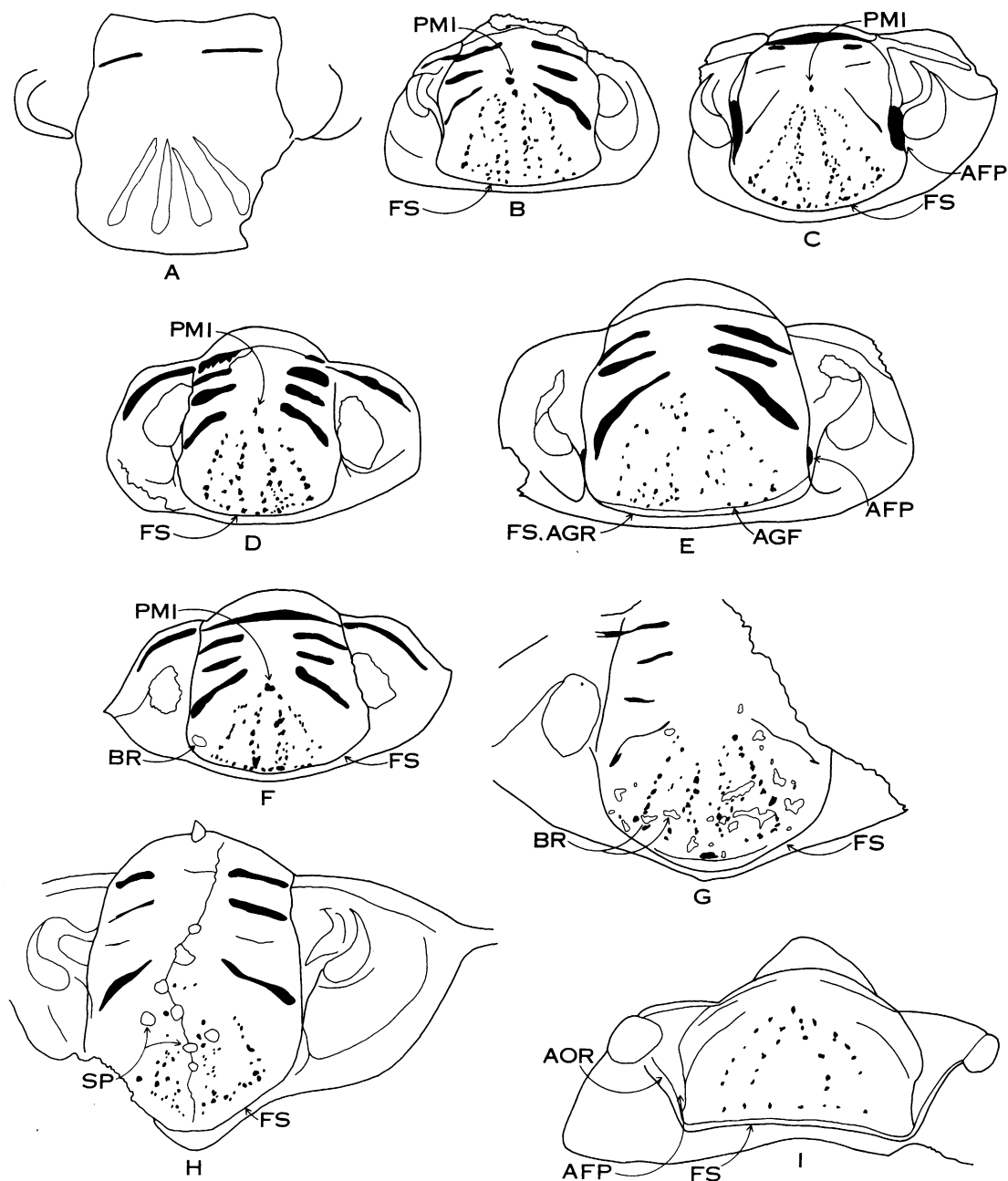
FIG. 2. Comparison of development of auxiliary impression system on anterior glabellar lobe of various calmoniid taxa. All specimens oriented in oblique frontal view. Redrawn from camera lucida sketches. *Abbreviations:* AFP, axial furrow pit; AGF, anterior glabellar furrow; AGR, anterior glabellar ridge; AIS, auxiliary impression system; AOR, anterior ocular ridge; BR, break in the surface of the cuticle or internal mold; FS, facial suture; PMI, posterior median impression; SP, spine or base of broken spine. A. *Andinacaste legrandi*. AIS developed as raised continuous ridges on external surface of cuticle. Latex cast, paratype NMNH 245638 (latex cast AMNH 36709). See figure 25H. B. *Phacopina*
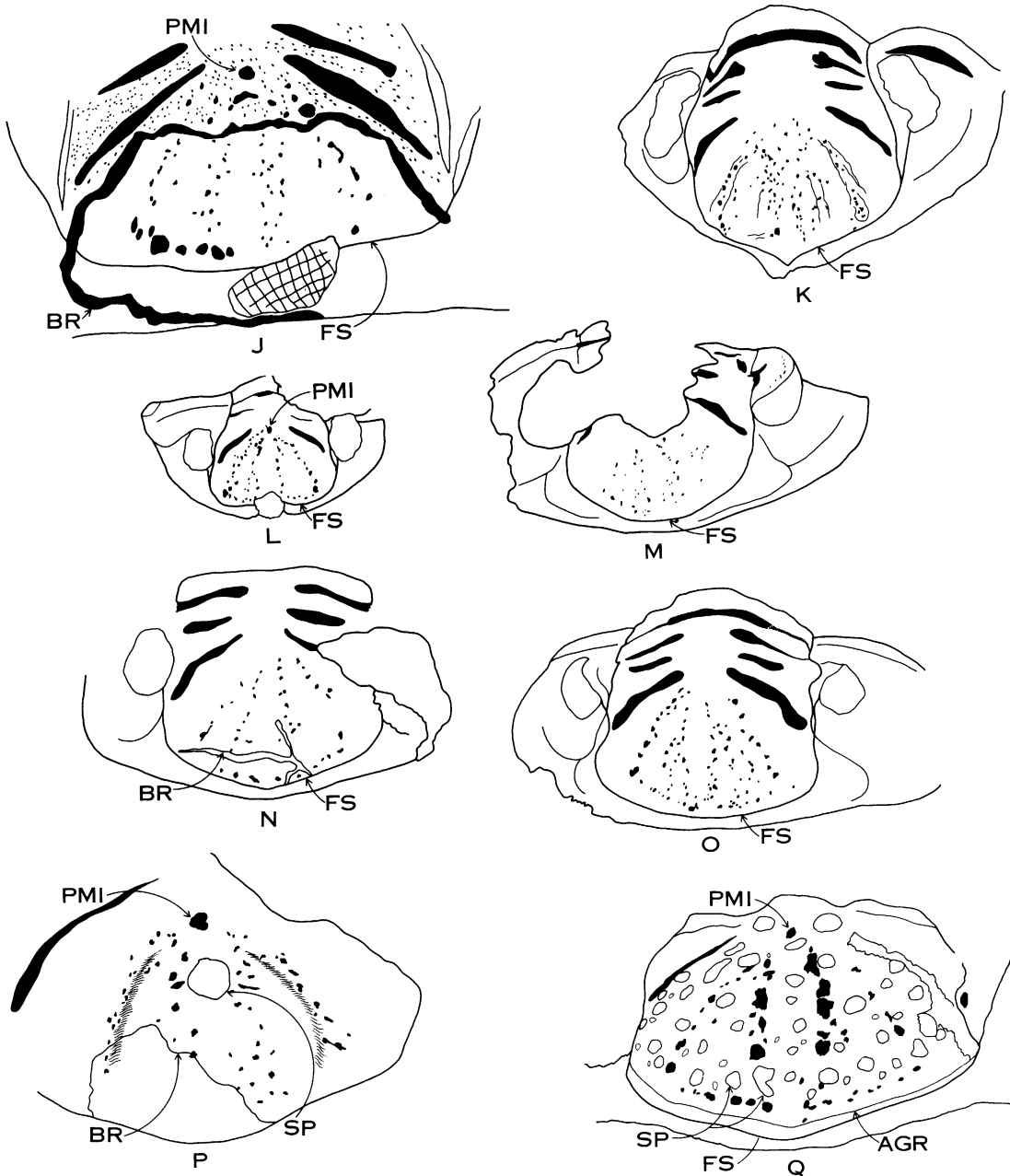
convexa. AIS developed as visceral scars, preserved as pads on internal mold, except PMI, which is developed viscerally as a pad. Internal mold, holotype NMNH 245627. See figure 22A–E. C. *Vogesina* sp. AIS developed as pads on internal mold. AMNH Smith Collection, Chacoma, Bolivia. D. ?*Acastoides* sp. AIS developed as pads on internal mold. NMNH 245624, Icla Formation, Padilla, Bolivia. See figure 18D. E. cf. *Pennaia* or ?*Acastoides* sp. AIS developed as depressions on poorly preserved granulated external surface of cuticle. NMNH Collection, Gamka Poort, South Africa. F. *Calmonia* sp. AIS developed as scars on internal mold, except PMI, which are developed as a pad. NYSM specimen, Pebble Island, Falkland Islands. G. *Deltacephalaspis* (*Deltacephalaspis*) *magister*. AIS developed as pads on

basis of a single specimen of (then) uncertain age, from Rurrenabaque, Beni Department, Bolivia. We have had some 50 specimens from three additional localities available to us for the present study, and it is now clear that *Parabouleia* is a valid genus restricted to the *Scaphiocoelia* Zone. The glabellar morphology of *Parabouleia* is less advanced than in *Bouleia*, and was cited (Eldredge, 1972a) as intermediate between *Bouleia* and other more "conventional" calmoniids. The eye morphology was unknown on the holotype; the present study has revealed, astonishingly, that this otherwise primitive (with respect to *Bouleia*) genus has the entire ocular-palpebral complex reduced to a slender spike apparently devoid of lenses.

It is thus difficult to derive *Bouleia dagincourti* directly from *Parabouleia calmonensis*. Virtually all other *Scaphiocoelia* Zone species possess anatomical specializations that likewise prohibit hypotheses of an ancestral-descendant relationship between them and their younger relatives. These peculiarities are the very features which also allow accurate segregation of species within the *Scaphiocoelia* Zone. In addition to the "eye stalk" of *Parabouleia,* the main anatomical differences among *Scaphiocoelia* Zone species involve *peripheral* anatomical features, especially the great diversity in structure of the genal angle and spine, contour of the lateral cephalic border, relative convexity of the entire cephalon, morphology of the anterior cephalic border at the midline, and the course of the anterior branch of the facial suture. Also the axial and especially the distal extremities of the thoracic segments, and the shape and other aspects of pygidial morphology, serve to distinguish all the species described below. So, in some aspects these taxa are as well differentiated morphologically as are the younger, better known calmoniid taxa.

Yet, as would be expected in the oldest (known) segment of a radiation, many of the *Scaphiocoelia* Zone calmoniids are less well differentiated from each other, presumably because of the retention of relatively more numerous primitive calmoniid character states in these older taxa (see Stitt, 1971, for a similar claim for Cambrian trilobites). These characters are especially rampant in the axial region of the cephalon, but also include eye placement, size, and palpebral and visual surface morphology, as well as a host of "ornamental" features and characteristics of the genae. Although most, if not entirely all, of the *Scaphiocoelia* Zone calmoniids are typical "Phacopina" (*sensu Treatise*) in

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internal mold. Holotype, NMNH 245616. See figure 13A, B. H. *Deltacephalaspis (Prestalia) tumida.* AIS developed as faint non-pustulose depressions on external surface of cuticle. Latex cast of holotype, NMNH 245617 (latex cast AMNH 36695). See figure 15C–E. I. *Bainella (Belenops) insolita.* AIS developed as depressions on internal mold. NMNH 245612. See figure 8A–D. J. *Bainella (Bainella)* "*acacia.*" AIS developed as pustule-free depressions on external surface of cuticle in posterior portion of anterior glabellar lobe, and as pads on the internal mold of anterior portion of anterior glabellar lobe. NYSM 5628, Pebble Island, Falkland Islands. See figure 4. K. *Schizostylus (Curuyella) granulata.* AIS developed as pads (and associated ridges) on internal mold. Holotype, NMNH 245620. See figure 17A–C. L. *Schizostylus (Schizostylus)* sp. AIS developed as "dark markings" ("dunkler stellen"—see Eldredge, 1971, Appendix A, p. 66) in cast of cuticle. AMNH Smith Collection, Chacoma, Bolivia. M. *Kozlowskiaspis (Romanops) borealis.* AIS developed as depressions within a groundmass of granules on external cuticular surface. Holotype, AMNH 36715. See figure 30A–C. N. *Kozlowskiaspis (Romanops) australis.* AIS faintly developed on internal mold. Holotype, NMNH 245630. See figure 32B, C. O. *Kozlowskiaspis (Kozlowskiaspis) superna.* AIS developed as pads on internal mold. NMNH 5867, Padilla, Bolivia. P. *Tarijactinoides tikanensis.* AIS developed as depressions on external surface of cast of cuticle. Paratype, AMNH 36751. See figure 37E, F. Q. *Malvinella haugi.* AIS developed as dark markings on external surface of cast of cuticle. AMNH coll., *Metacryphaeus cornutus* Zone, Pujravi, Bolivia.

the apparent non-functioning of the facial sutures at ecdysis, so that cranidia alone are infrequently encountered, it is in cranidial features that confusion sets in when identifying elements of the fauna. The relative sizes of the glabellar lobes, and degree of emplacement and direction of the glabellar furrows are especially so similar in many of these species that identification becomes difficult or even impossible when only the axial cephalic region is preserved on a given specimen. Many instances of confusion are cited in the discussions following each diagnosis of the individual taxa in an attempt to clarify the telling criteria that do allow accurate assignment. Suffice it to say, as an example, that cranidia of *Deltacephalaspis* (*Deltacephalaspis*) spp. are very similar indeed to those of *Kozlowskiaspis* (*Romanops*), new subgenus, which in turn look very much like both *Deltacephalaspis* (*Prestalia*), new subgenus and *Phacopina convexa,* new species. In fact, within the *Scaphiocoelia* Zone, it is only in *Tarijactinoides jarcasensis* Suárez Soruco and *Parabouleia calmonensis* that we find any significant deviation from this typical early calmoniid glabellar plan, which can be summarized as: moderately to lightly incised ("pencil line" in most cases) axial and glabellar furrows devoid of microgranulation, which otherwise typically covers the lobes; glabellar furrow 3p generally straight, and *not* in communication with the axial furrow; glabellar furrows 2p lightly incised, short, nearly directly transverse, and also not communicating with axial furrow; glabellar furrows 1p more deeply incised (always produced viscerally into apodemes), transverse, in communication with the axial furrows, but not confluent at the midline (i.e., no intercalating ring developed). This pattern is not very different from typical acastid morphology (Acastinae and Acastavinae) and is present in its typical form in the Silurian Bolivian genus described below as *Andinacaste.* We consider this morphology primitive for Calmoniidae; taxa in which the furrows are effaced or nearly so [e.g., *Bainella* (*Belenops*), new subgenus; *Phacopina* from the *Scaphiocoelia* Zone] are to be

considered derived, as are also those taxa where the axial and glabellar furrows are more deeply incised [e.g., *Schizostylus* (*Curuyella*), new subgenus, *Kozlowskiaspis* (*Romanops*), and *Tarijactinoides* from the *Scaphiocoelia* Zone].

The close similarity of the cranidia of so many of these taxa (as well as those from other Malvino-Kaffric sections and some taxa in younger units of the Bolivian section) immediately invites classifying these relatively older taxa into a discrete subdivision of the Calmoniidae. But this cranidial pattern is undoubtedly primitive for Calmoniidae in general (and thus perhaps a shared-derived feature uniting *all* calmoniids) but, as a primitive feature within Calmoniidae as a whole, therefore valueless for evaluating intergeneric relationships within the group as a whole. In point of fact there are abundant characters, which appear to be derived, which actually do serve to link many of these similar taxa with *Calmonia* itself. Thus *Bainella, Deltacephalaspis, Paracalmonia, Calmonia,* and perhaps *Schizostylus* appear closely related and to form a distinct division of the Calmoniidae. But *Kozlowskiaspis* (*Romanops*), as well as *Kozlowskiaspis* (*Koslowskiaspis*), while retaining a large array of features very similar to this core *Calmonia*-related group of taxa [especially similar to *D.* (*Deltacephalaspis*)], seems more closely related (as the plesiomophic sister-group) to another large division of the Calmoniidae centering around *Metacryphaeus*—a group which also includes *Malvinella* Wolfart, *Parabouleia, Bouleia,* probably *Typhloniscus* Salter, and several other as yet undescribed genera. All these issues are to be discussed at greater length in the future study of intergeneric relationships, but are broached here to illustrate the necessity, and possibility, of recognizing *vertical* relationships of the *Scaphiocoelia* Zone taxa. Their shared similarities are often due to primitive retentions, which can mask the more interesting and accurate relationships that the melange of *Scaphiocoelia* Zone taxa have with the more clear-cut and better differentiated taxa in younger sediments. Finally, we note that

the conservatism of glabellar characteristics, while the structural variety of other anatomical regions is very great, agrees well with the bulk of historical experience with the majority of other trilobite groups.

OTHER ASPECTS OF CALMONIID MORPHOLOGY

Many calmoniid taxa, especially those from the *Scaphiocoelia* Zone, have the anterior branch of the facial suture transecting or "cutting across" the anterolateral corner of the anterior glabellar lobe. Useful as a diagnostic feature, this morphological peculiarity raises several questions of homology and phylogenetic relationships. Most of the genera listed above as especially close relatives of *Calmonia* [except *Bainella* (*Bainella*)] show this feature to some degree, while more advanced groups appear to have lost it (i.e., the *Metacryphaeus* group, as well as the *Probolops* group, which includes *Tarijactinoides*, *Probolops* Delo itself, probably *Cryphaeoides* Delo, and several other as yet undescribed genera). Thus this feature appears to have some phylogenetic significance. However, some Ordovician Dalmanitacea (e.g., species of *Kloucekia* from Spain—personal observ., but see also Hammann, 1974, for further examples) also develop this feature. Although we have continued to use this as a diagnostic feature, it should be emphasized that its utility as a source of phylogenetic inference is complicated by the fact that its development depends upon two factors which vary independently. The course of the anterior branch of the facial suture is virtually identical in all calmoniids (except, of course, at the midline). From the anterior margin of the visual surface, the suture runs nearly straight forward, only slightly inclined anteroproximally, becoming reflected mesially only upon reaching the cephalic border furrow (if defined) or the anterior cephalic border itself. Two conditions are necessary for the branch to transect the anterolateral corner of the anterior glabellar lobe: (1) the eye must be set in close to the axial furrow, such that the

anterior margin actually abuts the axial furrow, and (2) the axial furrows must diverge sharply anterior to the eye, or, in other words, the anterior glabellar lobe must be expanded anterolaterally. The "*Calmonia* group" [as listed above, but excluding *Bainella* (*Bainella*)], as well as *Phacopina, Schizostylus,* and *Kozlowskiaspis* (as these taxa are emended below) all have rather small eyes set in close to the axial furrows, and varying degrees of anterolateral expansion of the glabella. Thus in all of these taxa, to varying degrees, the facial suture transects the anterolateral corner of the anterior glabellar lobe. In *Acastoides* and *Andinacaste,* the eyes are similarly located, but the axial furrows do not diverge appreciably anterior to the eye, so the facial suture remains entirely distal to the anterior glabellar lobe. Nor is the glabella transected in such disparate genera as *Bainella, Metacryphaeus, Bouleia,* and *Cryphaeoides,* though in each of these the glabella is expanded laterally, in some cases to a very great extent (e.g., *Bouleia*). However, unlike *Acastoides* and *Andinacaste,* the eyes in these genera are removed from the immediate proximity of the axial furrows, and, running directly anteriorly, the facial sutures simply do not encounter the anterior glabellar lobe. Thus mere presence or absence of facial suture transection of the anterior glabellar lobe is of uncertain phylogenetic significance.

Transection of the glabella does more than create confusion in phylogenetic analysis. It raises an important question of homology, for in a group otherwise considered to be monophyletic, how precisely are we to define the anterior glabellar lobe? The conventional definition cites axial and preglabellar or anterior border furrows (or simply, the anterior border) as the lateral and anterior bounding features. This is not entirely satisfactory because (1) the course of the facial suture is conservative and invariant in most calmoniids; (2) the auxiliary impression system is always proximal to the suture no matter how deeply the suture appears to encroach over the glabella, and (3) less importantly, in some taxa, the axial furrow

is effaced anterior to the eye, so there is no clear lateral topological definition between the glabella and the anterior region of the librigena. From these considerations we are inclined to homologize the anterior glabellar lobe as that area proximal to the anterior branch of the facial suture, realizing that functionally, external expression of the anterior glabellar lobe would include a librigenal section functioning (e.g., in burrowing) as an anterior glabellar lobe. However, viscerally (as judged by the auxiliary impression system), only that portion of the lobe proximal to the facial suture would be the anterior glabellar lobe, in functional terms. This view is thus partially based on the conclusion that the visceral morphology is the more important in defining the limits of the anterior glabellar lobe.

Yet clearly this view is also unsatisfactory, for two reasons: in the remainder of the calmoniids, plus nearly all the rest of the suborder Phacopina (*sensu Treatise*, Harrington et al., 1959) we would be forced to consider the axial furrow and portions of the librigena proximal to the facial suture (i.e., in those cases where such a condition exists) as a part of the anterior glabellar lobe. This is totally unsatisfactory, both for the sake of maintaining historical usage and because it is biologically implausible. Similarly, even in cases where the facial suture does transect the glabella (e.g., *Schizostylus*), the facial suture frequently *leaves* the "glabella," transects the border furrow, and runs along the anterior border, frequently along the median anterior border process (when present). We are left in a quandary as far as precise definition of the anterior glabellar lobe, suitable for all Phacopina, or even all Calmoniidae, is concerned. For the remainder of this paper, we use "anterior glabellar lobe" in its conventional sense, even when transected by the facial suture or where precise furrowed boundaries are lacking at the anterolateral margins. But we emphasize that in cases where the facial suture is described as "cutting across" or "transecting" the anterolateral corner of the anterior glabellar lobe, the course of the facial suture itself has not

changed so much as have position of the eye *or* the course of the axial furrow anterior to the eye.

Several other descriptive morphological terms are used throughout the text that are either new or relatively unfamiliar. "Standard orientation" is used, particularly in describing the lateral aspect of the cephalon, following the usage of Eldredge (1972b, p. 61; more explicitly defined in Eldredge, 1973, p. 295). Based on Clarkson's (1966) study of the functional morphology of *Eophacops musheni,* the cephalon is oriented with the dorsal margins of the two visual surfaces placed in the same horizontal plane. We use the expression "shouldering" or "shouldered" to refer to the pronounced change of inflection of the lateral cephalic border. Only in a few calmoniids is the lateral border developed as a smooth curve (e.g., *Vogesina* Wolfart)�‛. In the majority of calmoniid genera, the anterior border is rather gently inclined posterodistally anterior to the glabella; at some point (variable intergenerically), but usually in the vicinity of the anterior region of the eye, the lateral border is sharply reflected posteriorly, creating the distinctive prominence we have called the "shoulder." See figure 15C–E, for the typical development of the shoulder in *D. (Prestalia) tumida.*

"Dishing" or "dished" refers to the concave surface of the librigena developed especially directly distal to the eye and near the lateral border furrow, and developed (e.g., in *Deltacephalaspis*—see fig. 11 for examples) especially in those taxa with a broad librigena, where the eye socle (Shaw and Ormiston, 1964) and portion of librigena adjacent to the eye are steeply sloping, with the slope becoming progressively less steep distally, and bounded by a prominent lateral border. We have used the expression "anterior ocular ridge" for the prominent ridge running down the anterior surface of the ocular prominence (i.e., if the eye is elevated on a distinct conical prominence of the gena—e.g., *Bainella*; see figs. 2I, 3A, B) on or adjacent to which the facial suture is located. The expression "anterior glabellar

ridge" (or furrow) refers to the structure, also associated with the facial suture, which runs across the glabella (in taxa in which the facial suture transects the glabella only). It is always proximal to the anterior border furrow and ridge and may be continuous with the anterior ocular ridge (see fig. 2E and Q). Finally, we have used the word "dimple" to refer to relatively large, usually rather shallow, depressions of variable shape, seen on

both internal and external molds, on both the librigena and fixigena. Such depressions are generally devoid of other "ornamentation" (e.g., spines, tubercles, or microgranulation) and, of course, are well known in many other Phacopina, Cheirurina, and other trilobite taxa. All other morphological terminology conforms to *Treatise* (Harrington et al., 1959) usage, except where explicitly noted in the text.

SYSTEMATIC PALEONTOLOGY

FAMILY CALMONIIDAE DELO, 1935

Bainella Rennie, 1930

Bainella Rennie, 1930, p. 344; Struve, 1959, p. O484; Baldis, 1967, p. 791.
Paradalmanites Pillet, 1954, p. 828.

TYPE SPECIES: *Bainella bokkeveldensis* Rennie, 1930, p. 349, pl. 10, figs. 1–4.

EMENDED DIAGNOSIS: Medium- to large-sized calmoniids with moderate to relatively great degree of cephalic arching. Shallow axial furrow pit present. Eyes raised on high palpebral prominences; anterior ocular and anterior glabellar ridges present. Occipital spine generally present; genal spines large, directed posterodistally. Axial rings of thorax constricted sagitally and produced into large axial spines. Pygidium micropygous, subtriangular to posteriorly rounded. Axis bluntly rounded posteriorly, not reaching posterior margin. Pygidial border sometimes with small anterolateral lappets; posterior border bearing terminal spine.

REVISED DESCRIPTION: Species of the genus *Bainella* are medium- to large-sized Calmoniidae with a moderate to relatively great degree of cephalic arching. The glabella is pentagonal to semicircular, and is bounded anteriorly by an anterior border ridge distal to the anterior section of the facial suture. The axial furrows are broad, shallow, straight, and only slightly divergent, and bear a shallow axial furrow pit which is devoid of ornament. Glabellar furrows 3p are shallow, inclined anterodistally, and are not

confluent with the axial furrows. Glabellar furrows 2p are shallow, transverse, and are not confluent with the axial furrows. Glabellar lobes 2p and 3p are thus coalesced distally. Glabellar furrows 1p are transverse, bear linear apodemal pits, and are variably confluent with the axial furrows. The occipital furrow is transverse, bears linear apodemal pits, and is deflected slightly anteriorly at the midline. The entire axial region of the glabella comprises a single smoothly curved surface.

The occipital ring generally bears a large median spine directed posterodorsally. The posterior border furrow is broad, transverse, and confluent with the shallow lateral border furrow. The posterior border is thick, becomes reflected posteriorly in the distal region, and is produced into a large, posterodistally directed genal spine. An accessory spine is variably present at the posterior edge of the juncture of the facial suture with the lateral cephalic margin. The lateral border is smoothly curved anteroproximally; it becomes reflected anteriorly anterior to the eyes, producing a shouldered effect.

The eye is raised on a high palpebral prominence, and is situated opposite glabellar lobes 2p and 3p, well anterior to the posterior border furrow. The visual surface is small, with from 20–23 dorsoventral files; it bears from 102–111 lenses, with as many as six subequally sized lenses in the median dorsoventral files.

The anterior branch of the facial suture is bounded proximally by the anterior ocular

ridge, which is confluent with the anterior glabellar ridge and furrow. The cephalic doublure is vertically directed posterolaterally; it divides anteriorly into a flat or concave median triangular area, and an anterolateral, dorsally reflected region (bilaterally) which becomes confluent with the anterior border dorsally.

The hypostoma is unknown. The auxiliary impression system is generally weakly developed, variably expressed as pits externally, and as scars and pads internally, of the acastid form of the triangular *dalmanitid* pattern. The posterior median impression is generally present on the external surface of the cuticle. Cuticular ornament consisting of small tubercles is lightly to densely scattered over the cephalic surface; larger tubercles are present in some species. The genae bear pronounced dimpling over the entire surface.

The thorax consists of 11 segments bearing pleural spines. The axial rings are constricted sagittally, and are produced into large axial spines directed posterodorsally. The pygidium is micropygous, and subtriangular to posteriorly rounded. The pygidial axis is defined laterally by shallow axial furrows and bears, insofar as is known, approximately eight axial rings, sometimes with axial nodes on the anterior rings. Eight or nine pleura are present. The axis is bluntly rounded posteriorly and does not reach the posterior border. Small marginal lappets are variably developed anterolaterally; the posterior border bears a terminal spine.

REMARKS: The elevation of the eyes onto palpebral prominences, the presence of an anterior ocular ridge and its extension, the anterior glabellar ridge, and the sagittal constriction of the thoracic axial rings are the features which best serve simultaneously to tie all referred species together within this genus, and to differentiate *Bainella* from all other Calmoniidae. (*Tarijactinoides* and *Probolops* resemble *Bainella* in having the thoracic axial rings sagittally constricted and produced into large spines.) We regard these characters as synapomorphies for the included species, thus autapomorphic for the genus as a whole. These morphological features, as well as others, are described and discussed

in further detail under *Bainella* (*Belenops*) *insolita* (Wolfart) below. Referred species and their distributions are given under the subgenera below.

Bainella (*Bainella*) Rennie, 1930

EMENDED DIAGNOSIS: Species of *Bainella* with only moderate cephalic arching and moderate inflation of the anterior glabellar lobe. Anterior glabellar lobe distinctly pentagonal, produced into sharp point anteromedially. Facial suture not, or only slightly, transecting anterolateral corners of anterior glabellar lobe. Glabellar furrow 3p usually straight (slightly sinuous in *B. sanjuanina* Baldis). Glabellar furrows 1p not, or just barely, confluent with axial furrows. Anterior region of cephalic doublure only slightly reflected dorsally, confluent with dorsal surface. Thorax and pygidium as for genus.

REFERRED SPECIES: We refer the following species to *Bainella* (*Bainella*): *Bainella bokkeveldensis* Rennie (type species by original designation) from the Bokkeveld beds, South Africa; *B.* "*acacia*" (non Schwartz, 1906; *sensu* J. M. Clarke, 1913a), Pebble Island, Falkland (=Malvin) Islands; and, with some question, *Bainella sanjuanina* Baldis from the Talacasto Formation of the Cordilleran sequence of Argentina.

This emended diagnosis is to be considered provisional pending a thorough restudy of included species; we have based this diagnosis on literature evaluation plus the following limited materials: *B. bokkeveldensis*—one internal cephalic cast (genae damaged) and an internal cast of a thorax and articulated pygidium, Bokkeveld beds, Gamka Poort, South Africa. NMNH collections; see figure 3. *B.* "*acacia*" (*sensu* Clarke, 1913a): one generally well-preserved external cast of a cephalon, Pebble Island, West Falkland Islands. NYSM collections; see figures 4, 5. In addition we have examined the following material figured as *Dalmanites* (*Mesembria*) *acacia* described and figured by Clarke (1913a, 1913b), all from Pebble Island: NYSM 9715 (=13358/1) internal and external (artificial) casts of the right and median area of a cephalon; NYSM 9716
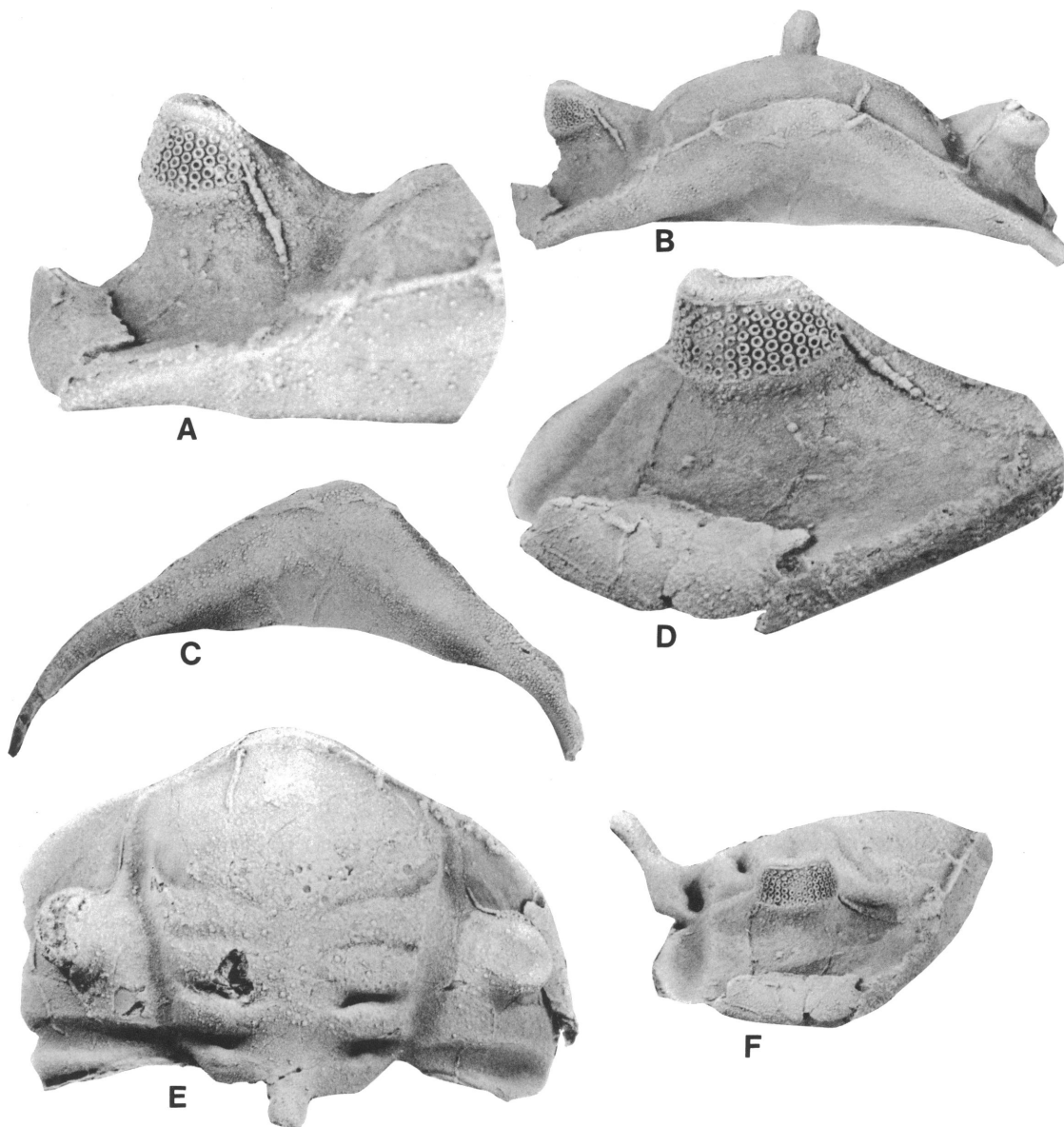
FIG. 3. *Bainella (Bainella) bokkeveldensis* Bokkeveld beds, Gamka Poort, South Africa. NMNH 245610. Internal mold of cephalon. A. Anterolateral view of right eye, showing distinct anterior ocular ridge proximal to trace of facial suture. ×4. B. Frontal view, ×2. C. Ventral view, ×2. D. Detailed view of right visual surface, ×4. E. Dorsal view, ×2. F. Right lateral view in standard orientation. ×2.

(=13358/2), an external cast (artificial) of a nearly complete cephalon with damaged eyes; NYSM 9717 (=13358/3), portion of thorax sectioned to show thoracic axial spines; and NYSM 9718 (=13358/4), cast of interior of right half of a cephalon with damaged eye.

Possibly other species from South Africa
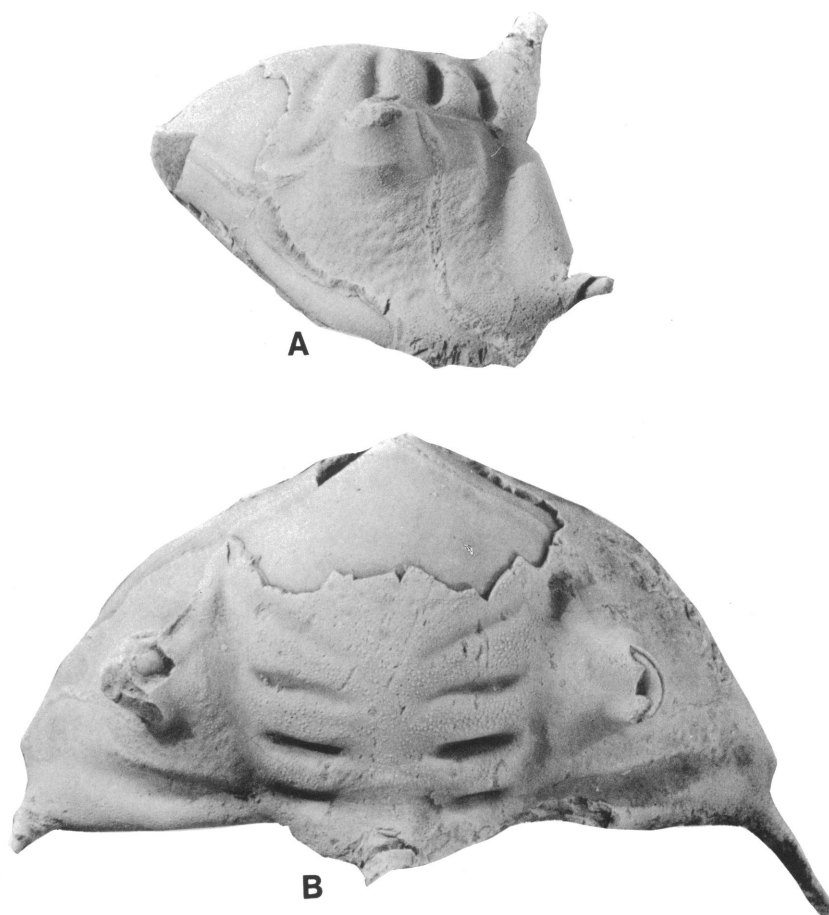
FIG. 4. *Bainella (Bainella)* "*acacia.*" Pebble Island, Falkland Islands. NYSM 5628. Specimen with cuticle nearly intact. A. Left lateral view of cephalon, ×2. B. Dorsal view of cephalon, ×2.

may prove referable to *Bainella (Bainella)* [see Rennie, 1930, for an extensive discussion of the problems of identification and synonymy of the various taxa described by Salter (1856), Lake (1904), and Reed (1925)]. Rennie (1930, p. 345) also referred *Dalmanites (Anchiopella) baini* Reed, 1925 from the Bokkeveld beds, to *Bainella*; we regard that allocation as provisional. Struve (1959) with question assigned *Phacops ocellus* Lake (another species from South Africa) to *Bainella*; this species appears to lack the palpebral prominences and axial and genal spines of true *Bainella,* hence appears more

closely related to genera such as *Acastoides* Delo or *Pennaia* Clarke.

The species of *Bainella (Bainella)* from Pebble Island, West Falkland Islands, was identified as *Dalmanites (Mesembria) acacia,* a species described by Schwartz (1906) from the Bokkeveld beds of South Africa; we here follow Rennie (1930, p. 348–349), who found this species to be unrecognizable in South Africa, and who therefore restricted the name to the type specimen. We note that Struve (1959) nonetheless seems to have accepted *Phacops acacia* Schwartz as a valid South African species of *Bainella*. There is
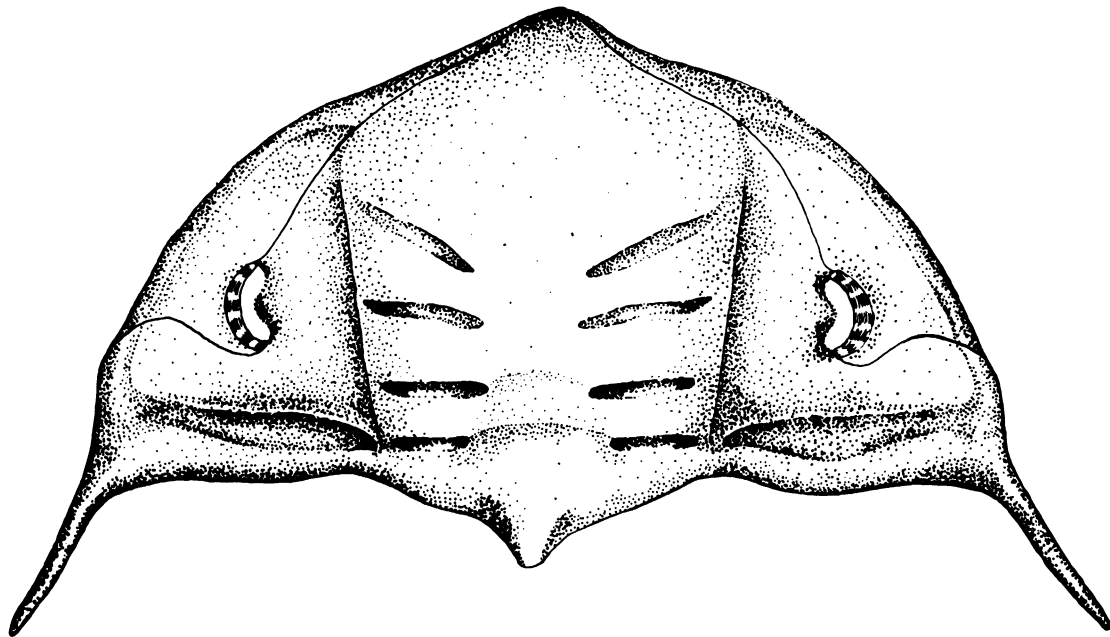
FIG. 5. Reconstruction of cephalon of Bainella (Bainella) "acacia," based on specimen illustrated in figure 4.

no doubt, in any case, that the name "acacia" should not be applied to the Falkland Island undoubted species of Bainella (Bainella). We also concur with Richter that Clarke's taxon name "Mesembria" introduced as a catch-all name for a variety of austral "dalmanitids," "never attained nomenclatorial status" (Richter, 1959, p. O525), hence its absence from our synonymy list for Bainella.

Baldis (1967, p. 791) has pointed out that Bainella (?Bainella) sanjuanina may be conspecific with B. (Bainella) acacia sensu Clarke. We doubt this, as in B. sanjuanina, glabellar furrows 3p are rather sinuous [recalling Bainella (Belenops), new subgenus diagnosed below], glabellar furrows 2p and 3p are rather deeply emplaced (unique for the genus), and the cuticular surface is more coarsely tuberculate than other species definitely attributable to Bainella (Bainella). While Baldis was entirely correct, in our opinion, in referring the species sanjuanina to Bainella, the characters enumerated

above cause us to refer this species to Bainella (Bainella) with some doubt. Baldis (1967, p. 791) furthermore referred to "Bainella (?) ocellus (Lake) (1906) [sic] of Bolivia." We can find no reference to such a taxon in Lake's 1906 paper on Bolivian trilobites.

BAINELLA (BELENOPS), NEW SUBGENUS

TYPE SPECIES: Bainella (Belenops) insolita (Wolfart).

ETYMOLOGY: The name Belenops is derived from the city and environs of Belén, Bolivia, source of many of the finest specimens of the Bolivian Devonian fauna, including B. insolita, and from "ops," the Ancient Greek word for "eye," in allusion to the unusual conformation of the eye complex.

DIAGNOSIS: Species of Bainella with anterior cephalic margin distinctly rounded, and anterior glabellar lobe greatly inflated. Anterior branch of facial suture transecting a relatively small portion of the anterolateral
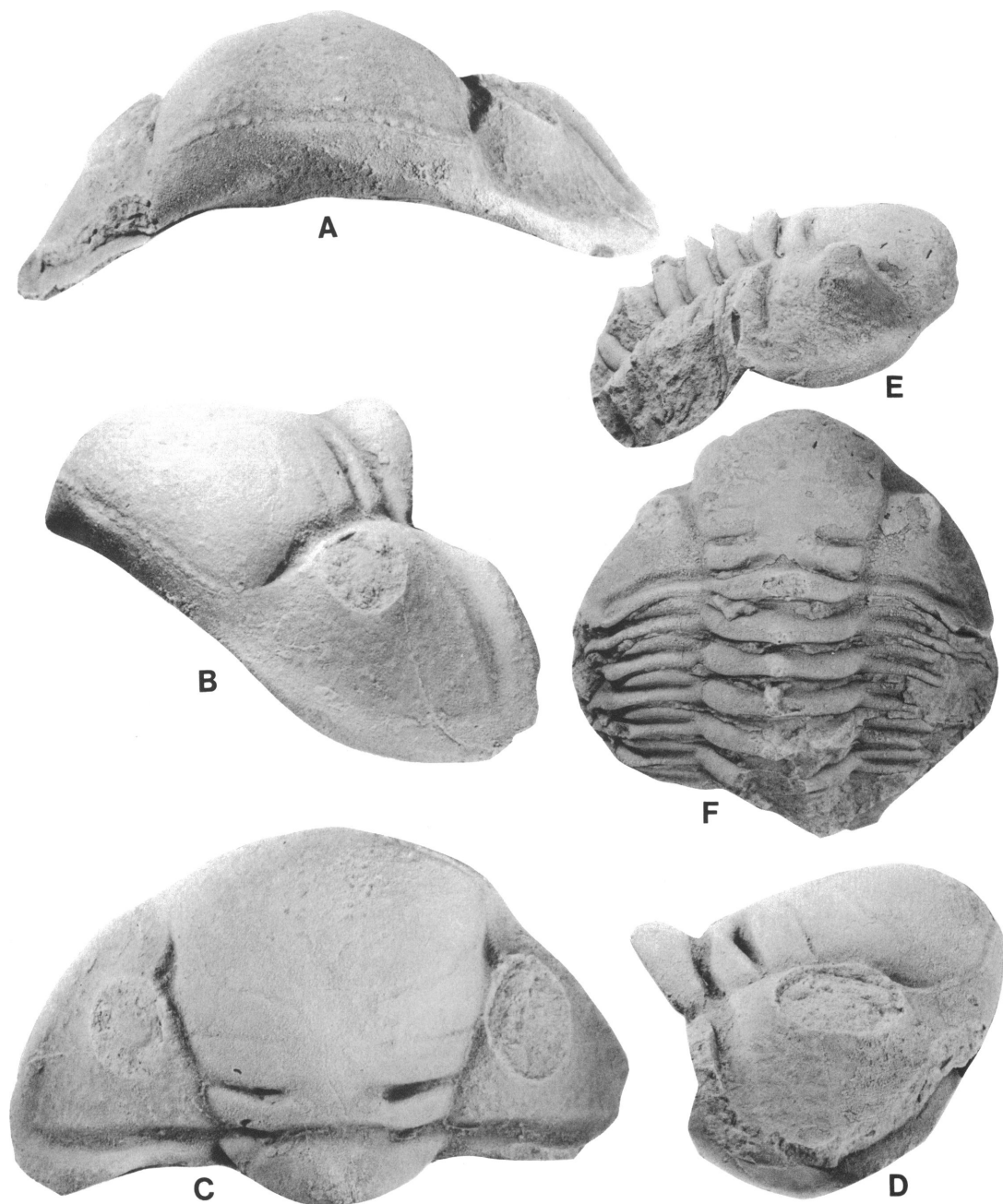
FIG. 6. *Bainella* (*Belenops*) *insolita*. A–D. NMNH 245611. *Scaphiocoelia* Zone, Lower Belén Fm., Belén, Bolivia. Frontal, left anterolateral, dorsal, and right lateral views of internal mold of cephalon, ×2. E, F. Same horizon, Tikani (=Estacion Bombeo Sica Sica), AMNH 36683 (Smith Coll.). Right lateral and dorsal view of internal mold of cephalon and anterior five thoracic segments, ×1.
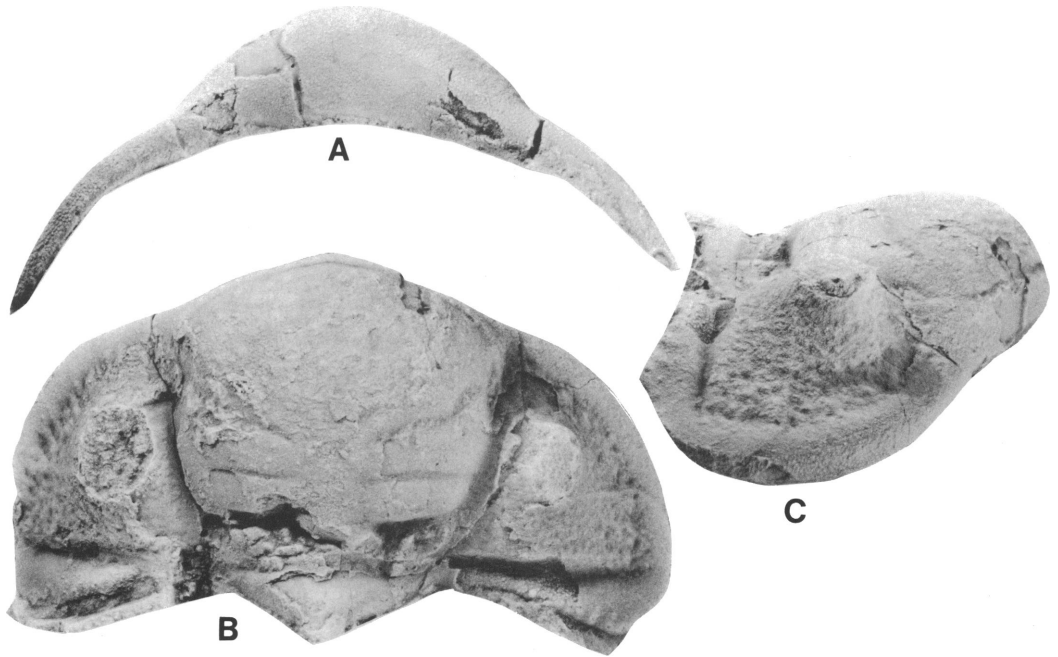
FIG. 7. *Bainella (Belenops) insolita*. A–C. *Scaphiocoelia* Zone, Lower Belén Fm., Tikani, Bolivia. AMNH 36684 (Braniša Coll.). Ventral, dorsal, and right lateral views of internal mold of cephalon, ×2.

corner of anterior glabellar lobe. Glabellar furrows 3p sinuous; 1p glabellar furrows wholly confluent with axial furrows. Antero-lateral region of cephalic doublure sharply recurved dorsally, confluent with dorsal cephalic surface. Occipital spine generally present, occasionally absent in some populations. Thorax and pygidium as for genus.

REMARKS: *Bainella (Belenops)* is erected for *B. (Belenops) insolita* (Wolfart) from the *Scaphiocoelia* Zone of Bolivia, and for *B. (Belenops) gamkaensis* (Rennie) from the Bokkeveld beds of South Africa. Rennie based *gamkaensis* on a single cephalon, referring it to *Bainella* Rennie, and noting its more conspicuous differences from the type species, *Bainella bokkeveldensis*. The much greater inflation and round shape of the anterior glabellar lobe, and the fact that the anterior branch of the facial suture transects the glabella to a much greater extent than in any known species of *Bainella (Bainella)*, serve to unite these two species and distinguish them from *B. (Bainella)*.

Bainella (Belenops) insolita (Wolfart)
Figures 2I; 6–9

Acastoides insolitus Wolfart, 1968, p. 113–115, pl. 21, figs. 2–3.

REVISED DESCRIPTION: The cephalon of this species is roughly semicircular in dorsal view in standard orientation. The entire exoskeleton is highly arched. In anterior view there is a broad, prodigious anterior (cephalic) arch, and the thorax and posterior marginal profile of the pygidium are likewise quite convex. Posteriorly, the arching becomes progressively less pronounced, and the pleural field of the pygidium is only slightly inclined, its marginal border lying everywhere in the same horizontal plane.

The axial furrows, lightly impressed on the external cuticular surface, and somewhat deeper on the internal cast, diverge at an angle of from 25° to 30° between glabellar furrows 1p and the point opposite the middle of the distal edge of glabellar lobe 3p (opposite the anterior edge of the eye). Anterior to this
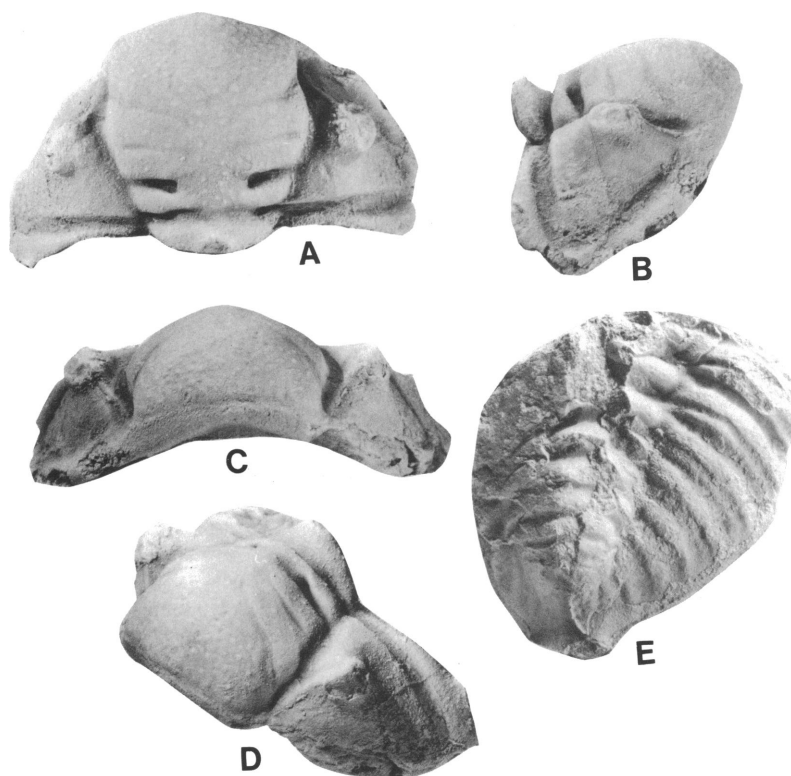
FIG. 8. *Bainella* (*Belenops*) *insolita*. A–D. *Scaphiocoelia* Zone, Gamoneda Fm., Curuyo, Bolivia. Dorsal, right lateral, frontal, and oblique left lateral views of internal mold of cephalon. NMNH 245612, ×2. E. *Scaphiocoelia* Zone, Lower Belén Fm., Colchani, Bolivia. Dorsal view of internal mold of partial pygidium, AMNH 36685 (Smith Coll.), ×2.

point, the axial furrows are deflected antero-ventrally into a shallow axial furrow pit (or *fossula* in Harrington et al., 1959). In smaller specimens particularly, the axial furrow pit comprises most of the area of the axial furrow anterior to the eye, and runs directly anteriorly. The distal wall of the axial furrow pit is formed by the anterior ocular ridge which runs anteroproximally, crossing the axial furrow, and becomes confluent with the anterior glabellar ridge. Anterior to the point where the anterior ocular ridge traverses the axial furrow, the axial furrow becomes shallower and particularly in larger specimens deflected more distally; thus, the proximad deflection of the axial furrow caused by the axial furrow pit delimits a slight "bulge" in the axial furrow opposite glabellar lobes 2p

and 3p. The axial furrow pit is invariably shallow and linear, never developed into a true apodemal structure (as compared with *Vogesina*); shallower on the external cuticular surface than on internal molds, the axial furrow pit is a thickening and ventral extension of the cuticle.

The anterior cephalic margin, in dorsal view in standard orientation, is formed by the anterior glabellar ridge and, medially, by the anterior border itself. The anterior margin is generally smoothly rounded, but may be slightly pointed in some specimens. Distally, the anterior border is reflected ventrally, confluent with the anterior doublure and not visible in dorsal view. In lateral view, glabellar lobes 1p, 2p, 3p, as well as the posterior half of the anterior glabellar
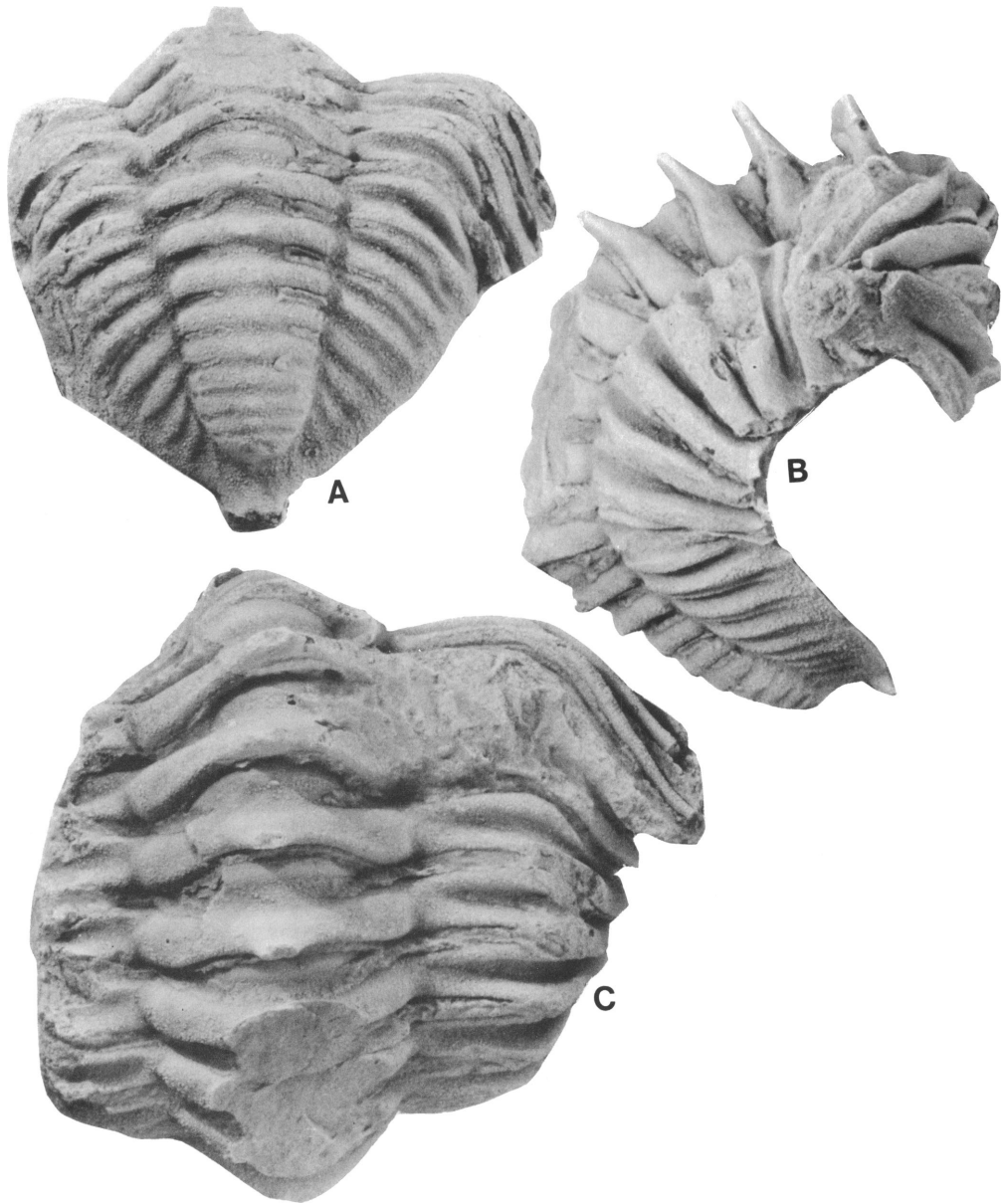
FIG. 9. *Bainella (Belenops) insolita*. A–C. *Scaphiocoelia* Zone, Lower Belén Fm., Tikani, Bolivia. Internal mold of thorax and pygidium, AMNH 36686 (Smith Coll.), ×2. A. Dorsal view of pygidium. B. Right lateral view of entire specimen. C. Dorsal view of middle region of thorax.

lobe, are gently inclined posteroventrally at an angle of roughly 10° from the horizontal. The anterior half of the anterior glabellar lobe becomes smoothly curved anteroven-

trally, becoming nearly vertical at the anterior border ridge. The anterior glabellar lobe is thus rather highly inflated for the family.

The anterior glabellar lobe is roughly

ovoid and is bounded anteriorly by the anterior border ridge; however, there is little break in slope between the anteriormost region of the anterior glabellar lobe, the anterior glabellar furrow, the anterior glabellar ridge, the facial suture and the anterior border ridge itself, so that all these structures lie in one nearly continuously curved surface. The facial suture transects the extreme anterolateral corners of the anterior glabellar lobe, distal to which the anterior glabellar lobe merges imperceptibly with the anterior border. The axial furrows are continuous with the shallow lateral border furrow, but an anterior border furrow is entirely lacking.

The posterior median impression is weakly developed as a thin, longitudinally elongate pad just anterior to the posterior margin of the anterior glabellar lobe. The auxiliary impression system is developed as pads on the visceral surface, and has been occasionally observed as unornamented (i.e., by granulation) pits on the external cuticular surface. The pattern is illustrated in fig. 2I, and is of typical acastid aspect.

Glabellar furrows 3p are relatively narrow and lightly impressed on the dorsal cuticular surface. The course of the 3p furrow is sinuous, forming two distinct but continuous moieties. The proximal moiety arises near the midline (the furrows are not conjoined medially) and curves anterodistally with its convexity oriented anteriorly. The distal moiety, more deeply impressed on internal molds (though not developed as apodemes) curves anterodistally and is concave anteriorly. The 3p glabellar furrows do not communicate with the axial furrows, although a shallow indentation, slightly below the glabellar surface, may run from the distal extremity of the 3p furrow to the axial furrow. The distal end of glabellar furrow 3p terminates just opposite the midpoint of the axial furrow pit.

Glabellar furrows 2p are developed as short transverse shallow grooves, not developed as apodemal projections ventrally. They do not reach the axial furrow; thus glabellar lobes 2p and 3p are distally coalesced. The wedge-shaped glabellar furrows 1p arise near the midline and run transversely, and

are confluent with the axial furrows. Proximally they are wide and shallow; midway along their course, they are deflected sharply ventrally into stout apodemal projections. They then become shallower and narrower near the axial furrows. Glabellar lobes 1p are wedge-shaped and are widest distally. The occipital furrow, broad and shallow on the external surface, is broad and deep on the internal mold, and communicates with the axial furrow. A pair of apodemal pits is developed just proximal to the axial furrows; the occipital furrow becomes shallower and reflected anteriorly at the midline. The occipital ring is arched well above the level of the posterior region of the glabella and is longest (sagittally—"sag.") at the midline. A stout median spine may be present, directed posterodorsally, arising from the posterior section of the occipital ring. Where no spine is present, the median section of the occipital ring slopes posterodorsally up from the occipital furrow and flattens out posteriorly, so that its highest point occurs at the posterior margin. (See below under Geographic Variation.)

The large genae are nearly horizontal posteroproximally, becoming moderately steeply reflected ventrally laterally. The thin posterior border is straight (transversely—"tr.") proximally, but widens (sag.) behind the eye so that the posterior cephalic border is deflected well posterior to the posterior margin of the occipital ring in plan view; distally the posterior border is reflected ventrally and produced into a smoothly curved genal angle which bears a short genal spine projecting at an exsagittal angle of roughly 40°, and lying in the same sloping plane as the distal area of the gena.

The posterior border furrow (narrow and lightly impressed externally; broader and deeper on the internal mold) is transverse, and reflected into a shallow genal border furrow laterally. The posterior border is likewise reflected into a lateral genal border ridge. The area of the gena distal to the eye is rather steeply sloped and somewhat concave, producing a "dished" effect.

The eye is situated on a high conical projection ("palpebral prominence") formed of

nearly vertical walls anteriorly, laterally and posteriorly, that arises smoothly from the genal surface. The eyes are small, being short in both length [Large Eye Index .285 according to Wolfart (1968, p. 114); we record a range of .282 in smaller specimens, decreasing to .218 in very large specimens] and in height. The palpebral lobe is horizontal and kidney-shaped, and is rather simple in that no discrete furrows are developed between the palpebral lobe proper and the visual surface, or between the palpebral lobe and palpebral area. The palpebral lobe bears muscle scars arranged in a concentric pattern just proximal to the facial suture (see Clarkson, 1975, pl. 6, for a similar pattern in some Phacopidae). The proximal surface of the palpebral area is not inflated as in phacopid and dalmanitid taxa, but rather slopes nearly vertically from the palpebral lobe, and is developed into a dorsal concave region and a less steeply inclined, somewhat concave ventral area running to the axial furrow and communicating smoothly with both the anterior and posterior regions of the gena. The eye, in relation to the total width of the gena, is set rather closely to the axial furrow.

The visual surface is bounded ventrally by a small, bulging eye socle which is covered with granules and set off from the genal surface below by the absence of the characteristic genal dimpling described below. The visual surface is rather small, bearing 22 or 23 dorsoventral files with a maximum of six lenses per file as seen in the specimens available to us which allow accurate counts. [Wolfart (1968, p. 115) reported 22 dorsoventral files with an approximate total of 105 lenses, with a maximum of six lenses per dorsoventral file]. The lenses are small, rather homogeneous in size, and project, insofar as is known, only slightly beyond the scleral surface. There is some evidence, on an internal mold, of a suture along the ventral margin of the visual surface, reminiscent of the "circumocular suture" described by Clarkson (1973) for olenid trilobites.

The facial suture is proparian and apparently not functional at ecdysis, although many specimens reveal some separation along the facial suture. The posterior branch arises on the ventral surface, cutting across the posterolateral corner of the gena transversely as a direct continuation of the line described by the ventral margin of the posterior border (which is itself reflected into a short doublure). At the cephalic margin, the suture is expressed dorsally and inclined sharply anteroproximally, curving across the genal border and then nearly transversely up the posterior region of the palpebral prominence; it is then reflected anteriorly along the dorsal margin of the visual surface. There is no genal sulcus or furrow developed along the posterior branch of the facial suture. The suture then runs down the anterior slope of the palpebral prominence, cutting across the anterolateral corner of the anterior glabellar lobe, and curving smoothly around the anterior glabellar lobe and meeting at the midline, just distal to the anterior glabellar ridge and furrow system described above.

The cephalic doublure is developed as a vertical wall on the posterolateral region of each gena. The ventral marginal wall of the cephalon is quite thin in that region, but becomes progressively thicker anteriorly along the genal margins, while the doublure remains short (tr.) and slightly concave. At the point below the anterolateral corner of the anterior glabellar lobe, the doublure begins a ventral reflection, becoming nearly horizontal at the midline. The hypostomal suture is convex anteriorly. The doublure is triangular under the anterior glabellar lobe, with the apex pointing anteriorly. The ventral marginal border of the gena becomes thicker and reflected dorsally under the anterior glabellar lobe, forming a rounded callosity smoothly confluent with the anterior border ridge. Thus the cephalic doublure is distinguished from the dorsal surface of the anterior region of the cephalon only by a sharp break in slope.

The hypostoma is, unfortunately, unknown.

Excluding the genal and occipital spines, there are five classes of "ornament" on the cephalon. Small granules occur nearly everywhere over the dorsal surface and anterior doublure. They are larger and most densely packed along the cephalic border and the an-

terior region of the glabella. These small granules are absent in the glabellar and axial furrows (hence permitting recognition that glabellar furrows 3p do not communicate with the axial furrows; the trough described above as connecting the 3p furrow with the axial furrow is granulate), including the axial furrow pits. When insertion sites of the auxiliary impression system are developed on the external surface, they are developed as flat, slightly depressed areas, and are completely devoid of granulation. The granulation is expressed solely on the external cuticular surface, and no perforations in them were observed.

The second class of "ornament" consists of tubercles quite larger in size than the granules. These are most prevalent on the anterior region of the cephalon, especially on the anterior border ridge, and are also variably developed (and often apparently absent) on the glabella, especially the anterior glabellar lobe. Where present, these structures are developed on the external surface and also reflected on internal molds.

Various muscle scars, and their patterns, have been described above. The auxiliary system is weakly developed both externally (as smooth depressions, where they are most easily distinguished from the larger "ornamental" tubercles) and internally as pads appearing as smooth depressions on the internal mold. The scars of the visual system are developed as concave depressions on the visceral surface, apparently not expressed externally, and appearing as smooth bumps on the internal mold.

Evidence of microtubules perforating the carapace is seen on some internal molds, showing as circular depressions with a small mound of matrix filling the center (see Eldredge, 1970 and 1971, for further discussion of these structures and their identification). In addition, a specimen from Presto El Peral, retaining highly weathered cuticular material along the left anterior ocular ridge and facial suture, shows that the cuticle, in this region at least, is riddled with very small vertical pores.

Finally, a very prominent pattern of "dimples" is developed over the entire genal area (both externally and viscerally) except on the genal border, giving the entire surface a corrugated appearance. The dimples are discrete, irregular (but usually rounded) depressions, generally bearing granules on the external surface, and are smaller and more numerous on the fixigena than on the librigena. On the distal wall of the librigenal moiety of the palpebral prominence, extending dorsally to the ventral margin of the eye socle, these dimples become linear, vertically directed and radially arrayed depressions, recalling muscle scars. The significance of these structures is unknown. While developed in various Phacopina and in other less closely related trilobites, the strength and extent of their development in this species is significant for the assessment of the relationships of B. (Belenops) insolita with other elements of the Malvino-Kaffric calmoniid fauna.

The thorax consists of 11 segments and is widest (in terms of axial ring width) at the sixth segment. Each axial ring is sagittally constricted into a thin, flat, posterodorsally inclined spine; the axial rings are widest (exsag.) adjacent to the axial furrows. The articulating half rings are separated from the axial rings by broad, granulated ring furrows. Distally each ring furrow bears a pair of stout apodemal projections.

The pleura run transversely approximately half their length, then become deflected downwards and inclined posterodistally, terminating in long thin posterodistally directed spines. Pleural furrows, rather shallow and narrow on the external surface, but more broad and deep on the internal mold, divide each pleuron into anterior and posterior moieties. The anterior moiety is developed as a slightly crescentic ridge in the proximal region; it becomes a flat surface inclined anteroproximally on the distal region, for sliding under the next anterior segment on enrollment. The posterior moiety of each pleuron consists of a thin ridge proximally, which runs posterodistally; the posterior moiety becomes wider (exsag.) in the distal, inclined region. Articulation between segments is accomplished by an anterior projection of each segment fitting into a shallow

posterior depression in the succeeding segment in the axial furrows and along a short transverse line of articulation along the proximal portion of the pleura. This latter line of articulation consists of a ridge on the posterior segment fitting into a groove on the anterior segment, and lies in a plane somewhat higher than that of the articulating mechanism of the axial furrows.

Each thoracic segment is covered with microgranules except on the articulating surfaces and in the pleural furrows. Larger tubercles occur in a single row along the posterior moiety of the pleuron.

The pygidium, excluding the terminal spine, is roughly triangular in outline, although the anterior margin is convexly rounded rather than transverse, and the lateral margins are also slightly curved. The axis consists of eight axial rings and a short, bluntly rounded terminal piece. The axis is moderately elevated above the pleural fields and set off by shallow, rather ill-defined axial furrows. The axis narrows posteriorly, is rounded posteriorly, and does not reach the posterior margin of the pygidium. Accessory half-rings are present on axial rings 2–5. Axial nodes (not true spines) are present on the more anterior axial rings. Apodemal depressions, progressively shallower and smaller posteriorly, are present on segments 1–5. There are eight or nine gently sloping pleura, the anterior three bearing pleural furrows. The margin bears short, ill-defined and generally poorly preserved lappets, particularly on the anterior two or three pleura. The length and morphology of the terminal spine is unknown; the terminal spine appears to have been directed horizontally, in a plane somewhat higher than the adjacent pygidial margin. The surface of the pygidium is covered with granulation. Dimples (muscle scars?) are present externally and internally between the posterior margin of the axis and the terminal spine.

REMARKS: *Bainella (Belenops) insolita* was first described by Wolfart (1968) as *Acastoides insolitus*. Wolfart (1968, p. 113–115) based his description on two cephala from the *Scaphiocoelia* Zone at Hiskachili, in the Belén region of Bolivia (holotype d308

in the collections of the Bundesanstalt für Bodenforschung, Hannover, West Germany, not examined). Our description, based on 73 cephala, 8 thoraxes, and 13 pygidia, is necessarily more complete. We disagree with Wolfart's description on only two points, the most important of which is that glabellar furrows 2p and 3p (respectively S2 and S1 in Wolfart's terminology) definitely do not reach the axial furrows (*contra* Wolfart, 1968, p. 114). This is clearly shown on external casts where these furrows are devoid of granulation. The only other area of disagreement is really a matter of terminology: Wolfart (p. 114) speaks of an "anterior axial furrow" behind the anterior branch of the facial suture (along the anterior region of the glabella). We have described an anterior glabellar ridge and anterior glabellar furrow in this position, and can only assume that Wolfart referred to the anterior glabellar furrow with his term. We do not believe that "anterior axial furrow" is appropriate terminology for Phacopina; it cannot be homologous in any strict sense with such grooves in other (primarily Cambrian) trilobites, as its scattered appearance in phacopids and dalmanitids is clearly neomorphic.

Wolfart (p. 115) allocated *insolitus* to the genus *Acastoides,* noting that the development of the palpebral prominences and the high occipital ring (true occipital spines are generally absent from specimens from the Belén area, including Wolfart's material—see below) set this species apart from all other species of *Acastoides.* It is true that the overall conformations of the cephala of species of these two genera are rather similar, but other details of cephalic anatomy (beyond those explicitly noted by Wolfart) and of course the conformation of the thorax and pygidium (unavailable to Wolfart) clearly align Wolfart's species *insolitus* with *Bainella.* These criteria are set forth in the diagnoses of the genus and the two subgenera above.

Bainella (Belenops) gamkaensis Rennie, 1930, was based on a single cephalon from Gamka Poort, South Africa. We have not examined this specimen; based on Rennie's description and illustration (Rennie, 1930, p.

353–354, figs. 14–17), the main differences between the two species appear to be in even greater inflation and rounding of the anterior glabellar lobe, and the presence of larger eyes with moderately well incised palpebral furrows in *gamkaensis*. Otherwise the two species are virtually identical.

GEOGRAPHIC VARIATION WITHIN
BAINELLA (BELENOPS) INSOLITA

Bainella (Belenops) insolita occurs in nearly all outcrops of the *Scaphiocoelia* Zone known to us to have produced trilobites (see table 1). Although there is no geographic or facies restriction of its distribution (i.e., when compared with most other calmoniid species of the *Scaphiocoelia* Zone fauna), some geographic variation is present. Thus, while most specimens have a pronounced occipital spine, only a high, protuberant occipital ring is developed on specimens from Belén, while specimens from nearby Tikani do have an occipital spine.

Three basic measurements (sagittal length of the glabella: LG; width of glabella at 1p lobe: PWG; width of glabella at axial furrow pits: AWG) were subjected to a simple principal components analysis (see Eldredge, 1973, for a description of procedures). Principal components are given in table 2. The first principal component, as is usually the case, is a simple overall size vector composed of nearly equal loadings on each variable. The second component contrasts posterior cephalic width with glabellar length and, to a lesser extent, with anterior glabellar width; a high score along this vector implies a relatively short cephalon with a low angle of divergence of the axial furrows. The third factor, which we shall not discuss further, implies a relatively short cephalon with a high angle of divergence of the axial furrows; specimen scores along this vector yielded no readily interpretable pattern.

A bivariate plot of the 23 specimen scores on principal components 1 and 2 is shown in figure 10. Specimens to the right of the plot (i.e., high scores on the second vector) imply relatively short heads with broad posterior glabellar widths, whereas those to the left

TABLE 2

Unrotated Principal Components for Analysis of *Bainella (Belenops) insolita*

	I	II	III
LG	.577	−.543	−.629
PWG	.579	.799	−.136
AWG	.576	−.256	.765

N = 24. LG: sagittal length of glabella; PWG: width of glabella at glabellar lobe 1p; AWG: width of glabella at axial furrow pits.

imply the reverse. The scores define a shallow parabola ("Kendall's horseshoe"), such that the highest scores on the first vector—a "maximization" factor of overall size—are in the middle of the range of variation of scores along the second component. That is to say, deviations from the "average" maximized cephalic size go in two different directions—toward longer cephala with relatively high angles of divergence of the axial furrows (to the left) or shorter cephala with lower axial furrow divergence angles. There is no ontogenetic (based on absolute size) structure to the plot. The interesting point is that the two northern localities utilized (Belén and Tikani) show most deviations to the left (i.e., toward longer cephala with higher axial furrow divergence angles) and only some to the right. Specimens from the remaining southern localities show deviations only to the right side of the plot—i.e., toward broader cephala with lower divergence angles. Though there is overlap, some geographic differentiation within *Bainella (Belenops) insolita* is apparent in terms of these three measurements. This geographic variation parallels the regional differences seen even more clearly in other *Scaphiocoelia* Zone genera—a pattern of vicariance between the La Paz-Belén area vs. the Icla-Tarija area primarily, with further more subtle differences present between the Icla and Tarija regions.

MATERIAL EXAMINED: NMNH Braniša Collection, eight cephala (including a part and counterpart) from Belén, seven cephala (including a part-counterpart) and a portion of a thorax from Curuyo, and a single ceph-

alon each from Presto El Peral, Agua Castilla and Tikani; AMNH Braniša Collection, 19 cephala (including a part-and-counterpart), a portion of a thorax, and five pygidia from Tikani, eight cephala, a thorax and two pygidia from Colchani, two cephala from Belén, two cephala from Sella Jarcas, a cephalon each from Puerto Perez and Agua Castilla, and a cephalon and a portion of a thorax from Curuyo; AMNH Smith Collection, 19 cephala, four thoraxes and six pygidia from Tikani, including a part and counterpart of a cephalon and of a thorax, and two cephala from Colchani. All specimens from the Lower Belén Formation, *Scaphiocoelia* Zone (Tikani, Belén, Colchani, the *Scaphiocoelia* Zone of the Icla Formation (Agua Castilla, Presto El Peral), or the Gamoneda Formation of the Tarija Department, all in Bolivia.

DELTACEPHALASPIS, NEW GENUS

TYPE SPECIES: We designate *Deltacephalaspis* (*Deltacephalaspis*) *comis*, new species, from the Gamoneda Formation, Curuyo, Bolivia, as the type species.

ETYMOLOGY: The name of this genus is formed by compounding three Greek words: *delta,* Greek letter, symbolizing triangular shape; *cephalon,* head; and *aspis,* spine, in reference to the distinctly triangular head with large genal spines characteristic of this genus.

DIAGNOSIS: Calmoniids with deltoid-shaped cephala. Genae distinctly dished. Posterior margin of cephalon recurved anterolaterally, produced into long genal spine projecting nearly transversely, to obliquely posterodistally. Cephalic furrows lightly impressed. Facial suture transecting anterolateral corners of anterior glabellar lobe; small preglabellar field present, comprising proximal portion of short spatulate anterior cephalic projection. Thorax with large pleural spines in posterior segments; eleventh pleural spine large, circular in cross section, and sharply reflexed posteriorly. Pygidium triangular, nearly isopygous, with distinct lateral border lacking spines or lappets. Ring

and pleural furrows indistinct. Axis terminating anterior to posterior pygidial margin; post axial field sloping abruptly to posterior margin, which bears a prominent spine. Axial spines variably present on some pygidial segments.

DESCRIPTION: Species of the genus *Deltacephalaspis* have flattened to moderately arched exoskeletons. The cephalon is distinctly deltoid or equilaterally triangular in gross outline. The genae are dished, with a distinct posterior border furrow confluent with the shallow lateral border furrow. The posterior border of the cephalon is nearly transverse from the axial furrow distally to the rear margin of the eye, and is then recurved anterodistally. The posterolateral corner of the cephalon is produced into a prominent genal spine of variable length, which variably projects nearly transversely (exsagittal angle about 5°) to obliquely posterodistally (exsagittal angle about 25°). The genal spine is circular in cross-sectional profile, and tapers to a point; it lies nearly in a horizontal plane in most species, or is reflected slightly dorsally, and forms, together with the genal border, the most ventral extension of the cephalon (in lateral view in standard orientation). The margin of the librigena is curved anteroproximally to a point opposite the anterolateral corner of the glabella; it is thereupon reflexed anteriorly, delimiting a short, spadelike anterior cephalic process. The lateral margins of the cephalon are thus distinctly shouldered in dorsal view. The portion of the anterolateral corner of the anterior glabellar lobe distal to the facial suture is rather steeply sloping and smoothly confluent with the librigena proper posteriorly, and is abruptly recurved to the flat, nearly horizontal surface of the cephalic doublure. The anteromedian portion of the cephalic doublure is triangular, and, also in ventral view, the anterolateral corners of the glabella are visible as small bulges distal to the doublure margin.

The axial furrows are nearly parallel, diverge only slightly, and are lightly impressed, becoming very shallow (nearly obsolescent) between the eye and glabellar
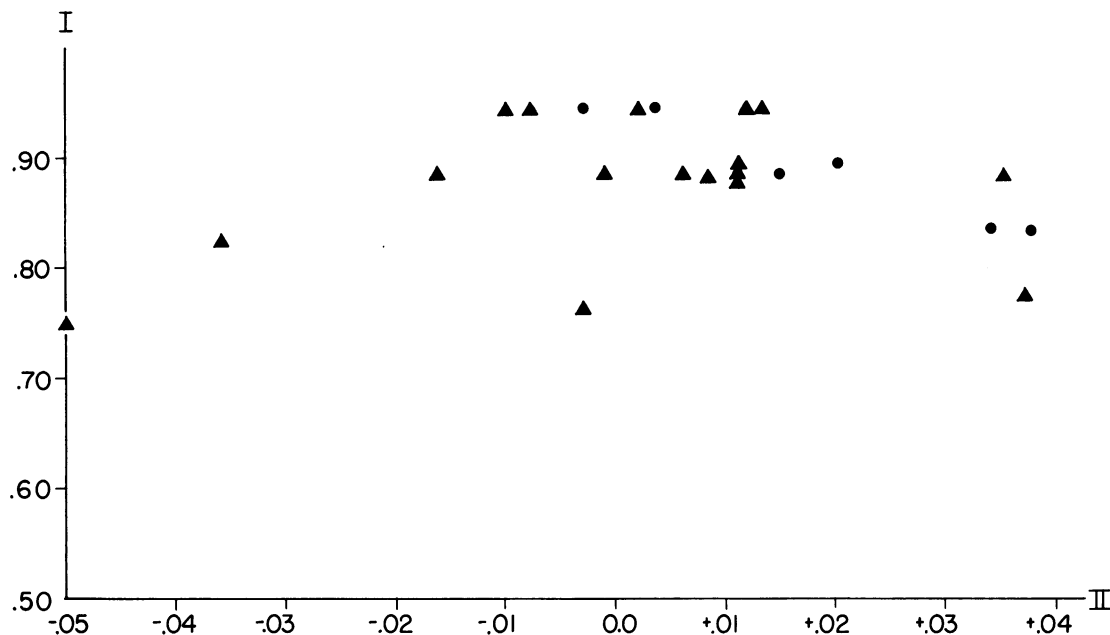
FIG. 10. Bivariate plot of scores of 23 specimens of *Bainella* (*Belenops*) *insolita* on factors I and II of an unrotated principal components analysis. ▲—specimens from northern areas of outcrop of the *Scaphiocoelia* Zone. ●—specimens from east-central and southern areas of outcrop.

lobes 2p and 3p. (The "shallow section" of the axial furrow actually reflects the fact that the axial furrow slopes anterodorsally from the posterior border furrow to the point directly opposite the eye, flattens out, and then slopes anteroventrally anterior to the eye.) Anterior to the eye, the axial furrows are broad and shallow, divergent, and merge indistinctly with the anterior region of the genae. No axial furrow pit is developed.

The anterior glabellar lobe is diamond-shaped. The facial suture runs directly anteriorly from the palpebrum across the axial furrow, transecting the anterolateral corners of the anterior glabellar lobe, thence becoming more sharply reflected proximally and meeting at the cephalic midline in a distinctly parabolic curve. The anterior ocular ridge is variably present; the facial suture is situated on the middle of a thickened ridge (anterior glabellar ridge) along the edge of the anterior glabellar lobe. Where the facial suture meets at the cephalic midline, a short, triangular

preglabellar field (horizontal or inclined anterodorsally) is developed, separated from the anterior glabellar lobe by a distinct break in slope. The anterior glabellar lobe is variably inflated, and ranges from nearly flat to moderately steeply inclined. The posterior branch of the facial suture is inclined slightly anterodistally, and is recurved at the lateral cephalic border anterior to the genal spine.

Glabellar furrows 3p are shallow, narrow, sometimes nearly effaced, and sinuous, with the proximal branch running obliquely anterodistally, and becoming reflected into a distal branch inclined more sharply anterodistally, and not communicating with the axial furrow. Glabellar furrows 2p are short, transverse, nearly obsolescent, and do not communicate with the axial furrows. Glabellar furrows 1p are also linear and transverse, but more deeply impressed on the external surface and developed ventrally as apodemes, and are confluent with the axial furrows. The occipital furrow is complete,

broad and shallow medially, and is developed as wide and deep invaginations distally, in communication with the axial furrows, and is developed as wide and apparently blade-shaped apodemes ventrally.

The entire median surface of the glabella forms a single curved surface, sloping posterodorsally (in lateral view) in the anterior region, and becoming nearly horizontal along the midline from the posterior one-third of the anterior glabellar lobe posterior through glabellar lobe 2p, thence gently sloping posteroventrally. The glabellar lobes are not inflated, but rather slope gently down distally to the axial furrows.

The occipital ring is smoothly curved, is widest (sag.) at the midline, and is constricted (exsag.) at the axial furrows. The proximal edge of the posterior border ridge is distinctly more narrow than the distal edge of the occipital ring; it widens distally and is posteriorly recurved as far posteriorly as the posterior edge of the occipital ring, before curving anterodistally.

The eyes are small and prominent. The posterior margins of the eyes are opposite glabellar furrows 2p, and the anterior margins are opposite the midpoint of glabellar lobe 3p. The visual surface is convex, bearing from 22 to 28 dorsoventral files. The dorsal surface of the palpebrum is in approximately the same horizontal plane as the midline of the glabella. The palpebral lobe is kidney-shaped, horizontal, and not sharply demarcated from the steeply sloping palpebral area except by a break in slope. The eye socle is tall, vertical, heavily granulated and recessed under the visual surface. The genal surface is sharply sloping laterally and anteriorly, and gently sloping posteriorly; it becomes shallower distally and recurved at the margin, producing a dished appearance.

The entire cephalon is covered with minute granules, particularly densely developed over the cephalic border, the anterior glabellar ridge, and the eye socle. Granules are sparse, in some cases absent, over much of glabellar lobes 1p–3p. The librigena has coarse dimples developed over its surface, especially in the dished region near the lateral border furrow. Smaller dimples are variably developed, seemingly irregularly, on the distal region of the fixigena. A small occipital spine is present in most species; small spines are developed, variably and irregularly, over the median region of the entire glabella in some species. The auxiliary impression system is of the acastid pattern (fig. 2G, H), with the impressions along the anterior margin of the field not strictly transverse, but rather running in parallel with the parabolic course of the anterior branch of the facial suture. The hypostoma is unknown.

The thorax [known only for *Deltacephalaspis* (*Deltacephalaspis*) *magister*, new species] has axial furrows lightly impressed and lacks axial spines [*n.b.*: *Deltacephalaspis* (*Deltacephalaspis*) *magister* lacks cephalic and pygidial axial spines, whereas they are present in other species. Axial thoracic spines may therefore prove to be present in *D.* (*D.*) *comis*, new species, *D.* (*D.*) *retrospina*, new species, and perhaps in *D.* (*Prestalia*) *tumida*, new subgenus, new species]. The pleural furrows are distinct, nearly linear, and inclined slightly posterodistally. The pleura terminate in short, slightly recurved spines on the anterior segments; the pleural spines become progressively larger posteriorly, are quite large and circular in cross-sectional profile on the eleventh segment, and are sharply reflexed posteriorly and are inclined somewhat ventrally, projecting below and lateral to the anterolateral corner of the pygidium.

The pygidium is triangular, roughly isopygous, rather steeply arched anteriorly, and has a distinct lateral border ridge which lacks spines or lappets, and which is separated from the pleural field by a broad, shallow indistinct border furrow. The pleural and ring furrows are all lightly impressed, and become obsolescent posteriorly; the interpleural furrows are extremely faint and are developed only in the anterior few segments. Only the anterior four pairs of pleura are distinctly developed. The axial furrows are lightly impressed; the axis tapers regularly posteriorly, and is set off from the pleural field rather sharply by a break in slope, especially posterolaterally. The axis has approximately seven axial rings anteriorly and

a long posterior section in which the ring furrows are indistinct. The axis terminates anterior to the posterior pygidial margin, and is obtusely rounded. A short postaxial pygidial field slopes abruptly to the posterior margin; a stout spine is developed on the posterior pygidial margin. Axial spines are developed irregularly on some (never all) segments in some species.

INCLUDED SPECIES: In addition to *D. (D.) comis,* we include *D. (D.) retrospina* from the Gamoneda Formation, Jarcas, Bolivia; *D. (D.) magister* from the *Scaphiocoelia* Zone of the Belén Formation in the La Paz-Belén-Sicasica region of northern Bolivia; *Deltacephalaspis (Prestalia) tumida,* from the *Scaphiocoelia* Zone at Presto el Peral, in the Icla region of Bolivia; and *D. (P.)* sp. A from the Lower Belén Formation (*Scaphiocoelia* Zone) at Belén.

REMARKS: This genus is quite distinctive and easily identified in well-preserved material. Criteria for recognizing the five included species are given in the appropriate places below. The above description, which patently is not restricted to autoapomorphic characters, is lengthy and is intended to help override two related problems in the identification of species of this genus from less than complete material: (1) the problem of distinguishing this genus from certain other calmoniids (e.g., *Paracalmonia, Calmonia*) within and outside Bolivia, and (2) the much more vexatious problem of distinguishing certain of the species of this genus from other sympatric species of other genera within the *Scaphiocoelia* Zone. This highly distinctive and unusual genus so closely resembles other taxa in certain of its characters that differentiation may be impossible on the basis of incomplete material.

It would be well, therefore, to specify the autapomorphic, or nearly autapomorphic, characters of this genus first. Its outstanding features are: (1) deltoid-shaped cephalon, i.e., the cephalon is in the shape of an equilateral triangle with very large genal spines projecting at a low angle (i.e., not quite directly transversely); (2) critically, the shape of the posterior border of the cephalon, which never projects posteriorly beyond the occipital ring, and which distally curves anteriorly before giving rise to the genal spine; (3) development of a short, spatulate anterior median cephalic projection, composed of the anterior border, parabolic anterior facial suture, and a small triangular preglabellar field; (4) near obsolescence of the glabellar furrows on the cephalon, and the ring and pleural furrows of the pygidium; (5) presence of a large, posteriorly reflected pleural spine on the eleventh thoracic segment; (6) termination of the pygidial axis anterior to the posterior pygidial border, and (7) development of a spine on the posterior margin of the pygidium. Although not entirely autapomorphic (perhaps only characters 1 and 2 enumerated immediately above can be so judged), in conjunction these seven character states or complexes serve to differentiate this taxon from all other calmoniid genera. *Paracalmonia* most closely meets these characters, but in that genus the anterior median cephalic projection is very long, the anterior section of the facial suture is apparently not reflected parabolically anteriorly, and there is both a metagenal and a "true" genal spine, and each is quite short. Otherwise *Paracalmonia* is phenetically closest to *Deltacephalaspis (Deltacephalaspis).* Other resemblances between *Deltacephalaspis* and other calmoniid genera emerge under the diagnoses of the subgenera and included species. When known through adequate material, species of this genus are highly distinctive and cannot be confused with other calmoniid taxa.

However, pragmatically, things are not so simple when dealing with poorly or incompletely preserved specimens from the *Scaphiocoelia* Zone fauna. In the Introduction we discussed the close resemblance most taxa from the *Scaphiocoelia* Zone bear to one another in terms of cranidial morphology. The general effacement of the glabellar furrows is a helpful clue in this case, though small specimens can still be confused with *Phacopina convexa,* new species, in which these furrows are also greatly reduced.

The real problem, however, is distinguishing two of the species of this genus from *Kozlowskiaspis (Romanops) borealis,* new sub-

genus, new species. There is no difficulty if the genae are known, but *Kozlowskiaspis* (*Romanops*) is similar to *D*. (*Deltacephalaspis*) in its cranidial, thoracic, and pygidial morphology and we have a number of specimens on hand that remain unassigned.

When genae are absent, the only two criteria which suffice to distinguish *D*. (*D*.) *magister* from *Kozlowskiaspis* (*Romanops*) *borealis* in the Belén area are shape of the anterior section of the facial suture (smoothly curved in *Kozlowskiaspis*) and the lateral profile of the anterior glabellar lobe, which is more steeply sloping in *Kozlowskiaspis*. Of great importance, of course, is that the posterior border is not recurved anteriorly in its distal region in *Kozlowskiaspis* but rather is nearly wholly transverse. Also, the glabellar furrows in *Kozlowskiaspis* tend to be somewhat more deeply impressed than in *Deltacephalaspis*.

Similarly, the thorax of *D*. (*D*.) *magister*, upon which the above diagnosis was based, is nearly identical with that of *Kozlowskiaspis* (*Romanops*) *borealis* from the same localities (and, incidentally, to that of *Paracalmonia* from Brazil as well). Both genera have simple (i.e., generalized) thoracic segments; the distinctive pleural spines are, however, unusual and present in all three taxa. They appear to be flatter and more hook-shaped in *Kozlowskiaspis*; perhaps the large pleural spine on the eleventh segment in *Deltacephalaspis* exceeds in size that of *Kozlowskiaspis*, but our evidence is as yet incomplete on this point. Suffice it to say, isolated thoraxes and portions thereof from the *Scaphiocoelia* Zone in northern Bolivia can be difficult, even impossible, to assign to one genus or the other, no matter how well they may be preserved.

The pygidia of *D*. (*D*.) *magister* and *K*. (*Romanops*) in both the Belén and Tarija re-

gions of Bolivia are also closely similar, though both pleural and interpleural furrows are better marked on *Kozlowskiaspis*. There seems to be no terminal spine on the pygidium of *Kozlowskiaspis*. However, there is one crucial difference: the posterior margin of the pygidium in *Kozlowskiaspis* is distinctly vaulted, and the axis, though terminating anterior to the posterior margin, nevertheless slopes gently (not abruptly, as in *Deltacephalaspis*) to the posterior border in an unbroken slope. The posterior margin of the pygidium is thus a highly reliable means of distinguishing these two taxa.

The subgenus *Deltacephalaspis* (*Prestalia*) is also easily confused with *Kozlowskiaspis* (*Romanops*). *Prestalia*, alone among species we assign to *Deltacephalaspis*, has a more highly inflated cephalon, and is indeed very similar to *Kozlowskiaspis* (*Romanops*) in general cephalic configuration. (The thorax and pygidium of *Prestalia* are unknown.) Small but important consistent differences do exist between these taxa, however. The anterior cephalic projection and reflection of the facial suture, shape of the genae, and shape, size, and position of the genal spines readily differentiate the two. Also, the eye of *Prestalia* is very prominent, nearly "stalked," and situated on a steeply sloping gena, whereas the eye of *Kozlowskiaspis* is set lower to the much more gently sloping surface of the gena. Although individual specimens may be difficult to assign, when adequately known there is no real difficulty in distinguishing *D*. (*Prestalia*) from *K*. (*Romanops*). As mentioned in the Introduction, despite their rather close phenetic resemblance, we have concluded that these two genera are not especially closely related. Their resemblance seems to stem from a marked degree of symplesiomorphy rather than convergence.

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FIG. 11. A–F. *Deltacephalaspis* (*Deltacephalaspis*) *comis*. *Scaphiocoelia* Zone, Gamoneda Fm., Curuyo, Bolivia. A, B. Dorsal and oblique left lateral views of latex cast of external mold of cephalon. Holotype, NMNH 245613 (latex cast, AMNH 36687), ×2. C. Dorsal view of latex cast of external mold of cephalon. Paratype, NMNH 245614 (AMNH cast 36688), ×2. D, E. Ventral and dorsal views of
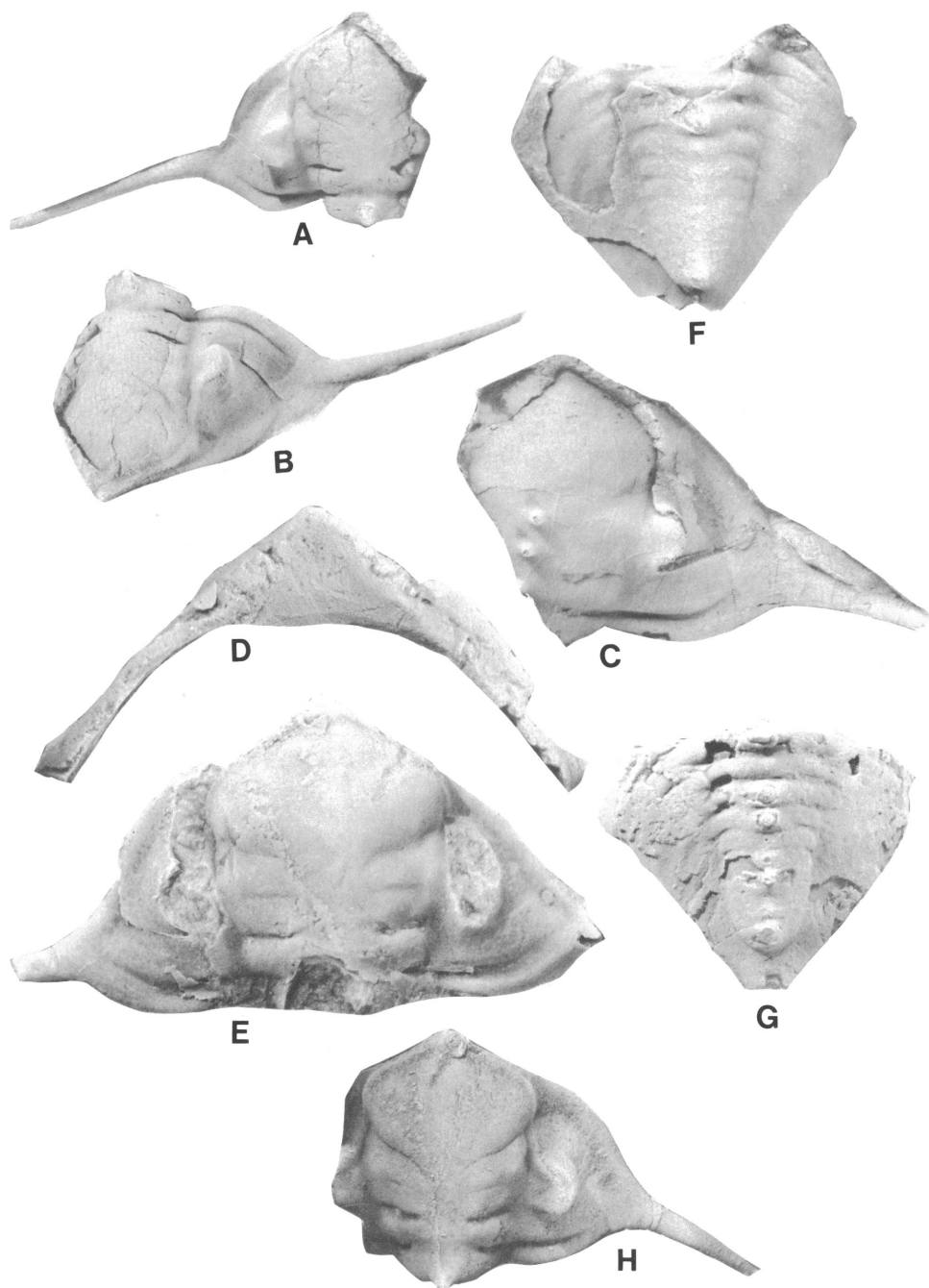
internal mold of cephalon. Paratype, NMNH 245615, ×4. F. Dorsal view of internal mold of pygidium. Paratype, AMNH 36689A, ×3. G, H. *Deltacephalaspis (Deltacephalaspis) retrospina*. Same horizon, Jarcas, Bolivia. G. Dorsal view of internal mold of referred pygidium. AMNH 36691, ×2. H. Dorsal view of latex cast of external mold of cephalon. Holotype, AMNH 36690 (latex cast is 36690C), ×3.

DELTACEPHALASPIS (DELTACEPHALASPIS),
NEW SUBGENUS

DIAGNOSIS: Species of *Deltacephalaspis* with distinctly flat, compressed cephalon, with shallow to moderate anterior arch, and relatively flat anterior glabellar lobe. Anterior median cephalic projection lying flat. Genal spines very long, in most cases, at least equal in length to sagittal length of entire cephalon. Distal portion of posterior border sharply recurved anteriorly; genal spine arising opposite posterior region of eye. Eye relatively small, Large Eye Index .27–.33, with 22–28 dorsoventral files; eye socle relatively short. Lateral genal fields only moderately sloping. Thorax and pygidium as for genus.

TYPE SPECIES: As for genus.

REMARKS: The three species included in the subgenus *Deltacephalaspis* (*Deltacephalaspis*) and their occurrences are given above and summarized in table 1. The type species, *D.* (*D.*) *comis*, is closely related to *D.* (*D.*) *retrospina*. Both are from the Gamoneda Formation in the Tarija Department of southern Bolivia. Together these species are the sister-group of *D.* (*D.*) *magister* from the northern region of Bolivia. Shared derived features, geographic variation, and points of difference among these species are given following their diagnoses.

Deltacephalaspis (Deltacephalaspis) comis,
new species
Figures 11A–F; 12A

TYPE SPECIMENS: Holotype, an external mold of a cephalon, NMNH 245613. Paratypes NMNH 245614, 245615 (two cephala), and AMNH 36689A (pygidium). All types from the Gamoneda Formation, Curuyo, Bolivia.

ETYMOLOGY: *Comis*, Latin for "beautiful."

DIAGNOSIS: A species of *D.* (*Deltacephalaspis*) with long genal spine, circular in cross-sectional profile, and projecting nearly horizontally at an angle of from 12°–15° posteriad. Genal spines not associated with facial sutures. Anterior ocular and anterior glabellar ridges pronounced; cuticular granulation densely developed. Eyes with 23 dorsoventral files.

DESCRIPTION: The cephalon of this species is markedly flattened, and has a broad shallow anterior arch. The axial furrows are broad, shallow, slightly divergent, and are inclined anterodorsally from the posterior border furrow to the point opposite the eye; anterior to the eye, the axial furrows are more deeply incised, run directly anteriorly, and are bounded distally by the anterior ocular ridge bearing the facial suture. The anterior ocular ridge merges with the pronounced anterior glabellar ridge at the anterolateral border of the anterior glabellar lobe. The anterolateral corner of the anterior glabellar lobe is thus transected by the anterior branch of the facial suture. The course of the anterior branch of the facial suture is as described for the genus. Distal to the facial suture, the anterolateral corners of the anterior glabellar lobe are nearly vertical, merging with the dorsally reflected anterior cephalic doublure to form the anterior cephalic margin. Ventrally, the doublure is triangular, flat, and has pronounced lateral ridges and a convex (anteriorly) hypostomal suture.

The genae have pronounced posterior border furrows and shallow lateral border furrows; the border furrows do not meet, but rather become obsolescent opposite the genal spines. The distal portion of the posterior border is thickened and recurved anteriorly. The genal spine is very long, and nearly circular in cross-sectional profile; it diverges posteriad from the cephalon at an angle of between 12° and 15°, and rises (distally) a few degrees from the horizontal. The base of the genal spine is set off posteriorly from the distal end of the posterior branch of the facial suture. The lateral border of the librigena is horizontal and is reflected moderately steeply proximally, producing a dished appearance. The eye socle is vertical and recessed under the visual surface. The visual surface is rather short (vertically) and the eye is rather small (Large Eye Index .27–.28); the visual surface has 82 lenses in the holotype,

arranged in 23 dorsoventral files, with a maximum of five lenses per dorsoventral file. The palpebral lobe is reniform, horizontal, and set off from the steeply sloping palpebral area by a sharp break in slope.

The entire cephalon is covered with very small granules, especially densely distributed on the anterior cephalic border, anterior glabellar lobe, and eye socle. The posterior region of the glabella and the occipital ring are less densely covered with granules; the occipital ring of the holotype specimen is nearly smooth. There is a small median occipital spine present on all available cephala; small median spines are variably present on glabellar lobes 1p–3p; spines are absent on the anterior glabellar lobe. The auxiliary impression pattern is incompletely known; it is developed as smooth patches devoid of microgranulation on the anterior glabellar lobe, and, insofar as it is known, it is closely similar to that described below for *D. (D.) magister*.

The thorax is unknown. The pygidium is as for the genus, with axial spines variably developed on the three available pygidia (i.e., on the fourth and seventh rings; the third ring and the posterior tip of the terminal axial piece; or altogether absent).

REMARKS: The description of *D. (D.) comis* is based on six cephala, including two external molds exhibiting fine details of ornament, and on three pygidia. This species differs from *D. (D.) retrospina* in its flatter cephalon and longer genal spines projecting at the rather low angle of from 12°–15° posteriad. *Deltacephalaspis (Deltacephalaspis) comis* differs from *D. (D.) magister* in having more pronounced anterior ocular and glabellar ridges, more pronounced ornament, an occipital spine, and genal spines basically circular in cross section, deviating only slightly from the horizontal in standard orientation and not associated with the distal portion of the posterior branch of the facial suture. For relationships among these species, see the discussion following the diagnosis of *D. (D.) magister*.

MATERIAL EXAMINED: Six cephala and three pygidia from the Gamoneda Formation
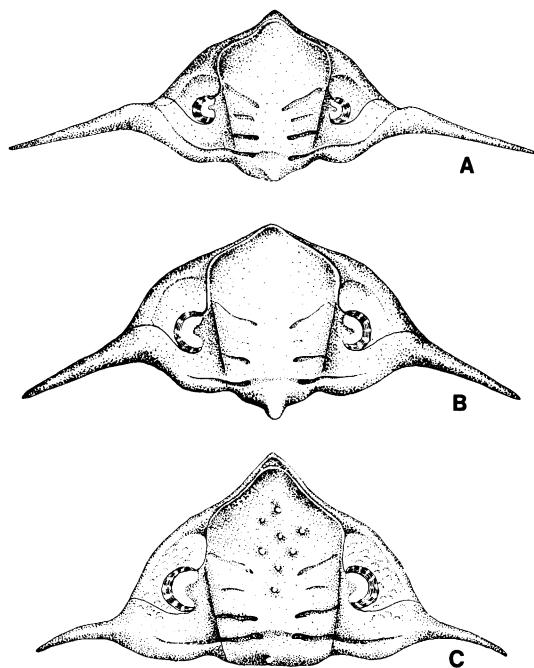
FIG. 12. Reconstruction of cephala of three species of *Deltacephalaspis*. A. *D. (Deltacephalaspis) comis* (based largely on holotype, fig. 11A, B.) B. *D. (Deltacephalaspis) retrospina* (based solely on holotype, fig. 11H) C. *D. (Prestalia) tumida* (based solely on holotype, fig. 15C–E).

at Curuyo, Tarija Department, southern Bolivia. Five cephala and one pygidium are from the Braniša Collection, NMNH; remainder are in the AMNH collections.

Deltacephalaspis (Deltacephalaspis) retrospina, new species
Figures 11G, H; 12B

TYPE SPECIMEN: The holotype is an external and internal (part and counterpart) mold of a cephalon from the Gamoneda Formation, Sella-Jarcas, Tarija Department, Bolivia; Braniša Collection, AMNH 36690A–C. We include a pygidium in the AMNH collections (AMNH 26691) from the same locality as a referred specimen.

ETYMOLOGY: The specific name is derived
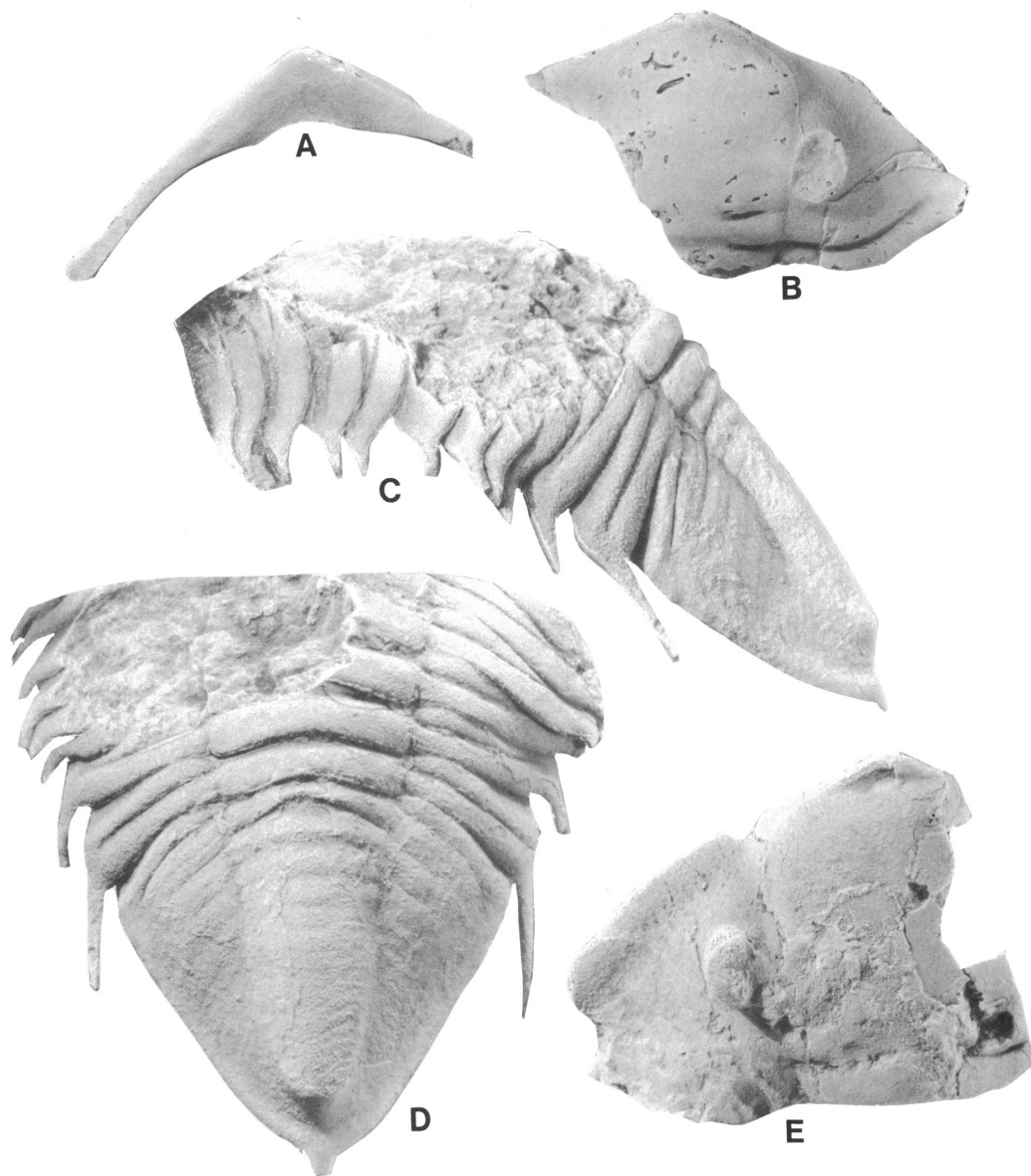
Fig. 13. *Deltacephalaspis (Deltacephalaspis) magister. Scaphiocoelia* Zone, Lower Belén Fm. A, B. Ventral and dorsal views of internal mold of cephalon, Belén, Bolivia. Holotype, NMNH 245616, ×2. C, D. Left lateral and dorsal views of thorax and pygidium, Colchani, Bolivia. Paratype, AMNH 36692 (Smith Coll.), ×2. E. Dorsal view of internal mold of cephalon closely associated in matrix with paratype AMNH 36692. AMNH 36693 (not designated as a type), ×2.

from retro, backwards, and spina, spine, in reference to the pronounced posterolateral inclination of the genal spine, the most striking feature of this species.

DIAGNOSIS: Cephalon flat, though distinctly more highly vaulted than in *D. (D.) comis*. Genal spine apparently relatively shorter than in *D. (D.) comis* and reflected posteriad

at an angle of approximately 25°. Eye with 22 dorsoventral files, with a maximum of five lenses per file. Large Eye Index .33. Thorax unknown. Single referred pygidium with axial spines on first, third, fourth, and seventh axial rings, plus terminal axial tip [thus embracing all known variation in D. (D.) comis] and with terminal spine of unknown length. All other characters as for D. (D.) comis.

REMARKS: *Deltacephalaspis retrospina*, known from a single well preserved internal and external mold (plus a single referred pygidium, clearly referable to the genus and from the same locality, though not definitely associated with the type cephalon), is identical with D. (D.) comis except in details of cephalic vaulting and size and inclination of the genal spines. For further discussion, see below under D. (D.) magister.

Deltacephalaspis (Deltacephalaspis) magister, new species
Figures 2G; 13

TYPE SPECIMENS: Holotype, NMNH 245616, a cephalon from the *Scaphiocoelia* Zone at Belén (Braniša Collection). Paratype, Smith Collection, AMNH 36692, a thorax and articulated pygidium (but not including two associated cephala), Colchani, northern Bolivia.

ETYMOLOGY: "*Magister*," Latin noun, in apposition to the generic name, in reference to the lordly, majestic size and form of this species.

DIAGNOSIS: A relatively large species of D. (*Deltacephalaspis*), with long, flattened genal spines projecting nearly transversely. Anterior margin of genal spine base formed by recurved distal portion of posterior branch of facial suture. All cephalic furrows greatly reduced. Anterior ocular and anterior glabellar ridges reduced or absent. Eye with 25 to 28 dorsoventral files. Axial spines lacking over entire cuticle.

DESCRIPTION: The cephalic width/length ratio of this species is relatively larger than for all other species of this subgenus, averaging approximately 2:1. The entire cephalon is relatively flat, with a broad and low anterior arch. The anterior ocular ridge and the anterior glabellar ridge are both reduced, and sometimes entirely absent. The cephalic doublure, in the anterior region, is as for other species; posterolaterally, it is flattened on the ventral surface, relatively thin below the eye, and expands in width posteriorly. The genal spines are broad at the base, relatively flat on the dorsal surface, gently rounded ventrally, and quite long. The genal spines project nearly transversely (projecting posteriad at a slight angle of from 5°–10°, and are inclined dorsally at an angle of roughly 20°–25° from the horizontal. The anterior margin of the genal spine base is formed by the recurved distal portion of the posterior branch of the facial suture.

The genal surface distal to the eye is gently sloping, accounting for a greater cephalic width than in other species. The eye is small (Large Eye Index .27); the visual surface is relatively tall, with 25 to 28 dorsoventral files bearing a maximum of eight lenses per dorsoventral file. The eye socle is not recessed under the visual surface.

The cephalon shows great reduction (near obsolescence) of the glabellar and axial furrows, and only faint granulation and genal dimpling. No occipital or other axial spines are developed. The auxiliary impression pattern (known from scars on the holotype—see fig. 2G) are of acastid type, consisting of two bilaterally symmetrical main rows of divergent scars and a strongly developed anteromedian pad. The posterior median impression is apparently absent. Scars are developed most strongly over the anterior half of the impression field. There is a short row of impressions present, inclined anteromedially, on the cephalic doublure. All other cephalic features are as in D. (D.) comis.

The thorax and pygidium are as described for the genus; the pygidium lacks axial spines.

REMARKS: *Deltacephalaspis magister* differs from D. (D.) comis and D. (D.) retrospina in its typically larger size, in the shape and inclination of the genal spine, the fact that the anterior margin of the base of the genal spine is bordered by the posterior branch of the facial suture, the greater effacement of cephalic furrows, lack of any
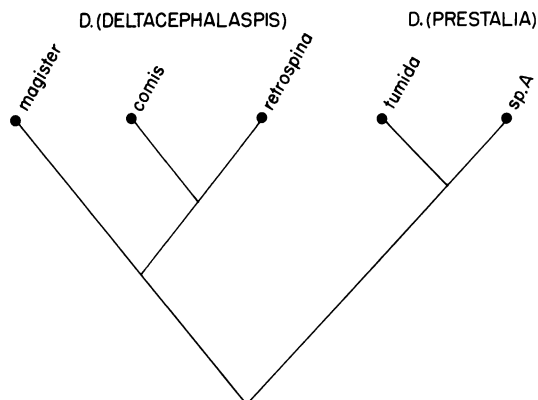
FIG. 14. Cladogram epitomizing relationships among the five species of *Deltacephalaspis* recognized in this paper.

axial spines over the entire exoskeleton, reduction or lack of a distinct anterior ocular and anterior glabellar ridge, a greater width/length cephalic ratio, and eyes bearing more dorsoventral files which themselves bear more lenses per file. It is the only species in which cephala have been found articulated, or closely associated, with thoraxes and pygidia. Thus pygidial morphology is definitely linked with cephalic morphology and provides the basis of referring indicated isolated pygidia to appropriate cephala in localities in southern Bolivia.

From northern Bolivia, *D. (D.) magister* is thus rather different from populations of *Deltacephalaspis (Deltacephalaspis)* in the south, and we have no hesitation in regarding it as a separate allopatric species. *D. (D.) comis* and *D. (D.) retrospina* are phenetically more similar to one another than either is to *D. magister,* and are allopatric vicariants within the southern region only. The case for recognizing these samples, from two nearby localities, as separate species is therefore not so compelling; however, the few morphological differences between the Curuyo and Sella-Jarcas populations seem to us sufficiently important to warrant naming and, as is the case with Recent organisms, whether to call two allopatric populations "species" or "subspecies" becomes a nontestable question incapable of further reso-

lution in the absence of further data. We elect to recognize *comis* and *retrospina* as distinct sister species (axial spines may serve as probable synapomorphies; the entire genus is sufficiently unique to prohibit lengthy debate over which character states among the five included species are primitive, and which derived). But these species are strictly morphologically defined, and their hierarchical rank is open to question; we do, however, claim that the amount and nature of the morphological differences between *D. (D.) magister* on the one hand, and *D. (D.) comis* plus *D. (D.) retrospina* on the other, coupled with their disjunct distribution, warrant the conclusion that they are biospecies exhibiting vicariance within the Andean geosyncline. The relationships of all species included in *Deltacephalaspis* are epitomized in figure 14.

MATERIAL EXAMINED: In addition to the type specimens detailed above, we have examined the following additional specimens of *D. (D.) magister:* two cephala, NMNH Braniša Collection; one cephalon from Belén, Smith Collection, AMNH; four cephala from Tikani (AMNH); two cephala, one associated with thorax-pygidium, and an additional thorax-pygidium, from Ayo Ayo, collected by Peter Isaacson (NMNH locality 17984). In summary, all specimens are from the lower part of the Belén Formation, *Scaphiocoelia* Zone, from four different localities in the Belén-La Paz region of northern Bolivia.

DELTACEPHALASPIS (PRESTALIA), NEW SUBGENUS

TYPE SPECIES: *Deltacephalaspis (Prestalia) tumida,* new species.

ETYMOLOGY: From Presto, a town in the Chuquisaca Department, Bolivia, at which the holotype of *D. (P.) tumida* was discovered.

DIAGNOSIS: (Based mostly on type species.) Cephalon highly arched, with pronounced anterior arch. Anterior median cephalic projection inclined anterodorsally at an angle of about 10°. Genal spine shorter than for *D. (Deltacephalaspis),* circular in

cross section, and arising well posterior to facial suture, and inclined dorsally at an angle of roughly 10°. Eye relatively large (Large Eye Index .30–.34). Lateral genal fields steeply sloping. Hypostoma, thorax, and pygidium unknown.

DESCRIPTION: (Based mostly on type species.) The cephalon is highly vaulted, with a pronounced anterior arch formed by steeply sloping genal surfaces. The lateral cephalic margin is distinctly shouldered. The front of the cephalon is prolonged into a tongue-like anterior projection reflected anterodorsally at an angle of roughly 10° (in lateral view); the anterior margin of the cephalon becomes reflexed vertically laterally, and merges with the librigenae. The anterolateral margin of the librigena curves gently posterodistally, and is then reflexed sharply posteriorly to the genal angle. The genal spine is stout, circular in cross section; it arises well posterior to the facial suture and extends posterodistally at an exsagittal angle of approximately 10°, and is inclined dorsally at an angle also of roughly 10°. The posterior border is thin proximally, becoming broader distally and slightly recurved anteriorly before giving rise to the genal spine; the posterior border is everywhere anterior to the posterior edge of the occipital ring.

The anterior ocular ridge is absent; the anterior branch of the facial suture transects the anterolateral corner of the anterior glabellar lobe. The anterior glabellar ridge, bearing the facial suture, is ill-defined laterally, and becomes pronounced anteromedially, forming a distinct parabolic ridge at the midline. A small preglabellar field is developed just proximal to the anterior glabellar ridge at the midline; the preglabellar field is elevated above the surface of the anterior median projection. The anterior glabellar lobe is moderately steeply sloping posterodorsally (in lateral view); the entire glabella is well inflated for the genus. The axial furrows are slightly divergent and fairly deeply incised (except just proximal to the eyes). No axial furrow pits are developed. Glabellar furrows and lobes are as for the genus as a whole.

The posterior border furrow is deeply in-

cised and confluent with the shallow lateral border furrow. The genae slope steeply to the nearly vertical eye socle; the eye socle is slightly concave and somewhat recessed under the visual surface. The eye is moderately large (Large Eye Index .30–.34) and extends from glabellar furrow 1p anteriorly halfway along glabellar lobe 3p; the eye is prominent and the visual surface is tall, though the palpebrum does not quite attain the height of the median region of the glabella. The eyes have 26 or 27 dorsoventral files, with a maximum of eight lenses per file, and a minimum count (left eye of holotype of type species) of 158 lenses.

The surface of the cephalon is covered with sparse, small tubercles, except on the posteromedian region. Six spines are asymmetrically developed on the posteromedian surface of the anterior glabellar lobe of the holotype of D. (P.) tumida; a seventh spine is developed in the region generally occupied by the posterior median impression; an eighth spine is developed just to the left of the midline opposite glabellar furrows 2p. A small median occipital spine is present. [None of these spines are developed on the additional two cephala we have assigned to D. (P.) tumida.] The auxiliary impression pattern is faintly seen as smooth patches on the external surface, and is incompletely developed. The auxiliary impression pattern conforms to the acastid type, except that the anterior row follows the parabolic course of the anterior branch of the facial suture (see fig. 2H). Dimples are developed on the genae as for the genus. The hypostoma, thorax, and pygidium are known.

Deltacephalaspis (Prestalia) tumida, new species
Figures 2H; 12C; 15C–E

TYPE SPECIMEN AND MATERIAL EXAMINED: Holotype, an external mold of a cephalon, Braniša Collection, NMNH 245617 (latex cast AMNH 36695), *Scaphiocoelia* Zone, Presto El Peral, Chuquisaca Department, Bolivia; referred specimens (*not* paratypes) include a second cephalon from Presto El Peral in the NMNH Braniša Collection,
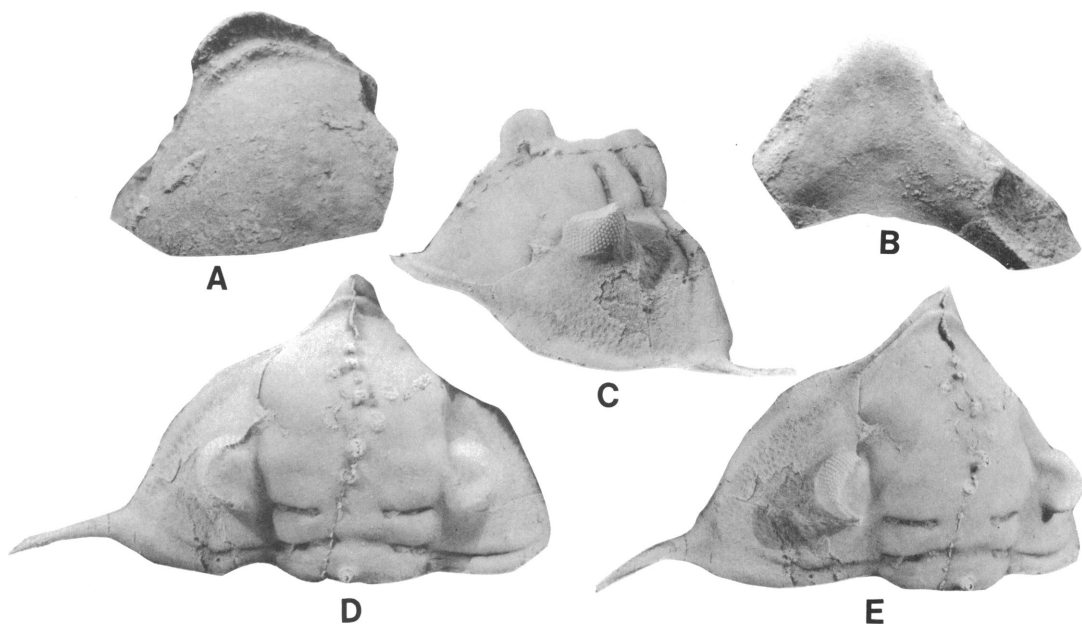
FIG. 15. *Deltacephalaspis* (*Prestalia*) spp. A, B. *D.* (*Prestalia*) sp. A. *Scaphiocoelia* Zone, Lower Belén Fm., Belén, Bolivia. Dorsal and ventral views of internal mold of fragmentary cephalon. AMNH 36694A (Braniša coll.), ×3. C–E. *D.* (*Prestalia*) *tumida*. *Scaphiocoelia* Zone, Presto el Peral, Bolivia. Oblique left lateral, dorsal, and oblique dorsal views of latex cast of external mold of cephalon. Holotype, NMNH 245617 (latex cast AMNH 36695), ×2.

and a single cephalon from the Gamoneda Formation at Curuyo in the Tarija Department (Braniša Collection, AMNH 36696).

ETYMOLOGY: From the Latin word meaning "tumid," in reference to the inflation of the glabella and relatively high vaulting of the cephalon.

DIAGNOSIS: [Based only on characters homologous with those preserved in *D.* (*P.*) species A diagnosed below.] A species of *D.* (*Prestalia*) with anteromedian cephalic process narrowly based and terminating in a distinct point. Facial sutures meeting at midline in a distinctly more parabolic shape than in *D.* (*Prestalia*) species A. Cephalic ornament, in addition to microgranulation, when present, developed as broad-based, distinct spines.

REMARKS: The similarities between this species and *Kozlowskiaspis* (*Romanops*) *borealis* were discussed above under the diagnosis of the genus *Deltacephalaspis*. We conclude that the species *tumida* should be referred to *Deltacephalaspis* primarily because of the (1) outline of cephalon in plan view, which remains triangular despite its greater inflation; (2) the shape of the genae, which are recurved posteriorly (shouldered) and give rise to a large genal spine which projects nearly transversely; (3) presence of a tongue-like projection of the anteromedian region of the cephalon, and the concomitant parabolic shape of the anteromedian section of the anterior branch of the facial suture, (4) presence of prominent eyes on well-developed eye socles; (5) presence of an anterior glabellar ridge, and (6) close similarity in ornament pattern including distributions of granules, scars, dimples, and spines.

We choose to erect a separate subgenus for *tumida* and for *D.* (*P.*) species A to reflect our conclusion that, while they are collectively the sister taxon of *comis-retrospina-magister* (on the basis of the above six synapomorphic character complexes), nevertheless they can be readily differentiat-

ed in greater inflation of the glabella and other features given in the diagnosis of the subgenus *D.* (*Prestalia*).

Deltacephalaspis (*Prestalia*) species A
Figure 15A, B

MATERIAL EXAMINED: A single fragmentary cephalon (internal mold) from the Lower Belén Formation (*Scaphiocoelia* Zone), Belén, Bolivia. AMNH 36694. Braniša Collection.

DIAGNOSIS: A species of *D.* (*Prestalia*) with anterior median cephalic process broader and more bluntly rounded anteriorly than in *D.* (*P.*) *tumida*. Anterior branch of facial suture broadly rounded where confluent at midline. Cephalic micro-ornament as for subgenus; larger tubercles (or perhaps small spines) developed irregularly over anterior glabellar lobe, more numerous, but smaller, than those of *D.* (*P.*) *tumida*. Hypostomal suture distinctly convex anteriorly. Anteromedian region of cephalic doublure inclined anterodorsally at an angle of approximately 10°, essentially flat, but divided into three nested triangular areas: a posteromedian inner triangular area, depressed (in ventral view), a flat median triangular area, and a dorsally reflexed marginal triangular area.

REMARKS: Morphology of the anterior median process immediately allows assignment of the fragmentary cephalon to *D.* (*Prestalia*). General morphology of the anterior glabellar lobe, glabellar lobe and furrow 3p, and position of the eye also agree with homologous morphology of *D.* (*P.*) *tumida*. In addition, this specimen affords the only information available on the morphology of the anterior cephalic doublure.

There is simply insufficient morphological information available to warrant formal naming of a new species. However, the differences that do emerge upon comparison with *D.* (*Prestalia*) *tumida* are of the same general nature as those observed between other sister taxa (species) from the northern (Belén-La Paz-Sicasica) region and the southern (Tarija, but also including the east central Icla) region of Bolivia, fitting in with the general pattern of faunal variation within the

Scaphiocoelia Zone. Finally, we note that these two species are among the rarest of the calmoniid fauna of the *Scaphiocoelia* Zone, based on collections available to us.

SCHIZOSTYLUS DELO, 1935

Dalmanites: Kozlowski, 1923 (pars), p. 39.
Proboloides: Kozlowski, 1923 (pars), p. 53.
Schizostylus Delo, 1935, p. 410; Struve, 1959, p. 0487.

TYPE SPECIES. *Dalmanites brevicaudatus* Kozlowski, 1923, p. 39, figs. 6–8.

REVISED DESCRIPTION: The cephalon of *Schizostylus* is moderately to highly arched, and bears a moderate to very long anterior process. The anterior process is inclined anterodorsally from 35° to 50° from the horizontal plane in standard orientation, and is composed of the extension of the doublure ventrally and laterally; the dorsal and dorsolateral portion of the anterior process is composed of the anterior cephalic border (distal to the facial suture) and a preglabellar field, which itself may not be well differentiated from the anterior glabellar lobe proper. The lateral cephalic margin is gently curved anterodorsally from the genal angle, thence swings sharply upward at the anterior process. The anterior border is separated from the anterior glabellar lobe by a shallow anterior border furrow laterally. The doublure is produced as a deep trough on the anterior process, and is bounded by thick ridges formed by the ventral cephalic margin.

The anterior branch of the facial suture runs along the lateral wall of the anterior process and joins at the midline on the dorsal surface of the frontal process.[1] The facial su-

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[1] Kozlowski (1923, p. 40) in his description of *Dalmanites brevicaudatus* (type species of Delo's genus *Schizostylus*) wrote that the anterior branch of the facial suture "se poursuit tout le long de l'arête latérale de la pointe rostrale jusqu'à son sommet," or, in other words, that the facial suture is confined to the lateral margins, dividing the frontal process into dorsal and ventral halves. This description has been faithfully repeated in all subsequent treatments of *Schizostylus*. Examination of scores of specimens of *Schizostylus* (*Schizostylus*) (as revised and emended below) consistently failed to

ture then runs posterodistally along the steep slope of the anterior glabellar lobe, thus transecting the glabella. The anterior glabellar lobe distal to the facial suture is nearly vertical, and is separated from the cephalic border by a shallow broad anterior border furrow (obsolescent medially in most species); the anterior section of the axial furrow is nearly obsolete, with only a faint break in the slope separating the anterior glabellar lobe from the anterior region of the librigena. No anterior ocular ridge is developed; the anterior glabellar ridge, where developed, is broad, and is bounded proximally by a shallow anterior glabellar furrow, and distally by the anterior branch of the facial suture.

The anterior glabellar lobe proximal to the facial suture is steeply curved in the anterolateral region, and is only gently curved or nearly flat anteromedially. Glabellar furrows 3p are moderately deeply incised on both the internal molds and external casts; the 3p furrows are straight, running anterolaterally at an exsagittal angle of approximately 65°, and not communicating with the axial furrows. Glabellar furrows 2p are short, transverse, and do not communicate with the axial furrows; they are moderately deeply incised on both external and internal surfaces. Glabellar lobe 3p is triangular or wedge-shaped. Glabellar furrows 1p are deeply incised, communicating with the axial furrows distally, and transverse in most species (or concave anteriorly). The occipital furrow is continuous, shallow medially, bears apodemes laterally, and communicates with the axial fur-

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reveal the course of the facial suture along the frontal process. Long after the initial draft of this manuscript had been completed, a specimen of *Schizostylus* (*Schizostylus*) sp. was donated to the American Museum of Natural History by LeGrand Smith. The internal mold of the frontal process clearly shows the facial suture running along each side of the process, but then running up onto the dorsal surface and meeting at an acute angle on the dorsal surface at a point between one-fourth and one-third the length of the process from the anterior tip. The specimen, AMNH 42418a–c, was collected at Padilla, Bolivia, between the *Kozlowskiaspis* and *Francovichia* Zones.

rows. The occipital ring is only slightly elevated above the median region of the glabella, which slopes regularly posteriorly at an angle of approximately 15° in lateral view. A small occipital spine is variably present.

The axial furrows are shallow, nearly obsolescent, generally straight, and diverge at an angle of approximately 30°. The axial furrows slope anterodorsally from the posterior border furrow, reaching a maximum elevation opposite the midpoint of the distal wall of glabellar lobe 3p, then slope anteroventrally. A shallow axial furrow pit is developed as a linear deepening of the axial furrow just distal to glabellar furrow 3p.

The posterior border furrow is deep, nearly transverse, and slightly recurved anteriorly in the distal region near the genal angle. The posterior border ridge is thickened slightly in the distal region, and projects as far posteriorly as the posterior margin of the occipital ring. The genal spine is stout, projecting posteriorly (in dorsal view) as a smooth continuation of the lateral cephalic margin, at an exsagittal angle of between 135° and 140°. The genal spines are inclined steeply dorsally at an angle of between 15° and 40° from the horizontal in lateral view in standard orientation. The termini of the anterior cephalic process and of the genal spines all lie in nearly the same horizontal plane either below, or, more usually, above the level of the palpebral lobes. The posterior branch of the facial suture intersects the lateral cephalic margin considerably anterior to the base of the genal spine. The posterior branch is reflected sharply posterodistally across the genal border.

The genae are steeply sloping, generally without a distinct border furrow, or are dished with a pronounced border furrow (especially opposite the eyes) and nearly horizontal border. The eyes are small (Large Eye Index .27–.34), situated close to the axial furrows, and generally entirely opposite glabellar lobes 3p, or extending posteriorly opposite the anterior region of glabellar lobes 2p. The visual surface bears from 18 to 20 (possibly more) dorsoventral files, with no more than six lenses per file. The eye socle is present as a small concave depression beneath

the visual surface, smoothly gradational with the steep slope of the gena. The palpebral lobe is flat, reniform, and separated from the depressed palpebral area by a distinct furrow.

The doublure is incompletely known, produced anteriorly into a troughlike ventral portion of the anterior cephalic process bounded by steep walls. The hypostoma is unknown.

The auxiliary impression system (fig. 2K, L) is usually expressed as pads on the internal mold, and is occasionally also expressed as unornamented flat round areas on the dorsal cuticular surface. The posterior median impression is either absent of only faintly developed. The auxiliary impression pattern is acastid in aspect, with strong lateral rows bearing the largest impressions anterolaterally. A second row is developed proximally, bearing subsidiary rows nearing, but not covering, the midline of the anterior glabellar lobe. The pattern is very similar to that of ?*Acastoides verneuili* (see Eldredge, 1971 and figs. 2D and 18D, this paper).

Cephalic ornamentation consists of a groundmass of very fine granules in some species, or of larger, more widely scattered tubercles over a basically smooth surface. Dimples are prominently developed as transversely elongate depressions on the librigenae; dimples are larger and more densely packed near the genal border furrow, becoming fewer and smaller approaching the eye socle and are absent altogether on the surface of the eye socle. Dimples are smaller and more rounded on the fixigena, or are absent there entirely.

The thorax has shallow axial furrows. Axial spines are variably present; axial rings are medially constricted (sag.). The pleura are transverse, each terminating in a short laterally directed spine in the anterior segments; the posterior segments terminate abruptly in a flat (exsag.) line, with a short posteriorly directed spine present in some species. Panderian organs are present in the anterodistal portion of the pleuron in all segments. The pleural furrows are broad and deep (observed mainly on internal molds) and slightly sinuous, directed posterodistally

from the axial furrow, thence gently reflected anterolaterally in the distal region. The pleural field is gently curved, and is not strongly divided into horizontal proximal and steeply sloping distal sections.

The pygidium is micropygous and distinctly triangular in dorsal view. The axis has three distinct rings plus a large terminal piece consisting of four or five rings (demarcated by transverse furrows which do not communicate with the axial furrows) or with five distinct rings and a smaller terminal piece. Axial spines (if present on the occipital and thoracic axial rings) are present on the first two axial rings of the pygidium, and are occasionally present on the third ring as well. The axis does not reach the posterior pygidial margin, and is set off from the posterior pleural field by a sharp break in slope. The pleural field has approximately five pleura, with pleural furrows developed on the anterior three pleura. The pygidial margin is entire; the posterior margin is distinctly pointed, but does not bear a terminal spine. The ornamentation of the thorax and pygidium is obscure inasmuch as most specimens observed are internal molds.

INCLUDED SPECIES: Wolfart (1968, p. 110, 113) has suggested the possibility that *Schizostylus brevicaudatus* (Kozlowski), the type species of *Schizostylus* by original designation and by monotypy, is a senior synonym of *Proboloides cottreaui* Kozlowski. While there can be no doubt that the specimen illustrated by Kozlowski (1923, pl. 2, fig. 10a, b) as the type specimen of *P. cottreaui* is referable to *Schizostylus* (as first recognized by Braniša, in Ahlfeld and Braniša, 1960) the great variation among samples from the "Icla" and "Sicasica" faunas indicates that several species of *Schizostylus* are present in Lower Devonian Bolivian rocks younger than the *Scaphiocoelia* Zone units; hence synonymizing these two species is premature and should be deferred pending a thorough study of all available samples. Whatever the case may eventually prove to be, all populations of *Schizostylus* younger than the *Scaphiocoelia* Zone in Bolivia are referable to *Schizostylus* (*Schizostylus*). Aside from the new species from the *Sca-*

phiocoelia Zone described below, the only other taxon in South America possibly referable to *Schizostylus* is *Cryphaeus allardycae* Clarke, 1913 (types seen). *Dalmanites (Proboloides) ensifer* Reed, based on a single cephalon from an unknown locality in the Bokkeveld beds of South Africa, has been referred to *Schizostylus* by Wolfart (1968, p. 113). The morphology of the anterior cephalic process in *ensifer* is indeed very reminiscent of that of *Schizostylus,* but details of eye morphology, genal spines, and the overall rather flattened nature of the cephalon, to the extent that these features can be accurately ascertained from Reed's (1925, pl. 8, fig. 4a–d) illustrations, are rather different from typical *Schizostylus*. Pending revision of both *allardycae* and *ensifer,* we tentatively allocate both to the new subgenus *Curuyella,* as ?*Schizostylus (Curuyella) ensifer* and ?*S. (C.) allardycae.* Note that, should these two species ultimately prove definitely referable to *Schizostylus (Curuyella)*, this would provide another nexus between the calmoniid trilobites of the Bolivian *Scaphiocoelia* Zone and the extra-Andean regions of the Malvino-Kaffriç Faunal Province.

REMARKS: *Schizostylus* appears to be closely related to the core group of calmoniids centering around *Calmonia* itself, and is perhaps most closely related to *Deltacephalaspis* and *Paracalmonia.* Although *Schizostylus (Schizostylus)* in itself is quite distinct from all other calmoniids, the relatively plesiomorphic new subgenus *S. (Curuyella)* described below, while sharing synapomorphies with *S. (Schizostylus)*, nevertheless clearly illustrates that *Schizostylus* shares its affinities with the core *Calmonia* group (see Introduction).

Criteria for distinguishing *S. (Curuyella) granulata,* new species from the *Scaphiocoelia* Zone, from other *Scaphiocoelia* Zone taxa are given following description of the species below. The genus as a whole, however, can be confused with two other calmoniid taxa, *Probolops glabellirostris* (Kozlowski) and *Cryphaeoides rostratus* (Kozlowski), from the "Icla" and "Sicasica" faunas, respectively. These two taxa are

themselves apparently closely related and in turn appear to be related to *Tarijactinoides jarcasensis* Suárez Soruco, discussed elsewhere in this paper. (See Introduction for discussion of the *Probolops* group). *Probolops glabellirostris* poses a particularly fascinating problem, as it is at first glance almost identical with specimens of *Schizostylus (Schizostylus)* cf. *brevicaudatus* with which it is apparently sympatric (see fig. 16). *Probolops* is only known from the Icla beds at Padilla, Chuquisaca Department, Bolivia. It was described on the basis of a single part and counterpart cephalon (Kozlowski, 1923, p. 52), and we have been able to locate only a single additional specimen, consisting of part and counterpart of a cephalon and associated thorax from the lower part of the Icla section at Padilla (above the *Scaphiocoelia* Zone) (fig. 16). *Probolops* shares with *Schizostylus* a general cephalic conformation, with a pronounced anterior median cephalic process, small eyes, similar cephalic vaulting, genal spines of approximately the same size and orientation (in dorsal aspect) and small occipital and axial thoracic spines. However, Kozlowski (1923, p. 52–53) was entirely correct in his assertion that, in *Probolops,* the anterior branch of the facial suture does not transect the anterior glabellar lobe, but rather runs just proximal to the cephalic border and connects at the midline entirely ventral to the anterior cephalic process. Furthermore, the cephalic process and genal spines of *Probolops glabellirostris* are not inclined dorsally as steeply as they are in *Schizostylus (Schizostylus)*. The presence in *Probolops* of a spine on the posterior region of the palpebral lobe, on the posterior cephalic border (proximal to the genal spines; the "metafixigenal" spines of Struve, 1959, p. 0486), and a homologous series on the pleura of the thorax, are further differences between these genera. These latter differences may seem trivial in view of the great amount of intra-specific variation in spine development in many calmoniid taxa described in this paper and elsewhere, but these particular spines are otherwise known only in *Tarijactinoides* and *Cryphaeoides* among previously described calmoniid gen-
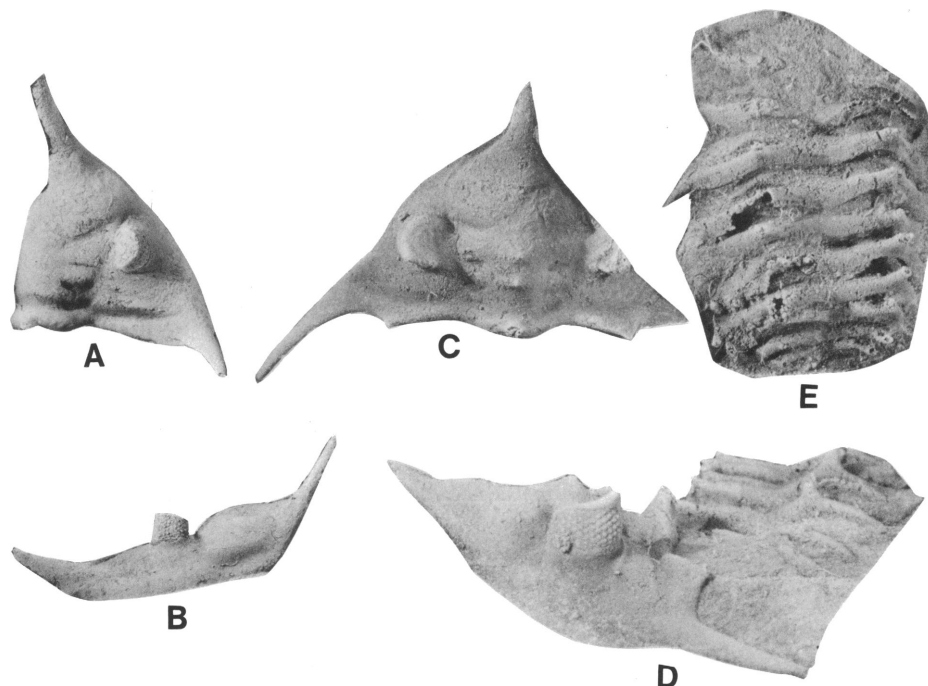
FIG. 16. Comparison of the homeomorphs *Schizostylus* (*Schizostylus*) cf. *brevicaudatus* and *Probolops glabellirostris*. Both specimens are from approximately the same horizon within the lower part of the Icla Formation (above the *Scaphiocoelia* Zone), Padilla, Bolivia. A, B. Oblique dorsal and right lateral views of latex cast of external mold of cephalon of *S.* (*Schizostylus*) cf. *brevicaudatus*, NMNH 245618 (latex cast AMNH 36697), ×2. C–E. *P. glabellirostris*. Dorsal (×3), left lateral (×4) views of latex cast of external mold of cephalon, and oblique dorsal view (×4) of latex cast of external mold of portion of thorax. NMNH 245619 (latex cast AMNH 36698).

era. We believe that the development of palpebral, metafixigenal, and serially homologous (to the metafixigenal) thoracic pleural spines are synapomorphies which, together with other features, serve to unite *Probolops* with *Tarijactinoides* and *Cryphaeoides,* together with a number of other as yet undescribed genera, into a coherent monophyletic group. Certainly, the course of the anterior branch of the facial suture as originally described by Kozlowski is sufficient in itself to separate *Probolops* from *Schizostylus*. (The pygidium of *Probolops glabellirostris* is unfortunately unknown still.) The extreme rarity of *Probolops,* and the relative commonness of *Schizostylus* at Padilla suggest that *Probolops glabellirostris* may be a genuine mimic of *Schizostylus* (*Schizostylus*) cf. *brevicaudatus*. However, such an assertion

warrants additional study; though figured here, we plan to redescribe *Probolops glabellirostris* in a future study.

Cryphaeoides rostratus may be confused with *Schizostylus* only insofar as both possess a long anterior median cephalic process. The anterior branch of the facial suture meets a short way up the dorsal surface of the cephalic process in *Cryphaeoides* and *Schizostylus* (*Curuyella*), while meeting much farther forward in *Schizostylus* (*Schizostylus*). *Cryphaeoides* may be distinguished from *S.* (*Curuyella*), however, in the fact that the facial suture does not transect the glabella in the former, but does so in the latter, and in other features mentioned above in conjunction with the discussion of *Probolops*. The difference between the course of the facial suture on the anterior process

in *S.* (*Schizostylus*) and *S.* (*Curuyella*) emerges in the following diagnoses.

SCHIZOSTYLUS (SCHIZOSTYLUS)
Figures 2L; 16A, B

EMENDED DIAGNOSIS: Cephalon highly arched; anterior process long, subconical, inclined anterodorsally at an angle of approximately 45–50°, smoothly continuous with gently sloping (posterodorsally) surface of anterior glabellar lobe. Anterior branch of facial suture continuous along dorsolateral margin of anterior process, gaining dorsal surface and meeting at midline one-fourth to one-third length of frontal process from anterior tip. Posterior border nearly straight, inclined slightly posterodistally. Genal spines relatively large, subconical, steeply inclined at an angle of approximately 35–48° from the horizontal. Small occipital spine variably present. Genae steeply sloping, with little or no development of lateral border furrow. Eyes prominent with 19 or fewer dorsoventral files. Cephalic surface generally smooth, or with large scattered tubercles. Thorax and pygidium as for genus; axis of pygidium with three distinct rings and large terminal piece.

REMARKS: Included species were tabulated under Remarks following the generic diagnosis. Excellent collections from a wide variety of localities and stratigraphic horizons are available for detailed studies of within and among sample variation in this highly interesting and unusual taxon, and we defer further comment pending such detailed work.

SCHIZOSTYLUS (CURUYELLA), NEW SUBGENUS

TYPE SPECIES: *Schizostylus* (*Curuyella*) *granulata,* new species, by original designation and by monotypy.

ETYMOLOGY: The name *Curuyella* is based on Curuyo, a town in the Tarija Department, southern Bolivia, near which the holotype and most referred specimens of the type species were collected.

DIAGNOSIS. Cephalon relatively flat for genus; genae relatively flat, hence entire ceph-

alon relatively broad. Anterior cephalic process shorter than for *S.* (*Schizostylus*), rather flat, triangular, terminating in sharp point, and inclined at an angle of approximately 35–40°. Anterior process separated from anterior glabellar lobe by a sharp break in slope, defining a distinct furrow [in contrast to the slight, gradational change in slope in *S.* (*Schizostylus*)]. Anterior branch of facial suture meeting at midline in a point on the dorsal surface less than halfway up the slope of the anterior cephalic process. Anterior process thus composed mostly of cephalic margin distal to facial suture, a short, triangular preglabellar field being defined proximal to the facial suture at the midline. Posterior border transverse, distally curved slightly anteriorly near genal angle. Genal spines relatively short and flat, inclined at an angle of approximately 15–20° from the horizontal. Occipital spine absent. Genae with distinct border furrows, and slightly dished. Genae becoming progressively more steeply inclined proximally, forming prominent mound supporting eye. Eye with 20 or more dorsoventral files. Cephalic surface generally covered with small granules.

Thorax and pygidium as for genus, lacking, insofar as is known, axial spines. Axis of pygidium with five distinct rings and relatively small terminal piece.

REMARKS: The relatively plesiomorphic nature of this subgenus has been discussed above under the genus as a whole. Although primitive in many respects, and retaining many characteristics in common especially with *Deltacephalaspis* (*Deltacephalaspis*), the nature (including size and position) of the eye corresponds closely to species of *Schizostylus* (*Schizostylus*), and the anterior cephalic process and genal spines, though less highly developed than in *S.* (*Schizostylus*), are clearly apomorphic features shared by the two subgenera. The course of the anterior branch of the facial suture is especially important in this regard, as the condition in *S.* (*Curuyella*) differs from *D.* (*Deltacephalaspis*) *comis* only in that the anterior glabellar lobe is inflated and a furrow separates the flat preglabellar field from the steeply sloping surface of the anterior glabellar lobe in *Cu-*

ruyella; no break occurs in *Deltacephalaspis*.

Schizostylus (Curuyella) granulata,
new species
Figures 2K; 17

TYPE SPECIMENS AND MATERIAL EXAMINED: Holotype, a part and counterpart cephalon, NMNH 245620. Two paratypes, NMNH 245621, and AMNH 36701, both cephala. In addition we refer a single thorax and articulated pygidium, AMNH 36700, to this species, but do not designate it as a type. Three additional cephala are known to us, two on a single slab in the Braniša Collections, AMNH, the other from an unknown locality (? Lower Belén Formation), in the Braniša Collection, NMNH 245622. All the other material is from the *Scaphiocoelia* Zone portion of the Gamoneda Formation, Curuyo, Bolivia.

ETYMOLOGY: Granulata, granulated, in reference to the distinctive ornamentation of this species.

DIAGNOSIS: As for subgenus.

DESCRIPTION: Excluding the anterior cephalic process and the genal spines, the general outline of the cephalon in plan view is roughly semicircular. The posterodistal margins of the genae are recurved anteriorly; the lateral margins of the genae swing smoothly anteroproximally, becoming more sharply reflexed tranversely opposite the anterolateral corners of the anterior glabellar lobe (producing a shouldered effect), then becoming abruptly reflexed anteriorly to form the cephalic process. The genal spines are short, flat, and inclined at an angle of approximately 35° (exsag., in plan view). In side view in standard orientation the cephalon is moderately arched, with the anterior process, median surface of anterior glabellar lobe, and the dorsal surfaces of the palpebral lobes in approximately the same horizontal plane. The genal spines are inclined at an angle of approximately 15–20° from the horizontal, whereas the anterior cephalic process slopes anterodorsally at an angle of approximately 35°–40°. The median region of the anterior glabellar lobe is roughly horizontal; posteriorly, the median surface of the glabella slopes gently back to the occipital furrow.

The axial furrows are straight and only slightly divergent. The axial furrows are relatively broad and lightly impressed; they are inclined steeply anterodorsally from the point of their inception opposite the occipital and posterior border furrows, anterior to the point midway along glabellar lobe 3p, and are then inclined anteroventrally. The axial furrow pit is developed as a thin, short, linear invagination (on the external cuticular surface—on internal molds it appears broader and shallower) opposite the distal terminus of glabellar furrow 3p; the axial furrow pit runs directly anteriorly (exsag.), causing a slight deflection in the course of the axial furrow, which then resumes its course diverging around the lateral margin of the anterior glabellar lobe. The axial furrows remain distinct throughout, and become confluent with the lateral and anterior cephalic border furrows just distal to the anterolateral corners of the anterior glabellar lobe.

The morphology of the anterior border, the anterior region of the anterior glabellar lobe, and the anterior cephalic process, is complex, and best described in relation to the course of the anterior branch of the facial suture. From the anterior margin of the visual surface, the facial suture runs anteriorly down the steeply inclined surface of the palpebral prominence which supports the ocular complex. The suture is set well away from the axial furrow and is not associated with a distinct anterior ocular ridge. The suture crosses the axial furrow a short distance anterior to the axial furrow pit, and transects the anterolateral region of the anterior glabellar lobe. The portion of the anterior glabellar lobe distal to the facial suture is nearly vertical and is bordered by the axial and anterior border furrows. Just proximal to the facial suture along its entire extent across the anterior glabellar lobe, a thin anterior glabellar ridge is developed which is relatively flat (i.e., sloping far less steeply than the area distal to the suture); this anterior glabellar ridge is set off from the remainder of the anterior glabellar lobe by an anterior glabellar furrow that is faintly developed laterally, but
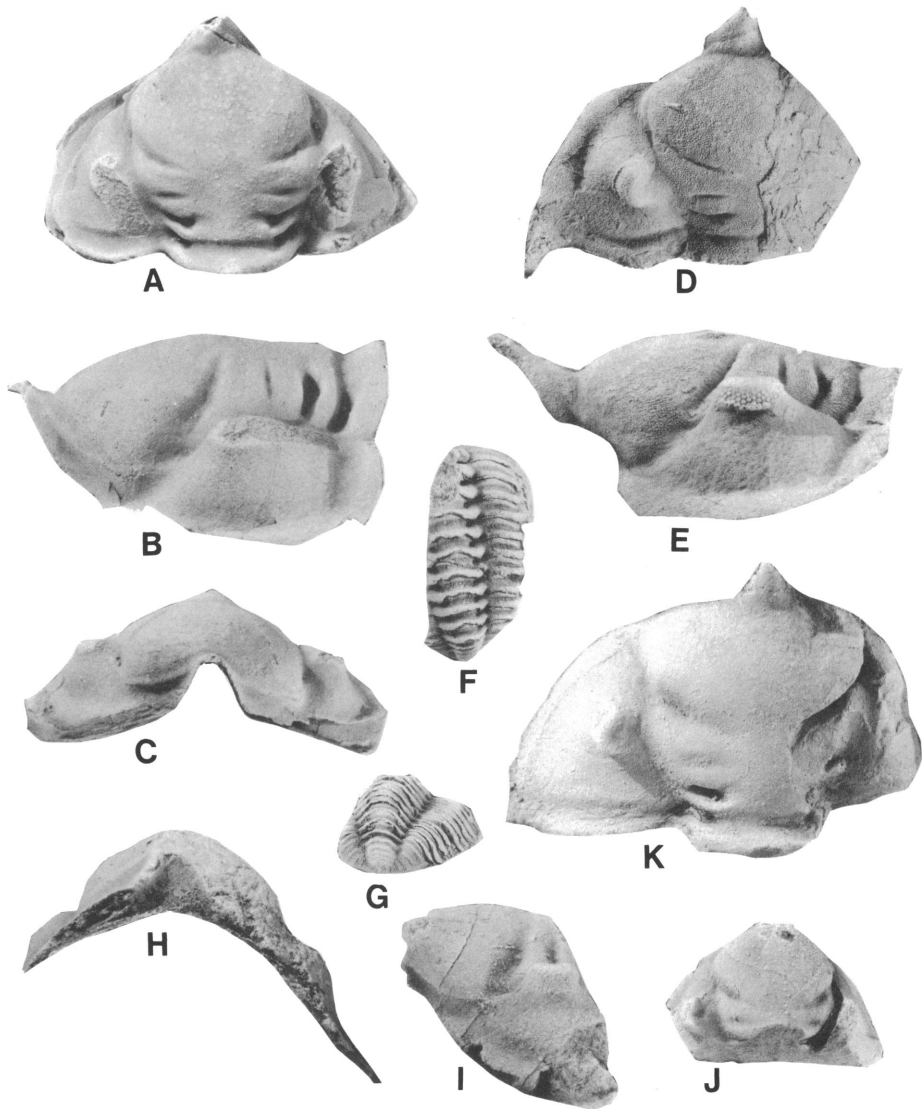
Fig. 17. *Schizostylus (Curuyella) granulata*. All specimens (except fig. 17K) from *Scaphiocoelia* Zone, Gamoneda Fm., Curuyo, Bolivia. A–E. Holotype cephalon, NMNH 245620 (latex cast of external mold, fig. 17D, E only, AMNH 36699). A–C. Dorsal (×2) (note pattern of auxiliary impression system), left lateral (×3) and frontal (×2) views of internal mold. D, E. Dorsal (×2) and left lateral (×3) views of latex cast of external mold. F, G. Dorsal and posterior views of internal mold of thorax and articulated pygidium, AMNH 36700 (Braniša Coll.), referred spec., ×2. H. Oblique ventral view of internal mold of cephalon. Paratype, NMNH 245621, ×3. I, J. Lateral (×3) and dorsal (×2) views of internal mold of cephalon. Paratype, AMNH 36701 (Braniša Coll.). K. Dorsal view of internal mold of cephalon, ×2. NMNH 245622, referred specimen. Precise horizon and locality unknown, probably *Scaphiocoelia* Zone, Belén region, Bolivia.

becomes more sharply incised medially. Approaching the midline, the facial suture continues in a roughly straight line anteroproximally, at the same time becoming reflected dorsally, and runs along the distal border of the anterior glabellar ridge. The anterior glabellar furrow, in contrast, is gently curved and confluent at the midline. Thus the anterior glabellar ridge becomes longer and distinctly triangular medially; inclined sharply anterodorsally, it forms a preglabellar field and is topologically the posteromedian portion of the anterior cephalic process. The remainder of the dorsal portion of the anterior cephalic process is formed by an extension of the anterior border ridge, which is likewise reflected anterodorsally and becomes rather flat and more distinctly triangular than in any other species of *Schizostylus*; though its true length is unknown, the portion of the anterior process distal to the facial suture and anterior border furrow is at least as long as the section proximal to the suture.

The ventral surface of the anterior cephalic process is formed by an extension of the doublure; as in related species, the ventral surface consists of a deep groove, widest posteriorly, bordered by steep lateral walls of the reflexed doublure. Proximally, the anterior doublure is a flat triangular area, bounded posteriorly by a gently but distinctly convex (anteriorly) hypostomal suture. Posterolaterally, the doublure is reflexed and closely associated with the dorsal cuticle.

The posterior branch of the facial suture runs transversely down and across the genal field and is reflexed posteriorly at the lateral border furrow. The suture is curved posteriorly at the lateral border furrow, and cuts across the lateral border well in advance of the genal spine. Ventrally the suture transects the doublure in a straight line, in line with the posterior border furrow of the dorsal surface.

The anterior glabellar lobe proximal to the anterior glabellar ridge and furrow is moderately inflated and generally ovate in outline. Glabellar furrows 3p arise near the midline roughly opposite the midpoints of the palpebral lobes, and run directly anterodis-

tally at an exsagittal angle of approximately 65° for about two-thirds its course, then becomes reflected sharply anteriorly (at a point roughly opposite the anterior margin of the eye), and terminates opposite the axial furrow pit without communicating with the axial furrow. Glabellar furrows 3p are relatively wide and deeply incised along their entire course (except near the proximal terminus) on both external casts and internal molds. The median glabellar field posterior to glabellar furrows 3p slopes smoothly and continuously at a slight posteroventral inclination, to the occipital furrow. Glabellar furrows 2p are very short, transverse, wide, and deeply incised, located roughly opposite the posterior margin of the eye; they do not communicate with the axial furrow. Glabellar lobe 3p is thus irregularly pentagonal in outline, and slightly inflated distally, and communicates distally with glabellar lobe 2p. Glabellar furrows 1p are very deeply incised and slightly curved (concave anteriorly), producing a ridgelike apodeme viscerally. The proximal end is bifurcate, with a short posterior ramus and a somewhat longer anterior ramus. Glabellar furrows 1p are in full communication with the axial furrows. Thus glabellar lobes 2p are roughly rectangular, with a slightly convex posterior border; their surfaces slope gently downward obliquely posterodistally. Glabellar lobes 1p are lower than 2p, and their surfaces are inclined in a similar fashion. Medially, the occipital furrow is continuous, quite shallow, and slightly convex anteriorly; distally it becomes more deeply incised and runs approximately transversely, communicating with the axial furrows. Glabellar lobes 3p are roughly as large as 1p and 2p combined; glabellar lobe 2p, in turn, is larger (in terms of comparative distal extent along the axial furrow) than 1p. The occipital ring is longest (sag.) medially, and is constricted distally; it is elevated above the posterior median glabellar field, and lies in roughly the same plane as the median region of the anterior glabellar lobe. The occipital ring lacks a median spine.

The posterior cephalic border consists of an arched ridge which in posterior view

slopes proximally down to the axial furrow, and distally to the lateral margin (proximal to the genal spine). In dorsal view, the posterior margin curves posteriorly out from the axial furrow forming a convex (posteriorly) arc, and then curves anteriorly distally near the base of the genal spine. The surface of the posterior border ridge is horizontal posteriorly, but slopes sharply downward into the broad posterior border furrow, which is also gently curved along its course between the axial furrow and the genal spine. The posterior border furrow is bounded anteriorly by a steep slope and a distinct ridge along the posterior region of the fixigena, a ridge which is roughly coincident in height with the posterior cephalic border ridge. The posterior border furrow becomes very shallow distally, and nearly disappears near the base of the genal spine. It communicates with the equally vaguely incised lateral border furrow; the librigenal section of the lateral border furrow, in contrast, is sharply incised opposite the eye, and becomes shallow again in the anterolateral region of the librigena. The shape and inclination of the genal spine were described above; in dorsal view the genal spine is nearly continuous with the curve of the distal margin of the lateral border. The lateral border is a flat ridge which is widest at the point just opposite the anterior region of the visual surface.

The fixigena is relatively flat distally, and slopes gently dorsally up to the posterior margin of the eye, and is then reflected ventrally down to the axial furrow, and merges with the steeply sloping palpebral area. In contrast, the librigena proximal to the lateral border furrow is nearly conical and somewhat "bulging" between that furrow and the eye socle, producing a high mound to support the eye. The eye socle is nearly vertical (actually somewhat concave on the internal mold) and is recessed under the visual surface. The visual surface slopes slightly dorsoproximally from the vertical throughout its extent. There are 20 (or perhaps slightly more) dorsoventral files bearing no more than five lenses per file in the central region of the visual surface. The lenses are densely packed and protrude well beyond the inter-

lensar sclera; some lenses appear slightly ovoid in the central region, indicating very close packing. The visual surface is relatively quite short (height) and small (length— Large Eye Index .27 for holotype).

The palpebral lobe is kidney-shaped, horizontal along its distal surface adjacent to the visual surface, and sloping proximally to the palpebral area, from which it is not distinctly set off. An unusual furrow, basically delineated by an absence of surficial granulation, runs from the base of the center of the palpebral lobe anteroproximally, communicating with the axial furrow near the front of the eye and serving to set the palpebral lobe off from the anterior region of the palpebral area. This furrow is not homologous with the "anterior ocular ridge" described for *Bainella* (*Belenops*) *insolita* and some species of *Deltacephalaspis,* and its functional interpretation and systematic significance are obscure.

The external surface of the cephalic cuticle is densely covered by a groundmass of (relatively) large granules (not as large as "true" tubercles). These granules are everywhere present except in the glabellar furrows and most portions of the axial furrows. Granules are present, but sparse, in the broad posterior border furrow. Granules are also less densely distributed over the posterior median area of the glabella, and, especially, over the occipital ring. Relatively deep dimples, linearly elongate (trans.) are numerous on the librigenae, especially in the lateral border furrow. Smaller, more rounded, less deeply emplaced and more scattered dimples are found over the entire fixigenal surface anterior to the posterior border furrow. All such dimples are smooth, i.e., devoid of granulation. On the internal mold, larger scattered tubercles (i.e., depressions on the visceral surface) are developed, especially on the anterior glabellar lobe, and seemingly in a random pattern. The pattern of the auxiliary impression system is developed externally as raised, relatively large mounds, usually with little or no covering groundmass of granulation. Viscerally, the system is developed as scars. There is a strongly developed outer pair of rows, and a narrow inner pair (nearly

parallel) recalling the pattern of *Acastoides* and other trilobites displaying the "acastid" pattern (see Introduction and fig. 2). A distinct posterior median impression is lacking. The hypostoma is unknown.

The thorax (known from a single internal mold referred to this species on the basis of its *Schizostylus*-like attached pygidium) consists of 11 segments. The axial rings are sagittally constricted. The pleura are gently sigmoid, and terminate in a blunt, flat edge; the distal pleural spine is either lacking, or not preserved, on the posterior segments. The pygidium of this referred specimen is relatively short and wide. The lateral margins are entire, and the posterior margin is distinctly pointed. The axis consists of five distinct rings and a terminal piece; there are five pleura, each bearing a pleural furrow, and fainter interpleural furrows are present along the entire pleural series. The axial furrows of both the thorax and pygidium are distinct, and the posterior margin of the pygidial axis is rounded, not reaching the posterior margin of the pygidium, but set off from the posterior pleural field by a sharp break in slope.

REMARKS: We have included a relatively longer, more detailed description of this species because of its unique morphology and excellent state of preservation. The features which serve to distinguish this species from others in the *Scaphiocoelia* Zone fauna are chiefly those which ally it to the genus *Schizostylus,* and were dealt with above. Isolated cranidia from the *Scaphiocoelia* Zone can be assigned to this species by their relatively great convexity and deep incision of the glabellar furrows; thus the problem of identifying *Scaphiocoelia* Zone calmoniids on the basis of cranidial characters (see Introduction for a discussion of this problem) does not involve specimens of *S.* (*Curuyella*) *granulata*. In addition, the single pygidium known to us from the *Scaphiocoelia* Zone which we attribute to ?*Acastoides* shows a more parabolic, rather than transverse terminal margin to the pygidial axis, as well as a more rounded posterior pygidial margin.

Finally, paratype AMNH 36701 (see fig. 17I, J) is rather unusual in several respects, and deserves special attention. An undoubt-

ed *Schizostylus* from the *Scaphiocoelia* Zone at Curuyo, this specimen (an internal mold of a cephalon with the posterior region, right eye, and anterior process destroyed) is relatively more convex (recalling younger species) and has a relatively larger (exsag. length) eye. We regard this specimen as a variant, rather than as a distinct taxon, but note its peculiarities in the hope that further collecting might reveal the significance of these two differences between this specimen and all (only 5) of the other cephala available to us.

ACASTOIDES DELO, 1935

Acastoides in one of only two genera of Calmoniidae (*sensu* Struve, 1959; the other is *Phacopina*) that is said to occur within both the Lower Devonian Malvino-Kaffric Province, and in areas of the Silurian and Devonian of the Northern Hemisphere (western Europe at least as far east as Turkey; see Haas, 1968, and Shergold, 1966). Delo (1935) designated *Acastoides henni* Richter, a German taxon, as the type species, and in view of this fact, and the moderate diversity within this genus outside the Malvino-Kaffric Province, we shall not attempt formal revision of the entire genus.

However, it is well to point out that specimens from the Malvino-Kaffric Province may not be correctly allocated to *Acastoides*. "*Acastoides*" *sensu lato* is essentially a generalized acastid with an inflated anterior glabellar lobe and a rather short, posterolaterally rounded ("phacopidized") pygidium. The margin is generally entire, but small denticles may appear on the ventral doublure on the anterior three segments (Struve, 1959). Indeed, Haas (1968) has recently figured the pygidium of his newly erected subgenus *A.* (*Talus*), showing the distinct development of five pairs of marginal lappets associated with a quite *Acastoides*-like cephalon. *Acastoides verneuili* (d'Orbigny) [?=*A. acutilobata* (Knod)] from the Icla and Sicasica faunas of Bolivia, is the only Malvino-Kaffric species other than *Acastoides insolitus* Wolfart [=*Bainella* (*Belenops*) *insolita* of this paper] yet to be re-
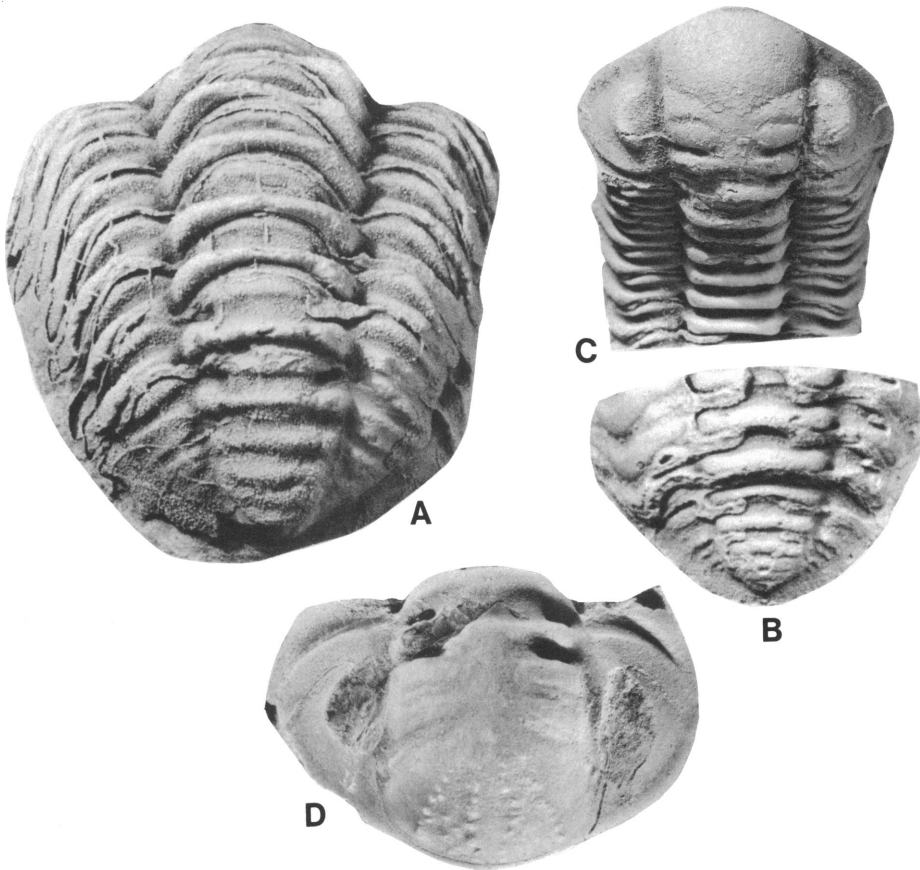
FIG. 18. *?Acastoides verneuili*. A. Dorsal view of internal mold of pygidium showing marginal lappets (spines). NMNH 245623, ×3. Specimen referred to this species with some doubt (see text). Icla Fm., Padilla, Bolivia. B. Dorsal view of internal mold of a pygidium definitely determined as *?A. verneuili,* for comparison with figure 18A. AMNH 36702 (Smith Coll.), ×3. Chacoma, Bolivia, precise horizon unknown. C. Dorsal view of internal mold of cephalon and anterior region of thorax, showing typical cephalic outline (in plan view) of austral *?Acastoides,* ×2. AMNH 36703 (Smith Coll.), Lower Sicasica beds, Belén, Bolivia. D. Oblique frontal view of anterior region of cephalon, showing pattern of auxiliary impression system developed as tubercles (i.e., matrix infilling of scars on visceral side of cuticle). ×3. NMNH 245624, Icla Fm., Padilla, Bolivia.

ferred to the genus *Acastoides*. We are in possession of a thorax and pygidium identical with that of *A. verneuili* (including the distinctly spined pleural tips) from the Icla beds at Padilla, on which are developed two large anterior pairs of lappets, and a minor third pair, on the pygidium (fig. 18A); though the specimen lacks a cephalon, *A. verneuili* is present in this fauna.

Aside from a rounded posterior outline,

the pygidia of the taxa from the Northern and Southern hemispheres differ markedly. Rounding, in and of itself, is common in other taxa, and can be considered an independent development, or even as a relatively primitive feature typical of many older acastids. Northern *Acastoides* have broader and generally relatively larger pygidia in which the axis is said to be relatively flat. Those from the Malvino-Kaffric Province tend to

have short and narrow pygidia, with a prominent axis bluntly rounded posteriorly and well set off from the posterior pleural field. Moreover, northern species tend to have well-inflated palpebral lobes, sharply set off from the palpebral area by a well-incised furrow, whereas southern forms lack a well-differentiated palpebral complex.

A further difference between austral and boreal species assigned to *Acastoides* involves the shape of the gena in plan (dorsal) view. In austral forms, the posterior border of the cephalon is recurved anterolaterally and the genal angle is roughly opposite the posterior margin of the eye (see fig. 18C). In boreal forms the genal angle forms the posterolateral corner of the cephalon, the usual situation in acastid-like trilobites. Specimens from the Icla Formation at Padilla, in fact, seem intermediate between austral "*Acastoides*" and species of *Calmonia* from the Falkland Islands with respect both to pygidial and genal morphology. The resemblance between northern and southern "*Acastoides*," then, boils down to relatively high inflation of the entire cuticle in both groups. This apparent conflict in distribution of similarities suggests the hypothesis that inflation of the anterior glabellar lobe and concomitant development of a posteriorly rounded micropygous pygidium occurred independently as a parallelism in the two hemispheres (as it indeed was independently achieved by *Parabouleia* and *Bouleia* within Bolivia itself). The hypothesis requires further test, but our observations do suggest that Malvino-Kaffric *Acastoides* may not be congeneric with boreal *Acastoides,* but instead may be the sister-group of the genus *Calmonia*. For this reason, we refer the new species from the *Scaphiocoelia* Zone, as well as *A. verneuili* itself, to ?*Acastoides*.

?Acastoides gamonedensis, new species
Figure 19

TYPE SPECIMEN AND MATERIAL EXAMINED: We designate a single weathered cephalon with three articulated thoracic segments as the holotype, NMNH 245625, from the Gamoneda Formation, Curuyo, Tarija De-partment, Bolivia. We designate a weathered pygidium articulated with two thoracic segments, from the same horizon and locality, as the paratype, NMNH 245626. These are the only two specimens of this species available to us.

ETYMOLOGY: The name *gamonedensis* is derived from Gamoneda, near Curuyo, and the name of the formation which has produced these specimens.

DIAGNOSIS: Cephalon less highly arched than in ?*A. verneuili*. Anterior glabellar lobe highly inflated and shouldering pronounced. Axial furrow pits present. Glabellar furrows lightly incised. Eyes small for genus; axial region relatively broad. Pygidium rather broad and flat.

DESCRIPTION: The cephalon of this species is roughly triangular in dorsal view, with a length/width ratio of approximately .47. The anterior glabellar lobe protrudes beyond the anterior border ridge, and the cephalon is slightly shouldered anterolaterally, in dorsal view. The axial furrows are lightly impressed and slightly divergent at an angle of approximately 20°. The anterior arch is broad and moderately shallow. The axial furrows are inclined dorsally from the occipital furrow to the point opposite glabellar furrows 2p, and are thence inclined anteroventrally. The axial furrow pits are present as linear (exsag.) narrow invaginations; anterior to the pits, the axial furrows are broad, shallow, more divergent, and continuous with the broad shallow lateral cephalic border furrow. The anterior branch of the facial suture traverses the axial furrow just anterior to the axial furrow pit, transecting only a very slight area of the anterior glabellar lobe, reaching the proximal margin of the anterior cephalic border ridge, and running continuously along the anterior margin of the anterior glabellar lobe.

The anterior glabellar lobe has a steep anterior slope in lateral view. It is inflated and roughly pentagonal in shape (in dorsal view); the posteromedian section of the anterior glabellar lobe is nearly horizontal. The entire median surface of the glabella is only slightly sloping posteroventrally. The occipital ring is elevated only slightly above the median
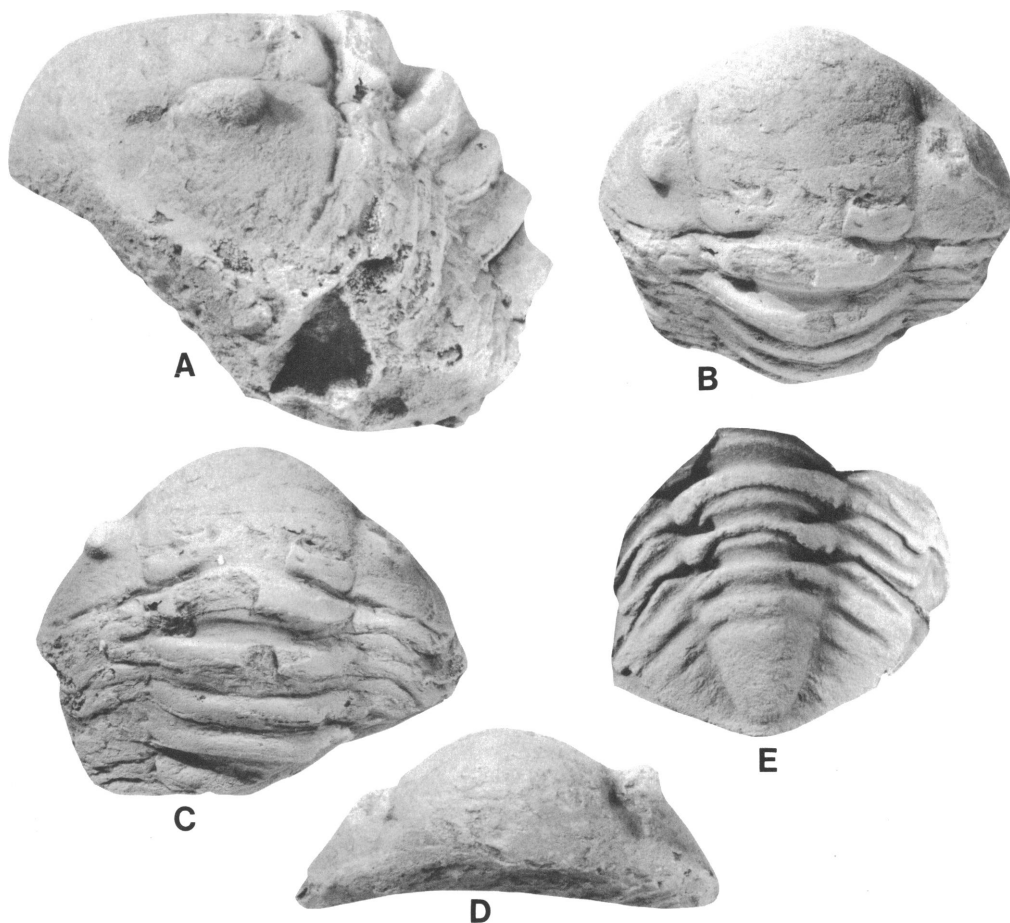
FIG. 19. *?Acastoides gamonedensis*. *Scaphiocoelia* Zone, Gamoneda Fm., Curuyo, Bolivia. A–D. Left lateral (×3), dorsal (×2), oblique posterior (×2) and frontal (×2) views of internal mold of cephalon and articulated anterior region of thorax. Holotype, NMNH 245625. E. Dorsal view of internal mold of pygidium. Paratype, NMNH 245626, ×3.

glabellar field, and does not attain the height of the anterior glabellar lobe (in standard orientation).

Glabellar furrows 3p are lightly impressed, nearly transverse for the proximal two-thirds portion, and are then reflected anterodistally, approaching, but not communicating with, the axial furrows. Glabellar furrows 2p are lightly impressed, wholly transverse, and do not communicate with the axial furrows. Glabellar furrows 1p are developed as deep transverse invaginations, running slightly anterodistally, and are apparently not contin-

uous medially. The occipital furrow is continuous medially, and is only slightly reflected anteromedially, with transverse apodemal pits developed laterally. The occipital and 1p glabellar furrows communicate laterally with the axial furrows. Glabellar lobes 1p–3p are slightly wider at the axial furrows than medially. The occipital lobe is narrowest (exsag.) at the axial furrow, and is widest (sag.) medially.

The posterior border ridge is transverse and widest proximally. The posterior border furrow is deepest and broadest proximally;

it is nearly transverse, and is apparently continuous with the faint lateral cephalic border furrow. The genal area is obscure, apparently terminating at an acute angle, but lacking a genal spine. The genae slope steeply laterally (librigenal surface), sloping more gently on the fixigenal surface. The librigenae are not dished, but rather are continuous in slope with the lateral border ridge. The eye is small both in length and in the height of the visual surface (Large Eye Index .28), and is situated close to the axial furrow opposite glabellar lobes 2p and 3p. The dorsal surface of the palpebral lobe lies in approximately the same plane as the median region of the glabella opposite glabellar furrows 2p. The eye socle is absent, and the visual surface arises abruptly from the librigenal surface. The morphology of the visual surface is obscure; the palpebral lobe is flat and not sharply demarcated from the palpebral area.

An anterior border ridge is present (not well preserved) and bears granules. The cephalic doublure and hypostoma are unknown. The auxiliary impression system and ornamental details (other than granules on the anterior border ridge) are unknown, except dimpling is developed on the genal surface, with larger individual dimples occurring over the librigenal surface especially near the lateral cephalic border furrow opposite the eye, and smaller dimples on the fixigena.

The thorax has broad, shallow axial furrows; the axis itself is relatively low and broad. The axial rings are not constricted sagittally. The posterior thoracic segments (i.e., on the paratype specimen) have linear pleural furrows, panderian protuberances, and small, posterodistally directed spines on the pleural tips. The pygidium of the paratype specimen is short and narrow ("phacopid-like"), with a length/width ratio of approximately .50. The axis is distinctly set off from the pleura, moderately well arched, with two distinct rings and a long tapering, bluntly rounded posteriorly terminal piece. (The pygidium is weathered, thus it is possible that additional rings have been obscured.) Four pleural furrows are visible, but no interpleural furrows are present on this

specimen. The pygidial doublure is reflected against the visceral side of the dorsal surface. No ornament or spines have been observed on either thorax or pygidium.

REMARKS: We have included the paratype specimen (NMNH 245626) in the description with some hesitation only because it was not directly associated with the holotype (and only known) cephalon. However, the paratype pygidium is clearly referable to ?*Acastoides* (*sensu* above discussion and as discussed further below), hence our decision to include it in the diagnosis and description. The axis of the posterior two thoracic segments and of the pygidium of this paratype specimen seems a bit more prominent than that of the anterior three thoracic segments articulated with the holotype cephalon, but we have observed the same increase in relative height of the axial lobe progressively down the thorax of complete individuals of ?*A. verneuili*, and are consequently confident that this difference between the two specimens is if anything in agreement with our decision to refer these two specimens to the same taxon. In view of the scant and rather poorly preserved nature of the material, we present only a relatively brief description of this species, fuller description to await the eventual discovery of additional and better preserved specimens.

?*Acastoides gamonedensis* differs from ?*Acastoides verneuili* in being slightly less highly arched. In addition, ?*A. verneuili* possesses a more highly inflated anterior glabellar lobe which protrudes further anteriorly producing a distinctly more shouldered effect. The genae of ?*A. verneuili* are also more steeply sloped and the lateral cephalic border furrow is more distinctly developed in that species than in ?*A. gamonedensis*. Axial cephalic and 2p and 3p glabellar furrows are also more deeply incised in ?*A. verneuili* than in the taxon from the Gamoneda Formation. The eyes of ?*A. verneuili* are relatively larger, extending the entire distance between glabellar furrows 1p and 3p, and taller, though standing at the same height relative to the more inflated median glabellar field, than in ?*A. gamonedensis*. The axis of ?*A. verneuili* appears to be relatively narrow-

er, and the axial rings somewhat more sagittally constricted than in ?*A. gamonedensis.* The pygidium of ?*A. verneuili* is relatively narrower and perhaps more highly arched than in ?*A. gamonedensis.* The axis of the former appears to be more bluntly rounded posteriorly, with a shorter terminal piece, though the morphology of ?*A. gamonedensis* is obscure in the single known pygidium. We shall defer extensive comparison with other Malvino-Kaffric species of ?*Acastoides* pending the necessary revision of these taxa.

?*Acastoides gamonedensis* is, as well as all *Acastoides*-like taxa, similar to some species of *Phacopina* Clarke. Species of *Phacopina* indeed are similar to ?*A. gamonedensis,* particularly in the weak development of glabellar furrows 2p and 3p, and the small eye positioned directly on the cheek with no true eye socle developed, and set in close to the axial furrow, and the posteriorly rounded pygidium. However, species of *Phacopina,* particularly *Phacopina convexa,* new species, described below from the *Scaphiocoelia* Zone of Bolivia, have a more convexly arched cephalon but a flatter, yet steeply sloping anterior glabellar lobe, and a longer and flatter pygidium, and thus easily distinguished from ?*A. gamonedensis.*

Pygidia of *Schizostylus* may be confused with "*Acastoides*" species; criteria for distinguishing the pygidium of *S. (Curuyella) granulata* from that of ?*A. gamonedensis* were given above following the description of *granulata,* and are not repeated here.

Finally, in terms of the cephalon only, ?*A. gamonedensis* is quite similar to *Bainella (Belenops) insolita.* The cephala of these two taxa have similar overall proportions, degree of inflation of the anterior glabellar lobe, development of the anterior arch, and weak implacement and general shape of glabellar furrows 2p and 3p. However, the eye of *B. (B.) insolita* is raised on a high cone formed from the gena and a definite, tall eye socle, and the eye is set out a relatively greater distance from the axial furrow. Also the lateral border furrows are well defined in *insolita,* producing a dished effect to the librigenae; furthermore, the occipital ring is raised high above the posterior median gla-

bellar surface, and, of course, frequently bears a large median spine. The doublure of the anterior region of the cephalon, while unknown in detail for ?*A. gamonedensis,* appears to conform to the normal, somewhat tumid, but rounded condition of ?*A. verneuili,* unlike the distinctly flat triangular posteromedian section, bordered by a dorsally reflected ridge confluent with the anterior cephalic border ridge in *insolita.* Isolated cephala lacking eyes *may* be difficult to determine; however, the thoraxes and pygidia of these two taxa differ in so many features that we believe further elaboration is unnecessary.

PHACOPINA CLARKE, 1913

Phacopina Clarke, 1913a (pars), p. 149; non Kozlowski, 1923, p. 49; non Swartz, 1925, p. 50; non Feruglio, 1930, p. 92, 94; Delo, 1940, p. 31 ff. (pars); Hupé, 1953, p. 236 (pars); Hupé, 1955, p. 261 (pars); Struve, 1959, p. O488 (pars); Wolfart, 1968, p. 120 (pars).
Jujuyops Baldis and Blasco (in Baldis et al., 1976), 1976, p. 215.

TYPE SPECIES: *Phacops braziliensis* Clarke, 1890, p. 15, pl. 1, figs. 1, 2.

REVISED DESCRIPTION: (Based on type specimens of *Phacopina braziliensis* (Clarke) and *Phacopina convexa,* new species, and *Phacopina padilla,* new species, as discussed under Remarks below.) Species of *Phacopina* are small calmoniids with a moderately to highly arched cephalon. The cephalic outline in dorsal view is nearly semicircular, with smoothly curved anterior and lateral borders (i.e., not shouldered), and a nearly transverse posterior margin. The entire dorsal cephalic surface is smoothly curvilinear, with no major abrupt breaks in slope of any feature. The axial furrows are broad and shallow on internal molds, and generally absent as discrete furrows on external casts, except as faint, narrow furrows anterior to the eye. No discrete axial furrow pit is developed. The axial furrows are nearly straight from the occipital furrow to a point opposite the distal terminus of glabellar furrow 3p, and then diverge sharply anterolaterally and merge with the lateral cephalic

border furrow. The anterior ramus of the facial suture is straight, inclined slightly anteroproximally; it runs just distal to the axial furrow, then traverses the furrow and transects the anterolateral corner of the anterior glabellar lobe opposite the distal terminus of glabellar furrow 3p. Near the anterior border furrow, the facial suture is deflected proximally, joining the anterior border furrow, and meeting at the midline in a smoothly rounded curve. The posterior ramus of the facial suture is nearly transverse, and is reflected posteriorly across the lateral cephalic border. The anterior border furrow is faint and shallow, and does not communicate with the lateral border furrow; the anterior border is a thin ridge.

The glabella is subquadrate, with the anterior margin expanded anterolaterally and slightly curvilinear, and convex anteriorly. All glabellar lobes plus the occipital ring lie in the same curved surface, with the median area arched above the distal ends of all glabellar lobes. Glabellar furrows 3p are lightly incised on internal molds; on the external surface, glabellar furrows 3p are not incised, but are indicated by the absence of cuticular granulation. Glabellar furrows 3p are essentially straight, and inclined at an exsagittal angle of approximately 60–65°; the 3p furrow is slightly sinuous in larger specimens of some species. When sinuous, the proximal portion of the furrow is widest, and the distal portion is inclined slightly more anterodistally. Glabellar furrows 3p approach, but do not communicate with, the axial furrows.

Glabellar furrows 2p are faintly incised on internal molds, and lightly incised or absent on the external surface, recognizable only by the absence of cuticular granulation; they are short, essentially transverse, and do not communicate with the axial furrows. Glabellar lobes 2p and 3p are thus fused distally and project slightly distally into the axial furrows. Glabellar furrows 1p are deeply incised, and are developed as broad apodemes distally (projecting viscerally, slightly posteroventrally) and as a narrow furrow on the external surface; they are roughly transverse, communicating with the axial furrows distally and sometimes "pinched" posterior-

ly near the middle of their course by a slight anterior projection of glabellar lobe 1p. Glabellar furrow 1p is not continuous medially. Glabellar lobes 1p are subrectangular and slightly wider at their exsagittal midpoint than at either end. The occipital furrow is slightly convex anteriorly at the midline, lightly incised (especially medially), with deep apodemes (which are narrower than those of glabellar furrows 1p) developed in the distal regions, and interrupted (on internal molds) by a slight projection of the occipital ring into the middle section of the apodeme. The occipital ring is smooth, convex, thus widest medially, with a straight (tr.) posterior margin.

The posterior border is nearly transverse, thinnest near the axial furrow, and becoming broader and projecting posteriorly to a point opposite the rear margin of the occipital ring in the distal region. The posterior border furrow is deeply incised, fairly broad on internal molds, narrow on the external surface, and becomes obsolescent at the genal angles and does not communicate with the broad, shallow lateral cephalic border furrow. The posterior border furrow runs slightly posterodistally from the axial furrow, and is then reflected directly transversely. The genal angles are obtusely rounded, and bear short spinules in some species. The lateral border is broad and inclined at the same angle as the remainder of the librigenal surface. The lateral border furrow is broad and very shallow; hence the librigena is not dished. The lateral border is confluent with the much narrower anterior border.

The eyes are of variable length (among species), and set in close to the axial furrows, with the anterior and posterior margins of the visual surface adjacent to the axial furrows. The palpebral lobe is reniform, flat, and concordant with the maximum height of the glabella. The palpebral furrow is faint to obsolescent. The palpebral area is minute, essentially a broadened area of the nearly obsolescent axial furrow.

The cephalic doublure is flat anteromedially and inclined anterodorsally at a slight angle. On internal molds, the posterior portion of the anteromedian area of the doublure

is depressed along the hypostomal suture, representing a visceral thickening of the cuticle. The hypostomal suture is slightly convex anteriorly. Posterolaterally, the doublure is reflected into vertical walls, closely associated with the dorsal cuticle. The ventral margin of the cephalon is thin posterolaterally. The hypostoma is unknown.

The entire external surface of the cuticle is crowded with exceedingly minute granules everywhere except in the axial and glabellar furrows. The auxiliary impression system is strongly developed as scars (i.e., nodes on internal molds), and is sometimes also developed as faint nodes on the external surface; the pattern is similar to that of ?*Acastoides*, with the central pair of exsagittal rows and distal pair diverging anteriorly, and with irregular rows of accessory scars developed anteriorly between the two major rows (figs. 2, 22E, G).

The genae are dimpled, with dimpling most strongly developed on the internal molds, and faint or non-existent on the external cuticular surface. Dimples are largest along the border furrow of the librigena, and are somewhat smaller and of coequal size on the remainder of the librigena and on the fixigena.

The axial rings of the thorax are widest distally; the axial furrows are sharply incised only on the posterior portion of each segment. The pleura are gently sloping; pleural furrows are deeply incised, straight, and run posterodistally at an exsagittal angle of approximately 110°. Pleural tips are flat and non-spinose.

The pygidium is rather flat, micropygous, rounded posteriorly, and the margin is entire. The axial furrows are distinct; the axis is rounded posteriorly, does not reach the pygidial margin, and tapers posteriorly, with four or five axial rings plus a terminal piece. The first (anterior) ring furrow is deeply incised, and bears an accessory half-ring. Ring furrows are progressively more lightly incised, becoming obsolescent, posteriorly. The anterior two pairs of pleura are distinct; pleural and interpleural furrows are developed only proximally for the first two pairs of pygidial pleura.

REMARKS: The foregoing revised description of *Phacopina* is based solely on the type species *P. braziliensis*, *P. convexa* from the Gamoneda Formation at Gamoneda and Sella Jarcas, Tarija, and *P. padilla* from the lower part of the Icla Formation at Padilla, Bolivia. Survey of all relevant literature shows *Phacopina* to be understood as a rare, small, moderately arched acastid with a smoothly curved anterior and lateral cephalic border, eyes set in close to the axial furrows, distinct anterior border ridge, anterior glabellar lobe only slightly inflated, and with generally effaced glabellar furrows. Most taxa referred to *Phacopina* are rather small and bear a striking resemblance of the genus *Eophacops* Delo of the Phacopidellinae. Suárez Soruco (1971) figured a single cephalon as *Phacopina* (?) sp. from the Gamoneda Formation (*Scaphiocoelia* Zone), at Jarcas, Bolivia, an identification we adopted throughout most of the course of our study of the trilobites of this fauna. Upon examination of most of the type specimens of all the species that have ever been allocated to this genus we frankly report that the situation is indeed messy. There are two basic problems in understanding *Phacopina*, the greatest being the miserable state of preservation of the type and topotype specimens of the type species. Also, *Phacopina* seems to be a grab bag of essentially plesiomorphic acastid-like trilobites with more or less effaced glabellar furrows. According to various authors, the genus embraces: (1) the type species *P. braziliensis* (Clarke, 1890) from the Maecuru sandstone; (2) various North American species described by Clarke, as well as by Williams and Breger (1916); (3) the Bolivian *Scaphiocoelia* Zone species figured by Suárez Soruco; (4) *Phacopina braziliensis* var. *chojnacotensis* Swartz, 1925 and *Phacopina bonarelli* Feruglio, both from the Silurian of Bolivia; (5) *Acaste devonica* Ulrich, 1892 and related taxa described by Wolfart, 1968 [under *Phacopina* (*Vogesina*)] from the Devonian of Peru and Bolivia; (6) *Scotiella*, a boreal Silurian genus regarded as a subgenus of *Phacopina* by Struve (1959), and (7) the recently described *Jujuyops* from Argentina, which we consider a

junior synonym of *Phacopina*. We have been prompted to review all these taxa and in so doing we have found them indeed generally quite similar. But special care must be taken in delimiting taxa and evaluating their affinities when the taxa in question are so generally plesiomorphic.

Clarke described the species *Phacops braziliensis* in 1890 (p. 15), basing his description on cephala only, two of which were figured. In that same publication, Clarke (1890, p. 16 and fig. 3) briefly described *Phacops anceps* from the "Upper Helderberg limestone at Cayuga, Province of Ontario." These two species were next discussed, briefly, in Clarke (1892), and more fully in Clarke's (1900) studies of the Oriskany fauna of Becraft Mountain, where a rare acastid was first described as *Phacops (Acaste)* cf. *anceps* Clarke, 1892, and later as *Phacops correlator*. In each of Clarke's two volumes of his large memoir, all previously described species were briefly discussed in conjunction with descriptions of material referred to *Phacops (Phacopidella) correlator* from the Gaspé sandstone (Clarke, 1908, p. 226) and *Phacops (Phacopidella) nylanderi* (1909, p. 96) from the Chapman sandstone of Maine. Finally, Clarke coined the generic name *Phacopina* in 1913 (1913a, p. 149 ff.), including *P. braziliensis, P. anceps, P. correlator,* and *P. nylanderi.* His diagnosis of the genus (1913a, p. 149) is as follows: "singularly compacted cephalon, elevated and somewhat protuberant glabella on which the furrows are almost extinct (the first two usually not showing except on compression or upon casts); rounded drooping cheeks, without spines and with relatively large eyes. . . . In *P. braziliensis* alone of all these species is the pygidium known and this is relatively large and heavy, multiannular without spines and blunt at the extremity." Clarke considered the group boreal, with the sole austral representative being *P. braziliensis* from the Lower Devonian of Brazil (Rio Maecuru).

We have summarized the history of Clarke's treatment of this group in order to trace the development of the concept of the genus *Phacopina.* [Williams and Breger, 1916, described another species of *Phacopi-*

na from the Chapman sandstone of Maine, as *Phacopidella chapmani,* in our opinion an evident synonym of *P. nylanderi* (Clarke), though this opinion is not shared by Delo (1940, p. 32). Delo (1940, p. 31–33), the only subsequent author to consider these North American Devonian species, briefly reviewed and refigured all of them. He recognized their acastid affinities, expressed doubt that all North American species would eventually prove to be congeneric, but otherwise retained Clarke's (1913a) assignment of them to *Phacopina.*] Reading Clarke's cited discussions of these species reveals inconsistencies and emendations in his remarks on nearly all of them; Clarke never refigured the specimens of *P. braziliensis,* nor did he ever figure the pygidium unknown to him in 1890, but briefly described by him in 1913. This pygidium was not included with the two type cephala in the collections of the National Museum of Natural History, which we have restudied (fig. 20A–C). The larger of the two is a cast, evidently struck from an external mold no longer in the collections. Two additional cephala, evidently topotypes, are associated with the type; all are catalogued as NMNH 23880. The poor quality of preservation prevents us from presenting a useful emended diagnosis of this species. However, the following morphological details are apparent, and are crucial to the interpretation of all other taxa attributed to the genus. The cephala are indeed small and smoothly curved (i.e., not shouldered). There is a thin but continuous anterior border ridge; the entire cephalon is rather depressed, and, particularly, the anterior glabellar lobe is only slightly inflated. The eyes are relatively large, approaching the posterior border furrow, and running anteriorly almost as far as the distal end of glabellar furrows 3p. Glabellar furrows 2p and 3p are all but invisible, whereas the 1p furrows are deep transverse apodemal grooves. The axial furrows diverge at an angle of approximately 35–40°, and, most significantly, as best shown on one of the topotypes, the anterior branch of the facial suture does indeed transect ["encroach" in Clarke's (1890, p. 15) terminology] the anterolateral corners of the glabella, though the
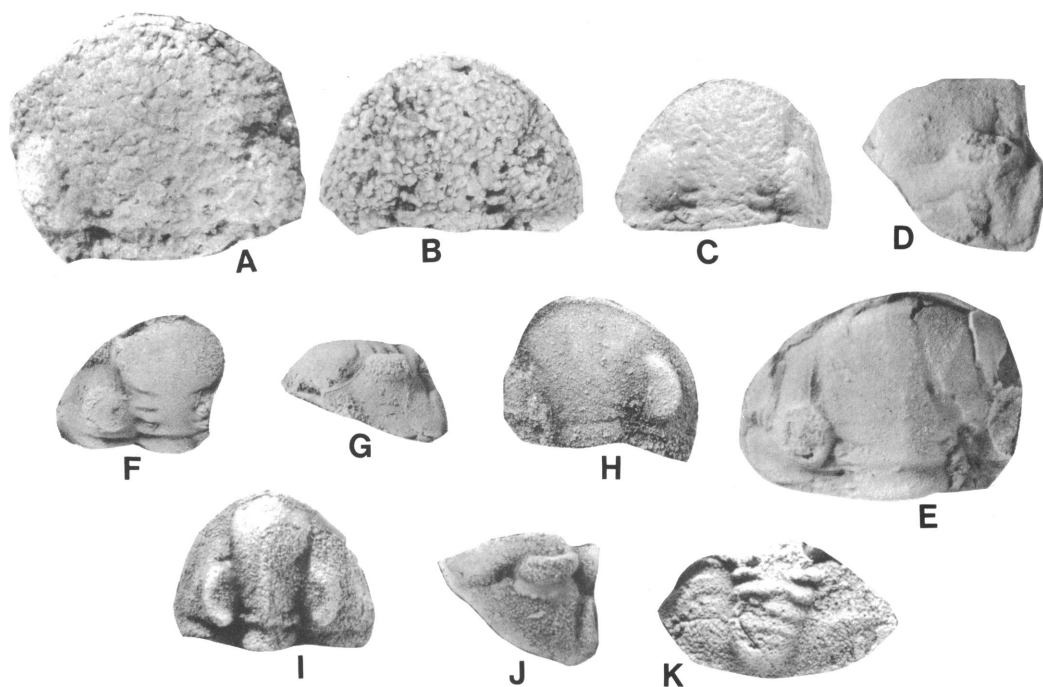
FIG. 20.   A–C. *Phacopina braziliensis*. Maecuru Fm., Rio Maecuru, Brazil. A. Dorsal view of internal mold of cephalon. Apparent topotype, NMNH 23880. ×6. B. Dorsal view of internal mold of cephalon. Syntype, NMNH 23880, ×4. C. Dorsal view of cast of external mold of cephalon. Syntype, NMNH 23880, ×3. D, E. *Phacopina anceps*. Onondaga Fm., Cayuga, Ontario. Left lateral and dorsal views of internal mold of cephalon. Holotype, NYSM 4609 (13880/1), ×5. F–H. *Phacopina correlator*. F, G. Dorsal and left lateral views of latex cast of external mold of cephalon. Glenerie Fm. ("Oriskany"), Becraft Mt., Hudson, New York. Holotype, NYSM 4611 (138821/1) (latex cast AMNH 36704), ×4. H. Dorsal view of latex cast of external mold of cephalon, ×3. Gaspé Fm., Gaspé basin, Quebec. NYSM 9825 (13882/2). I, K. *Phacopina chapmani*. Chapman Fm., Aroostook Co., Maine. I, J. Dorsal and left lateral views of internal mold of cephalon. ×5. Syntype, NMNH 59882. K. Dorsal view of internal mold of pygidium. ×5. Syntype, NMNH 59882.

amount of the glabellar corners thus isolated is far smaller than it is in, say, *Phacopina convexa* or *P. padilla*. Finally, we cannot evaluate Clarke's description of the unfigured pygidium.

With these salient features of the type species in mind, we shall now consider the various North American Devonian occurrences of *Phacopina*. *Phacopina anceps* (Clarke, 1890, p. 16, fig. 3, and fig. 20D, E, this paper) remains known from but a single cephalon from the "Onondaga" limestone of Cayuga, Ontario (NYSM 4609). In this spec-

imen the anterior portion of the anterior glabellar lobe is markedly inflated, but is not expanded anterolaterally, hence the facial sutures do not transect the anterior glabellar lobe. Furthermore a distinct axial furrow pit is developed in *anceps*—a feature totally absent in *P. braziliensis*. The eyes of *anceps* are large, apparently extending nearly as far posteriorly as the posterior border furrow. The genae are not steeply deflected ventrally.

In *Phacopina correlator* (from Becraft Mountain; NYSM 4611, an external mold of

a partial cephalon—see fig. 20F, G), the eyes are likewise large, the genae are subacute, and the facial suture does not transect the anterior glabellar lobe. Here again an axial furrow pit is present. Clarke (1900, p. 20) correctly stated that glabellar furrows 2p and 3p are relatively deeply incised, later incorrectly denying this (1908, p. 226). In our opinion, *P. correlator* (at least the type specimen from the Oriskany of Becraft Mountain) is best referred to an acastid genus such as *Acastella*. "*P. correlator*" from the Gaspé Sandstone (fig. 20H) is more like *P. anceps* (but lacking the inflation of the anterior glabellar lobe) and also has indications of an axial furrow pit, but is otherwise too poorly preserved for comparison with *Phacopina braziliensis*. We have not examined Clarke's type of *P. nylanderi* from the Chapman sandstone, but Clarke's figure (1909, pl. 22, fig. 1) resembles the other boreal taxa in its subacuminate genae; Williams and Breger's (1916) types of *P. chapmani* (see fig. 20H, I, J, K) consist of a cephalon and pygidium. The type cephalon, while laterally compressed, is moderately well preserved as an internal mold. The eyes are large as in *P. braziliensis*, but this species resembles *P. correlator* from Becraft Mountain in the presence of more markedly incised 2p and 3p glabellar furrows, presence of an axial furrow pit, and subacuminate genae. Indeed the cephalic outline of this species is shouldered, not lunate (as may be the case with Becraft Mountain *P. correlator*). The pygidium of *P. chapmani* is bluntly rounded, but the axis is distinctly set off above the pleural fields with distinct axial furrows. There are five axial rings plus terminal piece, and two pleura preserved. This is the only Devonian acastid pygidium yet described from North America; with reference to the Malvino-Kaffric fauna, it is more reminiscent of ?*Acastoides* than *Phacopina*—keeping in mind that we can only be sure of the pygidium of *Phacopina convexa* from Bolivia.

Finally, Dr. Pierre Lespérance has allowed us to examine five acastid cephala and cranidia (indicating functional facial sutures) from the Lower Devonian Indian Cove Member of the Shiphead Formation of the Gaspé Peninsula, Province of Quebec. These specimens will be described in a future paper. Suffice it to say at this juncture that the eyes are moderately large, the overall cephalic shape most closely resembles *P. correlator* from Becraft Mountain, an axial furrow pit is present, and the facial sutures are entirely distal to the anterior glabellar lobe.

We may conclude from this brief survey of the Appalachian Devonian acastids that, though all the specimens resemble *P. braziliensis* in a general way, they consistently differ from that species in having axial furrow pits and a "normal" facial suture pattern. Other differences of more doubtful significance also emerge, notably the inflated glabella of *P. anceps*, the more deeply incised 2p and 3p glabellar furrows plus the typically acastid subacuminate genal angle of *P. correlator* and *P. chapmani*, and the pygidium of *P. chapmani*. Inasmuch as axial furrow pits are developed in *Scotiella, Acaste,* and other Silurian acastids, as is the "normal" facial suture pattern, these probably cannot be cited as definitive evidence that all of these Appalachian taxa form a coherent group, discrete from the austral species of *Phacopina*. Indeed, we have already remarked that *P. correlator* and possibly also *P. chapmani* might better be allocated to *Acastella*. But a facial suture pattern transecting the glabella and absence of axial furrow pits might indeed serve to link the austral species of *Phacopina* and set them off from the Appalachian forms. The evidence is inconclusive, but such evidence as is available favors the hypothesis that Devonian acastids from North America have affinities with taxa other than the type and closely related species of *Phacopina* presently known from South America.

Phacopina convexa differs from *P. braziliensis* in total size, and, together with *P. padilla,* in a relatively smaller eye, a relatively larger section of the anterior glabellar lobe transected by the anterior branch of the facial suture, and by their greater convexity. We shall not formalize these differences by naming a new taxon to embrace the two Bo-

livian species; in our opinion, the Bolivian species, while more advanced than *P. braziliensis,* can easily be accommodated under an expanded and slightly revised concept of the genus *Phacopina.*

Struve (1959) recognized two subgenera of *Phacopina,* the nominate subgenus and *P. (Scotiella).* Our remarks above include only the former, and we reject Struve's lumping of all acastids with effaced 2p and 3p glabellar furrows into a single genus. Shergold (1967b), in his recent revision of some species of *Scotiella* from North America, clearly showed the acastid affinities of this genus. It appears that acastids *sensu lato* with reduced incision of glabellar furrows 2p and 3p were present in the Silurian and Devonian of both Northern and Southern hemispheres; *Scotiella* does not share the posteriorly rounded micropygous pygidium with true *Phacopina,* but this feature is developed fully in the Bolivian Silurian species of *Andinacaste* as described below. The evidence available suggests that the more accurate hypothesis is that the various few specimens referred to the Devonian species of *Phacopina* in North America actually share their affinities with *Scotiella* and *Acastella,* predominantly of North America and Europe; an additional possible shared-derived feature linking some of these taxa [e.g., *Scotiella logani* (Hall) and *P. anceps*] might be the faint median longitudinal glabellar ridge developed in both taxa.

We here figure (fig. 21) the type specimens of *Scotiella logani* for two reasons: Shergold (1967b) lists the types as lost, and one of the specimens clearly shows a well-developed palpebrum and rather large palpebral area (not preserved in any of the material illustrated by Shergold). In this feature *Scotiella* is a typical boreal acastid, similar indeed to the type specimen of "*Phacopina*" (? = *Acastella) correlator,* and totally unlike any known austral *Phacopina.* Northern and southern Devonian species of *Phacopina* in Clarke's original sense thus seem to have their affinities with Silurian species in their own respective hemispheres, rather than with each other across hemisphere boundaries.

We also exclude from *Phacopina* the well-known *Acaste devonica* Ulrich, first referred to *Phacopina* (and by all subsequent authors) by Kozlowski (1923, p. 49 ff., especially p. 51); Wolfart (1968) has erected a new subgenus *P. (Vogesina)* for this species, as well as for *P. (V.) lacunafera* Wolfart and *P. (V.) aspera* Wolfart. There is no doubt that *Vogesina* is a valid taxon, and we prefer to accord it full generic status. *Vogesina* shares with *Phacopina* only a general effacement of glabellar furrows 2p and 3p; however, in *Vogesina,* the genae are distinctly acuminate and are not deeply reflexed ventrally. The glabella of *Vogesina,* while slightly expanded distally, is indistinct anterolaterally and the facial sutures do not transect the glabella; glabellar furrows 1p are reduced to two short apodemal invaginations not communicating with the axial furrows, and there is a very deep axial furrow pit. Finally, the pygidium is distinctly triangular, with well-developed axial, ring, pleural, and interpleural furrows. This combination of primitive, advanced, and unique characters is highly distinctive and effectively isolates *Vogesina* from all other known Calmoniidae.[2] We emphasize that austral species referred to ?*Acastoides* probably form the sister taxon to austral *Phacopina,* and that *Vogesina,* far from being a subgenus of *Phacopina,* is not even particularly closely related to it as the resemblances between them seem in large measure to be primitive features.

The two species of *Phacopina* described below from the Bolivian Devonian are very similar indeed to Bolivian species of ?*Acastoides.* However, there are fundamental differences between them; the cephalon of *Phacopina* is far more highly arched—i.e., the vertical distance between the central region of the glabella and the lowest point on the genal margins, relative to the maximal width of the cephalon in dorsal view, is far greater in *Phacopina* than in ?*Acastoides.* Put

[2]New evidence suggests that *Vogesina* shares synapomorphies with *Malvinella*; data supporting this hypothesis will be presented in a separate study on the genera of Calmoniidae and their interrelationships.
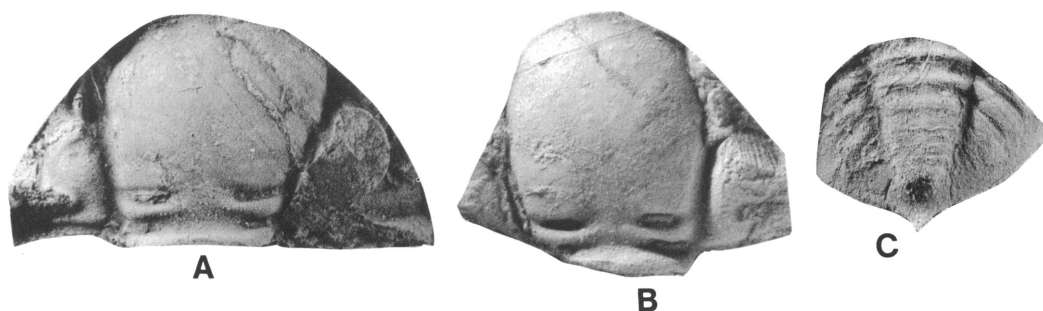
FIG. 21. *Scotiella logani*. Stonehouse Fm., Arisaig, Nova Scotia. A. Dorsal view of internal mold of cephalon. Syntype, AMNH 1660, ×3. B. Dorsal view of internal mold of cephalon. Syntype, AMNH 35971. ×3. C. Dorsal view of latex cast of external mold of pygidium. Syntype, AMNH 35972, ×3.

another way, the genae slope more sharply ventrally in *Phacopina* than in ?*Acastoides,* and the anterior arch is therefore greater in the former than in the latter. However, the anterior glabellar lobe of ?*Acastoides* is more inflated than it is in *Phacopina,* so, in that respect, ?*Acastoides* seems the more "inflated." Furthermore the frontal border of *Phacopina* (where the anterior border meets the cephalic doublure near the midline) is a sharp ridge, whereas it is developed as a bluntly rounded pustulose callus formed by the recurved doublure in all Malvino-Kaffric species of ?*Acastoides.* Then, too, in dorsal view the glabella protrudes beyond the curved outline of the librigenal border in ?*Acastoides,* producing the pronounced shouldered effect so typical of calmoniids, whereas in *Phacopina,* alone among the calmoniid genera of the *Scaphiocoelia* Zone, this shouldering effect is entirely absent. As a final general consideration of cephalic shape, the posterior border in ?*Acastoides* is reflected posterodistally, whereas it is more nearly transverse in *Phacopina.*

Such shape differences in themselves may not possibly suffice, though they do effectively segregate the various species allocated to each genus. Of far greater importance is the course of the anterior branch of the facial suture. In Malvino-Kaffric species of ?*Acastoides,* the facial suture remains just distal to the roughly straight axial furrows, and is then reflected smoothly around the front of

the glabella. In all species of *Phacopina* which we consider valid, the glabella has expanded anterolaterally and the facial sutures transect the anterior glabellar lobe. We find consistently that patterns developed by the anterior branch of the facial suture are stable within populations, stable among populations and species that share other features we may consider derived, and thus, for austral Calmoniidae at least, crucial to the recognition and diagnosis of genera.

The extraordinary development of truly minute granules all over the cuticular surface of well-preserved specimens of *Phacopina convexa,* new species (best seen on latex casts of external molds), is nearly unique: only *D. (Prestalia) tumida* shows a comparable development of such dense microgranulation. Further differences between *Phacopina* and ?*Acastoides* lie in eye morphology: in ?*Acastoides,* the posterior margin of the visual surface is not recurved as near to the axial furrow as it is in *Phacopina*—hence the virtual absence in the latter of a palpebral area. A final feature of the cephalon which invites comparison between these two genera is the greater obsolescence of furrows in *Phacopina* than in ?*Acastoides,* though some specimens of ?*Acastoides* we have examined (particularly from the Icla section at Padilla) also have greatly obsolescent furrows, particularly of glabellar furrows 2p and 3p.

The thorax of these two genera differ

mainly in the flattened distal pleural edges in *Phacopina*, as opposed to flattened edges bearing posterior spines in ?*Acastoides*. The pygidia are similar, but the axis of the pygidium in ?*Acastoides* is generally more sharply demarcated and more greatly inflated than in *Phacopina*, and, of course, the ring furrows of ?*Acastoides* are invariably more deeply incised than in *Phacopina*.

Phacopina convexa may also be easily confused with certain other *Scaphiocoelia* Zone taxa when only cranidia are compared; criteria for identifying *P. convexa* are given following its diagnosis below. The only other Malvino-Kaffric taxon readily confused with *Phacopina* is *Andinacaste*, new genus, described elsewhere in this paper, which has been variously called *Phacopina* and *Eophacops*. In *Andinacaste*, the facial sutures do not transect the glabella, the axial furrows diverge at a lower angle, the genae terminate in an acute point, the cephalon is distinctly shouldered and is not nearly so highly arched as in true *Phacopina*, and the glabellar surface slopes more gently than in *Phacopina*. We discuss these and other features more fully following the diagnosis of *Andinacaste*.

Phacopina convexa, new species[3]
Figures 2B; 22; 23A

Phacopina (?) sp. Suárez Soruco, 1971, p. 53, pl. 2, figs. 4, 5.

TYPE SPECIMENS: We designate NMNH 245627, a cephalon with associated portion

[3]We have recently obtained a copy of Baldis et al. (1976), in which Baldis and Blasco describe (p. 216) *Jujuyops nonoctubrensis* new genus and new species from the Lipéon Formation in the Río de los Tomates section, Zapla Hills, Jujuy Province, Argentina. We have synonymized *Jujuyops* with *Phacopina* above. The illustrations of *J. nonoctubrensis* (Baldis et al., pl. 5, figs. 1–4) reveal a striking similarity between *Phacopina convexa* newly described here, and *J. nonoctubrensis*. Should examination of the material from Argentina indicate that the two taxa are in fact conspecific, the name would become *Phacopina nonoctubrensis* (Baldis and Blasco). We shall continue to recognize *Phacopina convexa* until such time as examination of the types of *P. nonoctubrensis* and a direct comparison of specimens of the two species can be effected.

of thorax, as the holotype. AMNH 36706, a nearly complete enrolled specimen, is designated the paratype. Gamoneda Formation, *Scaphiocoelia* Zone, Curuyo, Tarija Department, Bolivia.

ETYMOLOGY: The specific name refers to the convex (highly arched) nature of the cephalon.

DIAGNOSIS: A relatively large species of *Phacopina* with small eyes (Large Eye Index .27–.34) set in close to axial furrows; top of palpebrum not elevated as high as central region of glabella. Visual surface short dorsoventrally, bearing approximately 20 dorsoventral files with a maximum of five or six lenses per file. Glabellar furrow 3p slightly sinuous. Genae smoothly rounded. Pygidium posteriorly rounded, micropygous, with five axial rings plus terminal piece, and four pairs of pleura developed only directly adjacent to axial furrows. Entire cuticular surface, save the axial and glabellar furrows, densely covered with minute granulation.

MATERIAL EXAMINED: Including type specimens, 14 cephala, two portions of thorax, and an external mold of a nearly complete, enrolled individual. All specimens from same horizon and locality as types. Six specimens from the NMNH Braniša Collection; one cephalon collected by Peter Isaacson, NMNH collections; and nine specimens in the Braniša Collection, AMNH.

REMARKS: *Phacopina convexa* is one of the smallest of the calmoniid trilobites in the fauna of the *Scaphiocoelia* Zone, thus its size alone helps identify it. However, *Deltacephalaspis* (*Deltacephalaspis*) *retrospina* from Jarcas and some specimens of *Schizostylus* (*Curuyella*) *granulata* are smaller than some of the larger specimens of *P. convexa* known to us. *Phacopina convexa* is readily confused with ?*Acastoides gamonedensis*, *Deltacephalaspis* (*Prestalia*) *tumida*, and *Kozlowskiaspis* (*Romanops*) *australis*. We have dealt with the *differentia* between *Phacopina* and austral ?*Acastoides* in sufficient detail under Remarks following the emended diagnosis of *Phacopina*; *P. convexa* is readily separated from *K.* (*R.*) *australis* by virtue of their completely different pygidial and genal morphology, as well as details of general
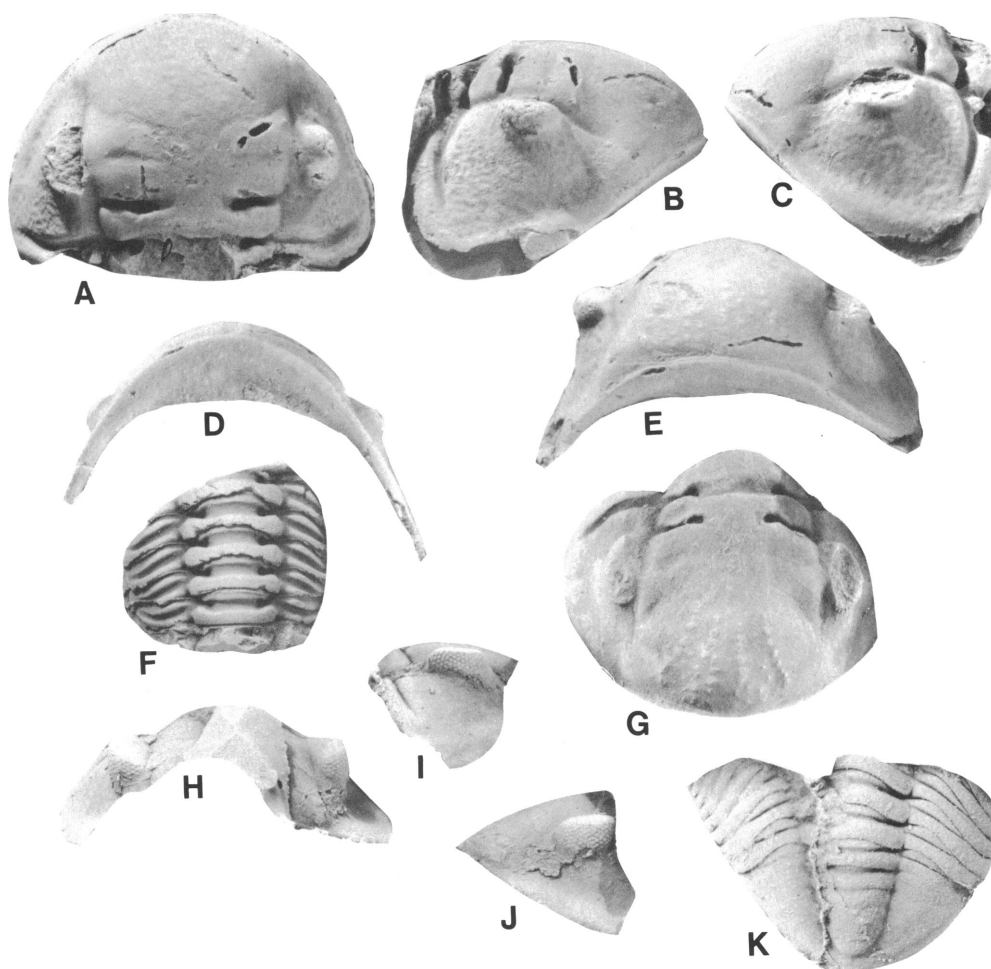
FIG. 22. *Phacopina convexa*. *Scaphiocoelia* Zone, Gamoneda Fm., Curuyo, Bolivia. A–F. Holotype cephalon and associated portion of thorax. NMNH 245627. A–E. Dorsal, right lateral, left lateral, ventral, and frontal views of internal mold of cephalon, ×3. F. Dorsal view of internal mold of portion of thorax, ×2. G. Oblique frontal view of internal mold of cephalon showing pattern of auxiliary impression system, NMNH 245628 (Isaacson Coll., locality #20018), ×3. H–K. Latex cast of external mold of nearly complete, enrolled individual. Paratype, AMNH 36706 (Braniša Coll.). H–J. Frontal, right lateral, and left lateral views of cephalon, ×3. K. Dorsal view of pygidium and articulated posterior portion of thorax, ×3.

cephalic shape (including greater degree of development of the anterior arch in *P. convexa* and absence of shouldering in this species). However, on cranidia alone, we are again faced with a very close resemblance between two taxa so different in other aspects of their anatomy. The shape of the gla-

bella, and size and direction of the glabellar furrows are nearly identical in the two species, though, of course, glabellar furrows 2p and 3p are usually more deeply incised in *K. (R.) australis* than in *P. convexa*. In addition, the eyes of *Kozlowskiaspis* are also set in very close to the axial furrows and are
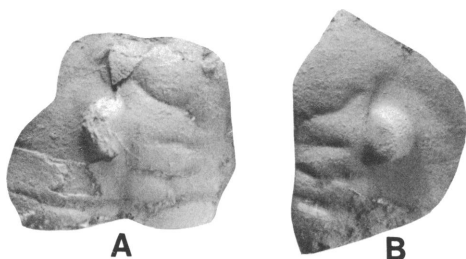
FIG. 23. Comparison of *Phacopina convexa* and *Kozlowskiaspis* (*Romanops*) *australis* showing close cranidial similarity between the two taxa. *Scaphiocoelia* Zone, Gamoneda Fm. A. *P. convexa*. Oblique dorsal view of latex cast of external mold of left side of cephalon, ×2. NMNH 245629 (latex cast AMNH 36707). B. *Kozlowskiaspis* (*Romanops*) *australis*. Jarcas, Bolivia. Dorsal view of latex cast of external mold of right side of cephalon. Holotype, NMNH 245630 (latex cast AMNH 36708), ×2. See figure 32B, C for views of internal mold of this specimen.

of about the same relative size, the facial sutures transect the glabella, and meet at the midline in only a moderately convex point (i.e., the facial sutures, though not forming a smooth arc as in *P. convexa,* do not meet in a distinct point as in, e.g., *Deltacephalaspis,* the other genus homeomorphic with *Kozlowskiaspis*). We dramatize the close cranidial resemblance between *K.* (*R.*) *australis* and *P. convexa* in fig. 23, which compares latex casts of external molds of a cranidium of each species. When confronted only with cranidia, we emphasize the sole remaining criterion that serves to distinguish *P. convexa* from all other taxa except *D.* (*Prestalia*) *tumida*: the development of a very dense groundmass of fine granules all over the glabella, usually still present in even poorly preserved material, though of course absent on totally exfoliated internal molds.

Finally, *D.* (*Prestalia*) *tumida,* bearing such a close resemblance to *K.* (*R.*) *australis* therefore may also be confused with *P. convexa.* We refer the reader to discussions following *K.* (*R.*) *australis* and *D.* (*P.*) *tumida* for criteria by which these taxa may be distinguished. The criteria for distinguishing *P.*

convexa from *K.* (*R.*) *australis* serve with even greater force to distinguish *P. convexa* from *D.* (*P.*) *tumida.*

Phacopina cf. Phacopina convexa
Figure 24G–J

REMARKS: A single enrolled, only slightly distorted specimen of *Phacopina* with the cuticle nearly entirely intact, is in the Braniša Collection of the National Museum of Natural History. Its tan coloring and general mode of preservation are very similar to specimens from the *Scaphiocoelia* Zone of the Lower Belén Formation in the Belén-Sicasica region of Bolivia. However, there is no locality information associated with this specimen.

In all aspects of its morphology, this specimen is identical to *Phacopina convexa* from Curuyo, except that the facial suture transects the glabella somewhat higher up the slope of the glabella, and swings around the anterior margin of the glabella somewhat more abruptly, delimiting a decidedly more pronounced anterior border. Also, though the cuticular surface is sufficiently well preserved to show the existence of small pores in some areas, the microgranulation so characteristic of *Phacopina convexa,* even on poorly preserved specimens from Curuyo, appears to be absent in this specimen. Rather, the cuticular surface appears smooth, with small granules (larger than those on *P. convexa* from the south) sparsely scattered over the surface, especially of the cephalon.

If we are correct in assuming that this specimen comes from the *Scaphiocoelia* Zone of northern Bolivia, the degree and kind of differences exhibited between it and *P. convexa* from the south would be comparable to the regional differences we have described for other taxa in this paper. Inasmuch as we have but the one specimen (fig. 24G–J), and no locality information, we simply refer this specimen to *Phacopina,* cf. *P. convexa* until such time as additional specimens may become available. We point out, however, that the assignment of this well-preserved specimen to *Phacopina* is not in
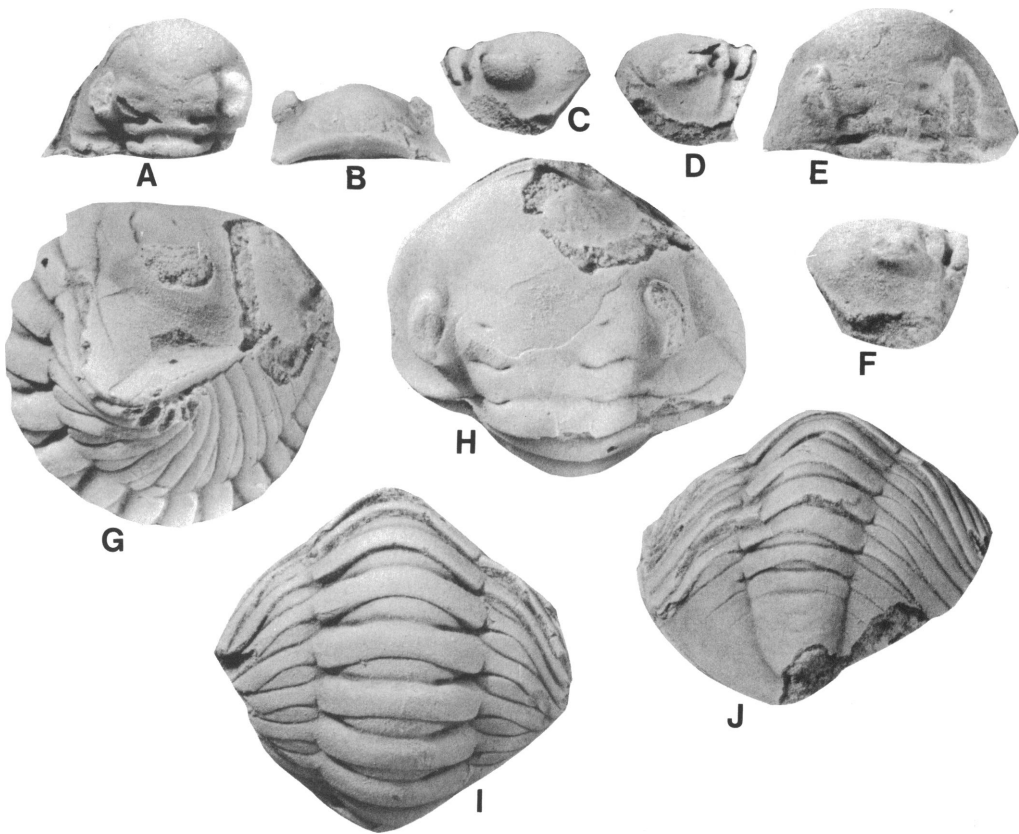
FIG. 24. *Phacopina* spp. A–F. *P. padilla*. Icla Fm., Padilla, Bolivia. A–D. Dorsal, frontal, right lateral, and left lateral views of internal mold of cephalon. Holotype, NMNH 245631, ×4. E, F. Dorsal and left lateral views of internal mold of cephalon. Paratype, NMNH 245632, ×4. G–J. *Phacopina* cf. *P. convexa*. Horizon and locality unknown, but presumably from *Scaphiocoelia* Zone, Belén Fm., Belén region, Bolivia. Dorsal view of cephalon, right lateral view of entire specimen, dorsal view of portion of thorax, and dorsal view of pygidium, of a nearly complete enrolled individual with cuticle intact. NMNH 245633, ×3.

doubt, and we have included this specimen in framing our concept of the genus *Phacopina*.

Phacopina padilla, new species
Figure 24A–F

TYPE SPECIMENS AND MATERIAL EXAMINED: This species is based on two small cephala (internal molds) from the Braniša Collection, National Museum of Natural History; both are from the lower portion of the Icla beds at Padilla, Chuquisaca Department, Bolivia. We designate NMNH 245631 as the holotype, and NMNH 245632 the paratype.

ETYMOLOGY: The specific name is based on the locality name where the specimens were collected.

DIAGNOSIS: Minute species of *Phacopina* with small, concave eye socle supporting visual surface. Eye relatively large (Large Eye

Index .36–.37), running between 1p and 3p glabellar furrows, elevated with palpebrum lying in same horizontal plane as central area of glabella. Glabellar furrows 3p straight, approaching but not communicating with axial furrows. Anterior slope of glabella slightly steeper than in *P. convexa*. Gena rounded, bearing small spine. Hypostoma, cuticular ornament, thorax, and pygidium unknown.

REMARKS: The larger, taller eyes, which are nevertheless still situated close to the axial furrows, and the small genal spine are the two most distinctive features of this species. At first glance, the specimens appear referable to *Acastoides* sp., which is abundant in the associated fauna. However, the general cephalic shape, the laterally expanded anterior glabellar lobe, with the facial sutures transecting the anterolateral corners, and the ridgelike anterior cephalic border—features so characteristic of *Phacopina*—are well developed in *P. padilla* and readily serve to distinguish this species from ?*Acastoides*. The species of ?*Acastoides* and *Phacopina* present in the Icla section at Padilla focus attention on a problem not unlike that posed by the *Scaphiocoelia* Zone calmoniids themselves: no fewer than four species, referable to four different genera, are very similar in many aspects of cephalic morphology, and may be readily confused. These taxa are *Phacopina padilla,* similar to ?*Acastoides* sp., which in turn is rather similar to *Kozlowskiaspis* (*Kozlowskiaspis*) *superna* Braniša and Vaněk (see section on *Kozlowskiaspis,* this paper), which in turn bears a resemblance to a new taxon (as yet undescribed) which is closely allied with *Calmonia* (see fig. 29, and further discussion under *Kozlowskiaspis superna* below). We intend to describe and discuss the taxa of the Icla beds, including those from Padilla, in a separate paper, but it is clear from preliminary work that the "radiation" which produced the diverse array of calmoniids already described in the literature (i.e., those from the younger Icla beds, and especially the even younger "Sicasica" beds in the La Paz region) was still in a rather formative phase in the early part of Icla depositional time, at least in the Padilla region.

ANDINACASTE, NEW GENUS

Phacopina: Swartz, 1925, p. 50; Feruglio, 1930, p. 92, 94; Wolfart, 1968, p. 121.
Eophacops: Ahlfeld and Braniša, 1960, p. 60; Wolfart, 1961, p. 75; Braniša et al., 1972, p. 24 ff.
?*Scotiella*: Wolfart, 1961, p. 76.

TYPE SPECIES: *Phacopina braziliensis* var. *chojnacotensis* Swartz, 1925.

ETYMOLOGY: The name *Andinacaste* is derived by compounding "andin" in reference to the Andes Mountains, and "acaste," in reference to the close similarity and presumed close affinity between this genus and the common trilobite genus *Acaste* Goldfuss.

DIAGNOSIS: Cephalon slightly shouldered. Glabellar furrows 2p and 3p variably incised, typically effaced or marked by narrow, lightly incised furrows. (In some populations, some specimens with more deeply incised 2p and 3p furrows.) Genae acuminate, occasionally bearing small genal spines. Eyes set in close to axial furrows; palpebral lobe generally demarcated from palpebral area by faint palpebral furrow. Anterior branch of facial suture not transecting anterolateral borders of anterior glabellar lobe. Pygidium micropygous and smoothly rounded posteriorly.

DESCRIPTION: Species of the genus *Andinacaste* are generalized acastid trilobites with a triangular, slightly shouldered cephalic outline. The axial furrows are moderately deeply incised, subparallel, and diverge at an angle of approximately 30°. An axial furrow pit is generally absent, but is rarely present as a minute apodeme. The anterior glabellar lobe is not inflated anteriorly, and curves smoothly posterodorsally; the highest point of cephalic convexity is situated between the proximal ends of glabellar furrows 3p. Glabellar furrows 3p are straight, run anterodistally at an exsagittal angle of 45°, and approach, but do not communicate with, the axial furrows. Glabellar furrows 2p run anterodistally at a slight angle, are convex anteriorly, and do not reach the axial furrows. Glabellar furrows 2p and 3p are variably incised on both the external cuticular surface and on internal molds; they are typically en-

tirely effaced or marked by narrow, lightly incised furrows. In some populations, some specimens exhibit rather deeper, "normal acastid" incision of glabellar furrows 2p and 3p. Glabellar furrows 1p are deeply incised, essentially transverse, developed as apodemes proximally and communicate with the axial furrows distally. All glabellar furrows arise very near the glabellar midline, defining a very narrow median glabellar area. The occipital furrow is shallow and convex medially. The occipital ring and all parts of the glabella lie in a single smoothly curved surface.

The posterior border is essentially transverse, and is recurved anterodistally approaching the genal angle. The genae are acuminate, and occasionally bear a small genal spine. The genae are essentially flat (i.e., not dished), with a very shallow lateral border furrow, and are inclined moderately steeply, forming a moderate anterior arch in anterior view. The eyes are variable in size, lack a discrete eye socle, and are set in close to the axial furrows. The palpebral lobe is generally demarcated from the palpebral area by a faint palpebral furrow (which appears to be obsolescent in some specimens).

The anterior border is a thin ridge, and is not produced into a discrete anterior process. The anterior branch of the facial suture is entirely distal to the axial furrow; it is recurved and runs just proximal to the anterior border, and thus does not transect the anterolateral corner of the anterior glabellar lobe. The doublure is essentially flat (depressed on internal molds). The hypostomal suture is slightly convex anteriorly; the hypostoma is unknown.

The auxiliary impression system is typically acastid—i.e., two major subparallel rows of scars on each side, which diverge anterodistally (fig. 2A). The posterior median impression is faint or absent. The entire cuticular surface is densely covered with minute granulation.

The thorax exhibits only slight axial tapering posteriorly through segment seven. The axial rings are simple; the axial furrows are deeply notched on the posterior region of each segment. The pleural tips are apparent-

ly flat. The pygidium is micropygous and smoothly rounded posteriorly. The axis is well set off from the pleural region, and nearly reaches the posterior margin of the pygidium; it consists of four, rarely five (and, in one case, eight) axial rings (generally only the anterior two being demarcated by well-incised ring furrows) and has usually two, and rarely as many as five, pairs of pleura. The pleural furrows are generally weakly developed on the anterior two pleura, but are also rarely present on pleura three, four, or five.

REMARKS: We include all Bolivian Silurian acastids known to us (detailed below under species diagnoses) in *Andinacaste*. We have erected this genus only after a thorough search of the literature and comparison with boreal Silurian material has convinced us that the complex of characters presented by the Bolivian material is not duplicated in any other previously described genus. The generalized acastid nature of *Andinacaste* is clear, however, and our initial reluctance to create a new generic name stems partly from our desire to determine a more precise age for the various "Silurian" formations which are the source of the material described by Salfeld (1911), Kozlowski (1923), Swartz (1925), Feruglio (1930), Wolfart (1968), and in the present paper.

We also refer the two taxa described by Wolfart (1961, p. 75 ff.) from the Lower Llandovery of Paraguay as *Eophacops*, new species A and *Scotiella obsoleta perroana*, new subspecies, to *Andinacaste*. *Eophacops*, new species A conforms very closely to *Andinacaste legrandi* described below, as judged from Wolfart's figures (Wolfart, 1961, pl. 5, figs. 1–2). The taxon described as *Scotiella obsoleta perroana* (Wolfart, 1961, pl. 5, figs. 3–5) is more difficult to identify from the illustrations, resembling both *Andinacaste* and, to a lesser extent, *Phacopina*. If these species are in fact of Lower Llandovery age, they are among the oldest of the acastid-calmoniid lineage.

Shergold (1966, 1967a, 1967b, 1968) has recently clarified, and greatly contributed to, our knowledge of boreal and Australian Siluro-Devonian acastids. Shergold's (1967b)

reappraisal of *Scotiella,* alluded to in our section on *Phacopina,* highlighted the problem posed by variable incision of the glabellar furrows, particularly 2p and 3p. Shergold's concept of *Scotiella* (1967b, p. 3 ff.) refers to among-species variation in the incision of these furrows. Below we discuss a similar case in a moderately large sample of *Andinacaste chojnacotensis* (Swartz) from the Catavi Formation at Tres Cruces, between Oruro and Cochabamba, Bolivia, but in this case there is every reason to conclude that this variation is within a single species, and possibly within a single population. Yet there is no clear-cut evidence for sexual dimorphism. In all other samples (including the types) of *A. chojnacotensis,* as well as *A. legrandi,* new species, which are all admittedly smaller than the Tres Cruces sample, glabellar furrows 2p and 3p are either faint or totally effaced. In any case, with respect to the depth of incision and its variation, *Andinacaste* resembles only *Scotiella* of all acastid taxa known to us, but must be excluded from that genus because *Scotiella* is further characterized by a more triangular pygidium with terminal spine, genae produced posterodistally, well-developed palpebral lobe and palpebral area, set off by a well-developed palpebral furrow, the eye set off relatively far from the axial furrow, presence of a definite axial furrow pit, and a moderately inflated anterior glabellar lobe.

In our opinion, specimens of *Andinacaste chojnacotensis* most closely approximate in overall morphology, including genal shape, species of *Acaste* Goldfuss itself—most notably *Acaste longisulcata* described by Shergold (1968, p. 20 ff.) from, we note, Lower Devonian rocks of Victoria, Australia. Indeed, *some* of the Tres Cruces specimens of *A. chojnacotensis* which exhibit rather deeply incised glabellar furrows appear all but identical with Shergold's figured specimens of *Acaste longisulcata,* with the exception of the rather more distinct palpebral lobe and furrow morphology, and larger eye, in *Acaste longisulcata.* Shergold described *A. longisulcata* as monomorphic in terms of depth of incision of the glabellar furrows—

as, of course, would be expected in *Acaste* and all related taxa except *Scotiella.* In this event, and given our observation that the *usual* condition of *Andinacaste* species is faint or effaced 2p and 3p furrows, we cannot refer the Bolivian material to *Acaste,* nor yet claim any especially close relationship with the Australian *A. longisulcata.* However, we note Shergold's (1968, p. 23) remark that "the eyes of *A. longisulcata* are perhaps closer to the glabella than in many species of the genus," and the fact that the glabellar furrows of *A. longisulcata* approximate more closely to the midline than in any other species of *Acaste*—prompting Shergold's choice of the specific name. We therefore hypothesize that *A. longisulcata* may in fact be closely related to *Andinacaste* and perhaps even more appropriately referred to this genus than to *Acaste.* Under no circumstance, however, can the generic name *Acaste,* with its full array of well-known species, be stretched to embrace the Bolivian material.

We reject the allocation of the Bolivian Silurian species to *Phacopina* because, as emended above, *Phacopina* has eyes even more closely set in towards the axial furrows, virtually no discrete palpebral morphology, rounded genae, a more strongly arched, non-shouldered cephalic outline, facial sutures which transect the anterior glabellar lobe, and a pygidium with a distinctly shorter axis than does *Andinacaste.* But these genera share general effacement of the glabellar furrows, basic similarity in glabellar design, otherwise similar thoraxes and pygidia, and a moderately dense covering of microgranulation all over the cuticular surface. [This granulation is present in most Silurian acastids and probably cannot be considered *ipso facto* as evidence of close affinity between *Phacopina* and *Andinacaste.* It is also present, in similar form, in ?*Acastoides, Schizostylus (Curuyella),* and *Deltacephalaspis.*] In view of the features which characterize *Andinacaste, Phacopina* emerges more strongly than ever as overall the most plesiomorphic taxon in the Lower and Lower Middle Devonian complex of
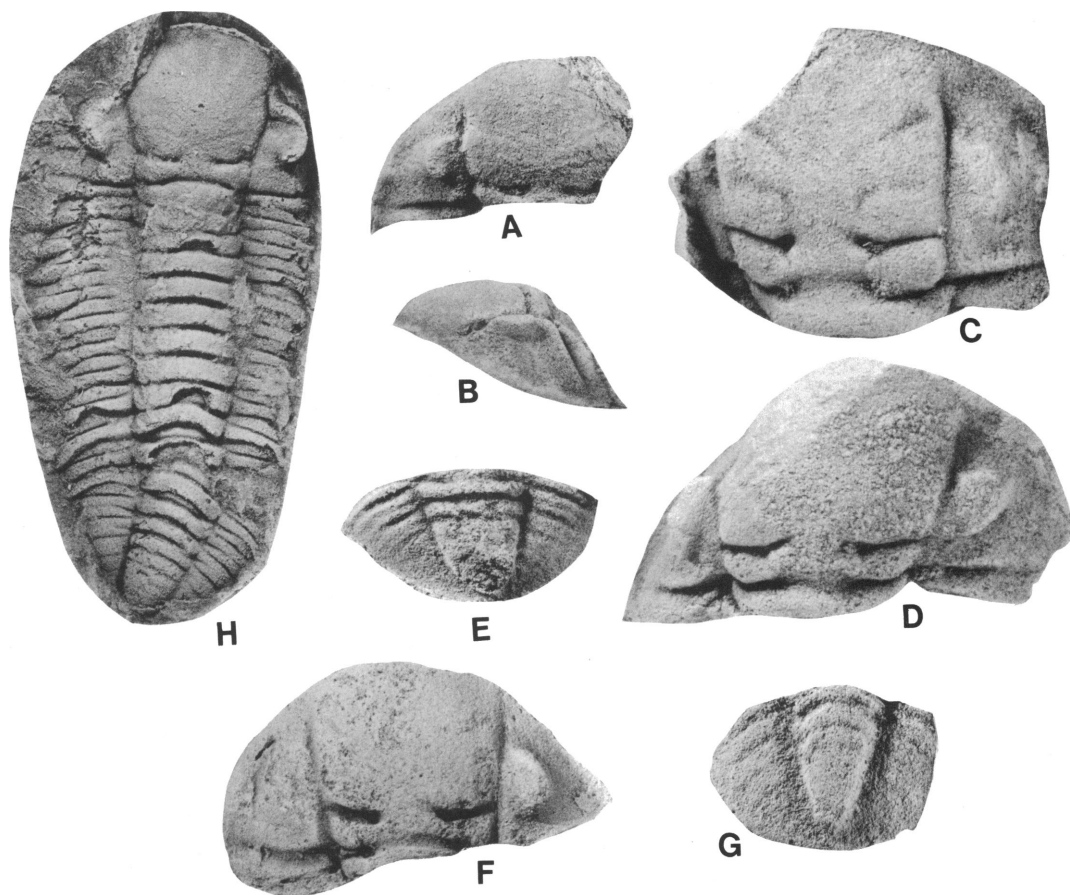
FIG. 25. *Andinacaste* spp. A–G. *A. chojnacotensis*. A–E. Catavi Fm., Tres Cruces, Bolivia. Isaacson coll., NMNH. A, B. Dorsal and left lateral views of internal mold of cephalon. NMNH 245634, ×3. C. Dorsal view of latex cast of external mold of cephalon, NMNH 245635, ×4. D. Dorsal view of internal mold of cephalon, NMNH 245636, ×4. Figures A, C, and D illustrate the variability in incision of the glabellar furrows within this sample of the species. E. Dorsal view of internal mold of pygidium, NMNH 245637, ×3. F, G. Chojñacota, Bolivia. Syntypes (two of three). F. Dorsal view of internal mold of cephalon, NMNH 165859, ×3. G. Dorsal view of internal mold of pygidium, NMNH 165858, ×3. H. *Andinacaste legrandi*. Sora Sora, Bolivia. Dorsal view of latex cast of external mold of a complete individual. Paratype, NMNH 245638 (latex cast AMNH 36709), ×3.

acastid and calmoniid trilobites in the Malvino-Kaffric faunal province. The opposite side of the coin is equally true: *Andinacaste*, more than any other taxon known to us, most closely approximates the expected hypothetical common ancestral morphotype for the entire Malvino-Kaffric Devonian calmoniid radiation.

Andinacaste chojnacotensis (Swartz)

Figure 25A–G

Phacopina braziliensis (Clarke) var. *chojnacotensis* Swartz, 1925, p. 50, pl. 1, figs. 8–10.
Phacopina chojnacotensis: Feruglio, 1930, p. 92, pl. 20, figs. 18, 19, ?20; Wolfart, 1968, p. 122, pl. 22, fig. 8, 9, pl. 23, figs. 4–6.

Phacopina bonarelli Feruglio, 1930, p. 94, Pl. 20, figs. 20, 21.

EMENDED DIAGNOSIS: A species of *Andinacaste* with glabellar furrows 2p and 3p variably totally effaced, or moderately deeply incised. Genae acuminate to sharply rounded, with genal angle approximately opposite (tr.) posterior margin of occipital ring. Short genal spine present on some specimens. Eyes small (Large Eye Index .27–.36) with posterior margin just anterior to distal edge of glabellar furrow 1p, and anterior margin reaching about midway along distal edge of glabellar lobe 3p. Pygidium with generally only anterior two axial rings and pleural pairs well differentiated, and posterior segmentation generally obscure.

REMARKS: Wolfart (1968, p. 122 ff.) has given an accurate diagnosis and description of this species, to which we refer the reader for fuller details. Our object in presenting this shorter account is simply to highlight those features in which those Silurian specimens of *Andinacaste* agreeing with Swartz's types differ from *Andinacaste legrandi* described below.

Specimens of *Andinacaste* come from a variety of localities in the Catavi and Cordillera Real formations. The age of these formations is difficult to assess, as fossils are generally poorly preserved and poorly understood, and seem to contain faunules of widely differing ages (especially the Cordillera Real Formation, which seems to contain segments of the Ordovician, Silurian, and Lower Devonian periods—see Braniša et al., 1972). Swartz's type specimens (NMNH 165857, 165858, 165859) of *Phacopina braziliensis* var. *chojnacotensis* (see fig. 25F, G) from Chojñacota, Bolivia, are preserved as molds in a gray quartz sandstone. All other samples in our possession which exhibit the same complex of characters as developed in the type specimens come from similarly clastic units: the Catavi Formation at Tres Cruces, near Sayari, Bolivia (associated with a multiplicate rhynchonellid) where the fossils are preserved in reddish powder (presumably hematite or limonite) in a whitish gray quartz sandstone; the Catavi Formation

of Quime, Bolivia, preserved as limonite powder in a gray quartz sandstone; the Catavi Formation at Cerro Ticti, Cochabamba, Bolivia; and the Catavi Formation ("Chuquiaguillo sandstone") at Rio Achumani (Smith Collection, AMNH) associated with *Dalmanella tacopayana* Kozlowski and *Harringtonina* sp.

The largest sample of *Andinacaste chojnacotensis* we have examined, from the Catavi Formation at Tres Cruces (collected by Peter Isaacson and now in the NMNH collections), consists of some 45 cephala and cranidia (indicating presence of functional facial sutures) and six pygidia. The material is not well preserved, and in fact is variably deformed, so that we have not performed any statistical analysis of the sample. Instead, we figure three specimens (fig. 25A, C, D) to illustrate the variability of depth of incision of the glabellar furrows in this population sample. No obvious case for dimorphism can be made, nor have we been able to determine any allometry in genal angle shape or in pygidial features such as Shergold (1966, p. 190) has demonstrated for population samples of various acastid species.

Andinacaste legrandi, new species
Figures 2A; 25H; 26

Proetus sp. Salfeld, 1911, p. 208, pl. 1, fig. 3.
Cyphaspis sp. Kozlowski, 1923, p. 62, pl. 4, fig. 18.
"*Eophacops*" sp. Ahlfeld and Braniša, 1960, p. 60, pl. 3, fig. 1; Braniša et al., 1972, p. 24–25.

TYPE SPECIMENS AND MATERIAL EXAMINED: Four nearly complete specimens, two cephala, portions of three additional thoraxes and pygidia, from the Cordillera Real Formation, Huañacota, Chacaltaya and Viloco, Bolivia; one nearly complete specimen, ?Catavi Formation, Sora Sora, Bolivia. We designate AMNH 36710A, an external mold of an exceptionally well-preserved cephalon best exhibiting genal and eye morphology, and the cuticular granulation, as the holotype. Paratypes include NMNH 245638 (the Sora Sora specimen) and NMNH 245639, from Chacaltaya.
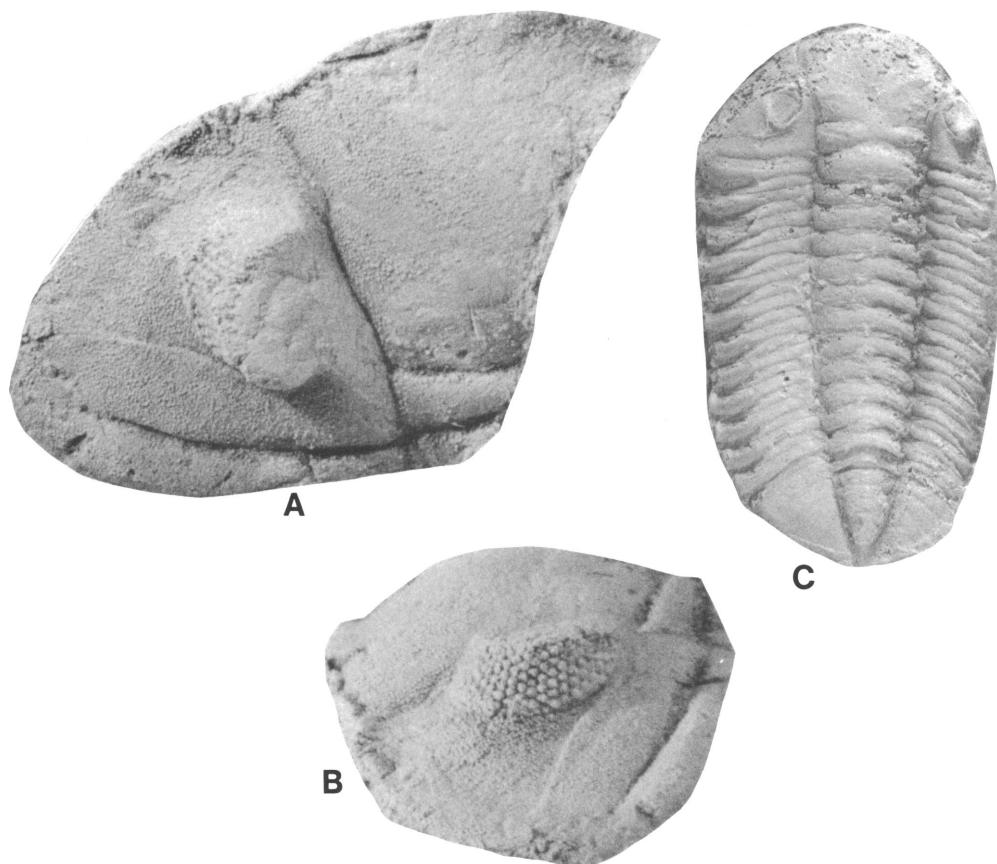
FIG. 26. *Andinacaste legrandi*. A, B. Cordillera Real Fm., Huañacota, Bolivia. Dorsal and left lateral views of latex cast of external mold of portion of cephalon. Holotype, AMNH 36710, ×10. C. Cordillera Real Fm., Chacaltaya, Bolivia. Dorsal view of internal mold of complete individual. Paratype, NMNH 245639, ×2.

ETYMOLOGY: This species is named for Rev. LeGrand Smith, collector of the holotype cephalon, and an accomplished and dedicated collector of Bolivian fossils whose efforts have contributed so heavily to this and other studies of Bolivian paleontology.

DIAGNOSIS: A species of *Andinacaste* with glabellar furrows effaced or incised as thin, faint linear depressions devoid of microgranulation. Genae sub-acuminate, without genal spines; posterior border recurved anterodistally with genal angle approximately opposite 1p glabellar furrow. Eyes relatively large for genus, set close to axial furrow, running from point opposite distal edge of glabellar furrow 1p anterior to point just posterior to distal terminus of 3p glabellar furrow. Eyes set on steeply sloping genal prominence, with no development of discrete eye socle. Palpebral lobe set off from palpebral area by conspicuous palpebral furrow. Eyes with approximately 25–26 dorsoventral files, with a maximum of six lenses per file. Large Eye Index .40–.44.

Pygidium with 5–8 axial rings and four or five pleura, with both pleural and interpleural furrows typically present.

REMARKS: The diagnosis of this species

documents the major differences between *A. legrandi* and *A. chojnacotensis,* differences we feel sufficiently great to warrant recognition of two separate species. We point out that the cuticular granulation described for the genus is only known for specimens of *A. legrandi,* as all specimens of *A. chojnacotensis* are internal molds, generally in a rather coarsely granular matrix.

The "schistes de la Cordillère Real" (Kozlowski, 1923, p. 10) have been most recently discussed by Braniša et al. (1972). At Huañacota, the matrix in which all of our specimens of *A. legrandi* are preserved is a dark grayish blue, slightly metamorphosed shale, and the specimens have been slightly flattened.

Ahlfeld and Braniša (1960, pl. 3, fig. 1) first noticed the differences between Cordillera Real specimens and those of *A. chojnacotensis* from the Catavi Formation at other localities. Also, *A. legrandi* is the taxon referred to as "*Eophacops*" sp. in the discussion of the Cordillera Real Formation in Braniša et al., 1972. The general conformation of this trilobite, especially the rather flat anterior glabellar lobe and the posteriorly rounded micropygous pygidium with, at least occasionally, reduced pygidial segmentation, indeed is strongly reminiscent of species of *Eophacops.* The acastid affinities of *A. legrandi,* however, are clearly shown by the morphology of glabellar furrows 3p and the typically acastid pattern of the auxiliary impression system. But the close agreement in general body size and conformation strongly suggests that these two only remotely related genera held many aspects of their mode of life in common.

KOZLOWSKIASPIS BRANIŠA AND VANĔK, 1973

Kozlowskiaspis Braniša and Vanĕk, 1973, p. 100, pl. 5, figs. 1–7.

TYPE SPECIES: *Kozlowskiaspis superna* Braniša and Vanĕk, by original designation and by monotypy.

REVISED DESCRIPTION: The cephalon of *Kozlowskiaspis* is roughly equilaterally triangular, rather flat, and distinctly shouldered. The anterolateral border runs poster-odistally at a low angle around the anterior glabellar lobe, and is then deflected sharply posteriorly along the genae. The anterior margin forms a sharply rounded point at the midline, and is not developed as a distinct anterior median process. The anterior arch is rather slight; the anterior glabellar lobe is moderately steeply sloping anteriorly, becoming nearly horizontal midway posteriorly along the anterior glabellar lobe. The entire central area of the glabella, occipital ring, and top of the palpebrum lie in nearly the same roughly horizontal plane in standard orientation.

The axial furrows are straight and diverge from the axial midline at a slight angle of roughly 5°–8° to a point opposite the anterior margin of the eye and the distal terminus of glabellar furrow 3p; the axial furrows then become sharply divergent anterodistally, becoming confluent with the shallow lateral border furrow. The axial furrows are moderately incised opposite the occipital ring and 1p glabellar lobes, become nearly obsolescent between the eyes and glabellar lobes 2p and 3p, and deepen anterior to the eye. A slight axial furrow pit is present proximal to the facial suture immediately opposite glabellar furrow 3p. The axial furrows are inclined anterodorsally opposite the occipital ring and glabellar lobe 1p; the central area between the eyes and glabellar lobes 2p and 3p is elevated to the same height as the palpebral area and glabellar surface. The anterior region of the axial furrow is steeply inclined anteroventrally.

The anterior glabellar lobe is trapezoidal; the anterolateral margin of the anterior glabellar lobe is slightly concave, reflecting a shouldering of the anterior border. Glabellar furrows 3p are moderately to lightly incised, and are rather broad and sinuous. The proximal portion of glabellar furrows 3p runs anterodistally at an angle of approximately 70°–75°, and the distal portion is reflected anteriorly and diverges exsagittally at an angle of approximately 50°–55°. Glabellar furrows 3p approach and appear (but in fact do not) to communicate with the axial furrows, being separated from the axial furrows by a slight ridge. Glabellar furrows 2p are likewise mod-

erately to lightly incised, transverse, do not reach the axial furrows, and lack apodemes. Glabellar furrows 1p are slightly inclined anterodistally and are shallow proximally; they become deeply incised distally and developed into broad (tr.) apodemes, and communicate with the axial furrows. The central area of the glabella is approximately 32 percent (range: 25%–37%) the total glabellar width between the eyes. The occipital furrow is broad and rather shallow medially, with the lateral portions more deeply incised and inclined slightly posterodistally, and with broad (tr.) apodemes developed. The occipital ring is smooth, longest at the midline, and elevated into the same curved surface as the glabella.

The posterior border is inclined slightly posterodistally, and is recurved slightly anteriorly near the genal angle. The genal angle is opposite the occipital ring, and bears a flat, broad, posteriorly directed genal spine. The lateral cephalic border furrows are very shallow.

The eyes are rather small in most species (Large Eye Index average .32; observed range .29–.42, N = 11), and are set in rather close to the axial furrows, with the posterior margin opposite glabellar furrow 1p, and the anterior margin extending to a point between one-half and three-fourths the length of glabellar lobe 3p. The eye socle is short and either vertical or slightly concave. The anterior branch of the facial suture is parabolic, transecting the anterolateral corners of the anterior glabellar lobe to a considerable extent in most species.

The cephalic doublure is flat, broadly triangular, and bears a triangular pattern of impressions with the apex directed anteriorly, near the midline. The hypostomal suture is slightly convex anteriorly. The hypostoma (known from the type species only) is short, and consists of a large, nearly flat central body, a broad border furrow, and a flat border ridge that is broadest posteriorly. The anterior wing is incompletely known; it is reflexed vertically and faces anteriorly. The wing process is unknown. The posterior wing is reflexed vertically and faces laterally; it is situated approximately midway along

the hypostomal length. At least two pairs of border spines are present; the more anterior one is opposite the posterior margin of the central body, and is rather short and directed posterolaterally, whereas the posterior spine is longer and directed posteriorly. The maculae are elongate grooves on the internal mold, inclined anterodistally (nearly indistinct on the external cuticular surface), and are near the anterior terminus of the border ridge just opposite the posterior proximal margin of the anterior wing.

The auxiliary impression system (figs. 2M–O and 27D) is developed in the typical triangular acastid pattern, viscerally as scars, pads, or both and externally (in one species) as depressions which retain the groundmass of granulation. The cephalic ornament, where known, is a groundmass of fine granules everywhere except in the major cephalic furrows. Genal dimpling is lightly developed in all species.

The thorax has well-pronounced axial furrows which converge only slightly posteriorly. The pleura are rather evenly arched, terminating in sharp, posteriorly directed, flat, bladelike spines. The distal pleural spines are flatter and shorter than in *Deltacephalaspis*. The pygidium is distinctly triangular, macropygous (approximately 120 percent the length of the cephalon), and is obtusely rounded posteriorly. The axis tapers posteriorly, nearly or completely reaching the posterior pygidial margin. The posterolateral margin is reflected sharply dorsally, creating a large posterior pygidial emargination (arch) in posterior view. The region posterior to the axis, where present, is short and steeply sloping. The pygidial border is flat and generally devoid of pleural and interpleural furrows. The pygidial margin is entire, except for two pairs of slight projections opposite the anterior two pygidial pleura in some species. The axis has from 9–13 rings, with the ring furrows moderately deeply incised. From 7–9 pairs of pleura are present; the pleural furrows are moderately deeply incised, and the interpleural furrows are obsolescent in some species, but faint to fairly well marked in others.

REMARKS: The uniquely shaped, rather

flattened cephalon of *Kozlowskiaspis* is distinctive. The size and location of the eyes, the glabellar pattern, and the transection of the glabella by the anterior branch of the facial suture call to mind *Deltacephalaspis* and other members of the *Calmonia* group (see Introduction), but the overall cephalic outline is distinctly "dalmaniticized," i.e., more like *Dalmanites* than any other calmoniid taxon except *Metacryphaeus*. Peripheral cephalic morphology—total outline, shape and position of genal spines, and nature of the anterior median region—readily distinguishes *Kozlowskiaspis* from all other calmoniids. The thorax of *Kozlowskiaspis*, however, presents few distinctive features except for the sharp, flat, posteriorly directed terminal pleural spines. These spines are to be found in *Deltacephalaspis* and *Metacryphaeus*, and isolated portions of thoraxes often cannot be identified. However, the more posterior spines in *Deltacephalaspis* are elongate and subconical, affording a measure of difference between the two genera. The pygidia of *Deltacephalaspis* and *Kozlowskiaspis* are likewise nearly identical, though the ring, pleural, and interpleural furrows are invariably fainter, the pygidial border is a slightly thickened ridge, the axis does not reach the pygidial margin, the posterior margin is only slightly arched, and there is a terminal spine in *Deltacephalaspis*. Nonetheless, fragments and otherwise poorly preserved pygidia are difficult to distinguish.

Metacryphaeus, of course, possesses a pygidium with distinctive marginal lappets (very similar to the thoracic terminal pleural spines) and, though earlier species (as yet undescribed) have rather triangular pygidia, the pygidia of most *Metacryphaeus* species are relatively shorter and more bluntly rounded posteriorly than in *Kozlowskiaspis*. We shall make other remarks concerning possibly confusing similarities with other taxa following descriptions of the species which we refer to *Kozlowskiaspis*.

Finally, we note that *Kozlowskiaspis* is presently known only from the Icla beds in the Padilla region of Bolivia, and from both northern and southern exposures of the *Scaphiocoelia* Zone of Bolivia. No taxon especially closely resembling *Kozlowskiaspis* has been described from any other horizon in Bolivia, or from elsewhere in the Malvino-Kaffric realm.

KOZLOWSKIASPIS (*KOZLOWSKIASPIS*)
Braniša and Vaněk, 1973

EMENDED DIAGNOSIS: Cephalon very broad (length/width ratio approximately .44), semicircular, with anterior border diverging posterolaterally from the midline at an angle of approximately 20°; shouldering pronounced, developed well distally to visual surface. Anterior border reduced and steeply inclined anteroventrally, and weakly pointed medially. Anterior border furrow obsolescent. Anterior glabellar lobe expanded strongly anterolaterally. Genae gently sloping and relatively broad.

Eyes small (Large Eye Index average .31; range: .30–.32, N = 7), set in close to axial furrows, with flat palpebral lobe and depressed, very small palpebral area set off from palpebral lobe by steeply sloping wall. Eyes with 23–24 dorsoventral files, with a maximum of six or seven lenses per file. Anterior cephalic doublure narrow, lunate.

Pygidium with 13 axial rings plus terminal piece, and approximately nine pleura, with interpleural furrows generally weakly developed or altogether absent. Pygidial border broad and smooth, with few traces of pleural furrows, and without marginal nodes; pygidial doublure flat, broad, closely adpressed to dorsal cuticular surface, and extending approximately one-third the length of the distal pleural field. Posterior vertical emargination very large; axis reaching posterior margin of pygidium.

REFERRED SPECIES: *Kozlowskiaspis* (*Kozlowskiaspis*) *superna* Braniša and Vaněk remains the sole species assigned to this subgenus. See comments under type species and following diagnoses of *K.* (*Romanops*), new subgenus, and its included species, below.

Kozlowskiaspis (*Kozlowskiaspis*) *superna*
Braniša and Vaněk
Figures 2O; 27; 28; 29B

Kozlowskiaspis superna Braniša and Vaněk, 1973, p. 100, pl. 5, figs. 1–7.
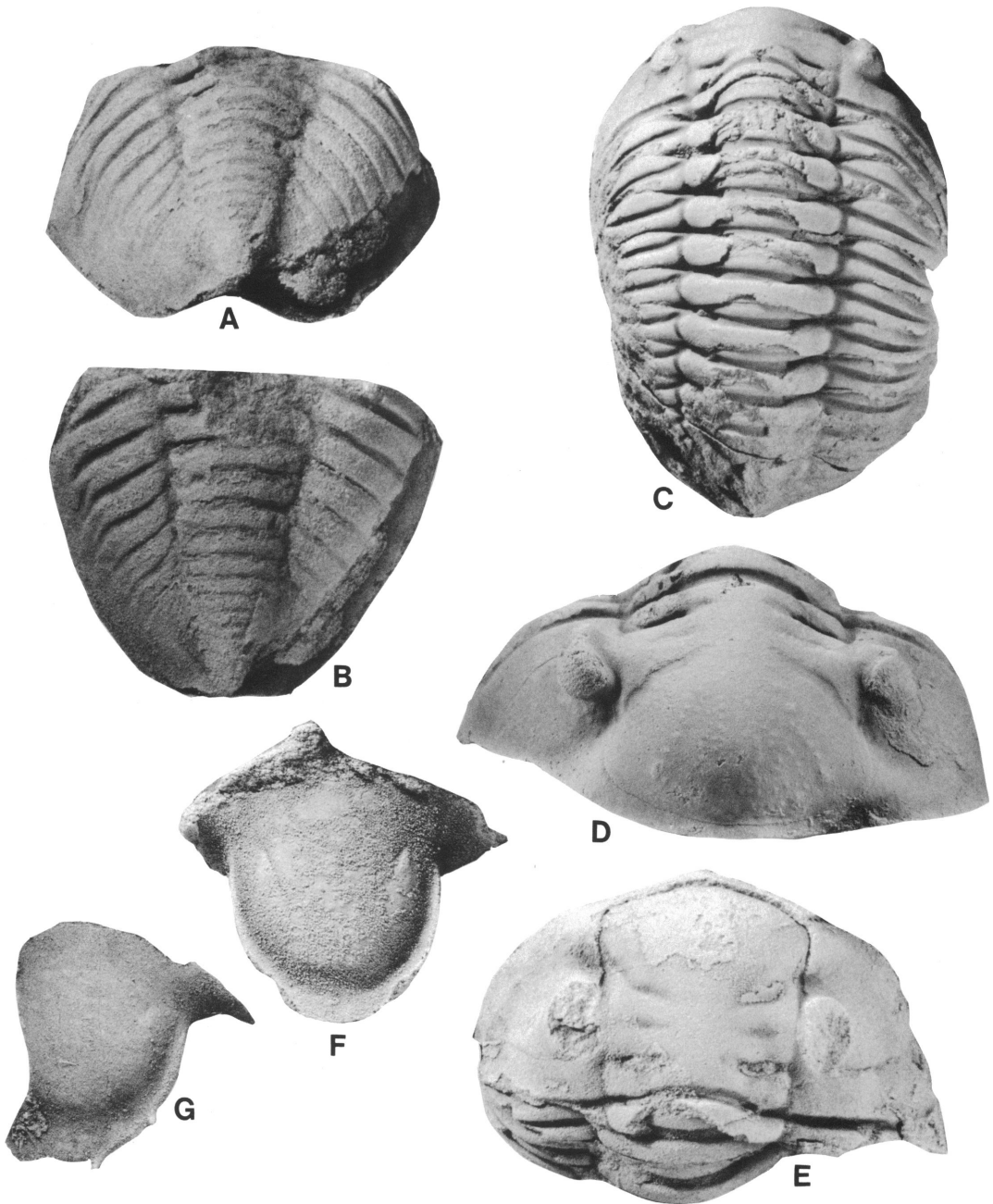
FIG. 27. *Kozlowskiaspis* (*Kozlowskiaspis*) *superna*. Icla Fm., all from Padilla, Bolivia, except A, B, from Otorongo, Bolivia. A, B. Oblique posterior (showing posterior arch) and dorsal views of internal mold of pygidium, AMNH 36711 (Smith Coll.), ×3. C, D. Dorsal view of internal mold of thorax (×2), and oblique frontal view of cephalon showing pattern of auxiliary impression system (×3). NMNH 245640. E. Dorsal view of internal mold of a cephalon, ×3. AMNH 36712 (Smith Coll.). F, G. External views of internal mold (F) and latex cast of external mold (G) of hypostoma, AMNH 36713 (Smith Coll.), ×4.
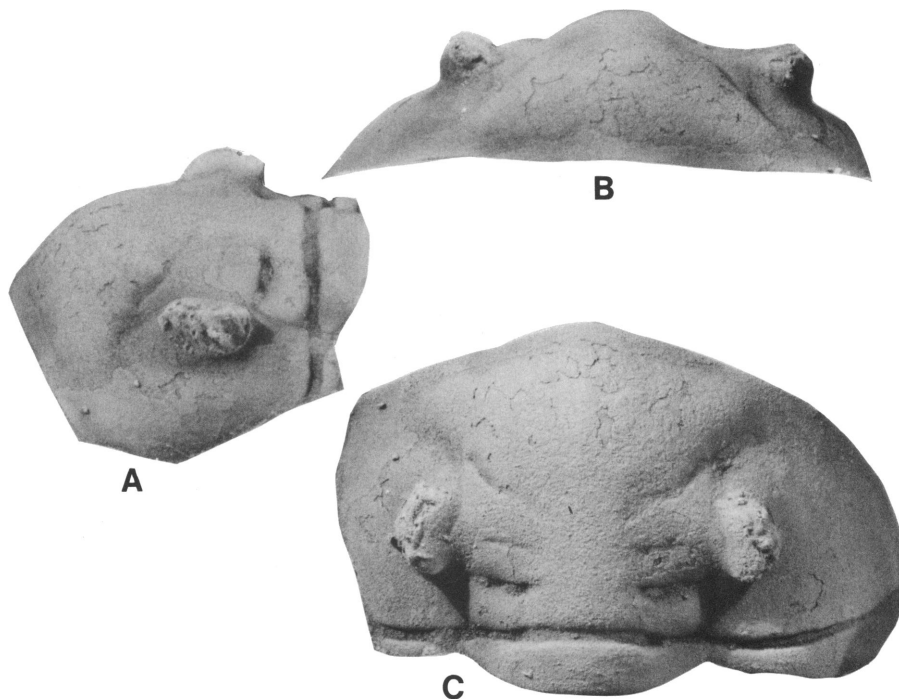
FIG. 28. *Kozlowskiaspis* (*Kozlowskiaspis*) *superna*. Icla Fm., Padilla, Bolivia. A–C. Oblique left lateral, frontal, and dorsal views of latex cast of external mold of cephalon. NMNH 245641 (latex cast AMNH 36714), ×3.

EMENDED DIAGNOSIS: *Kozlowskiaspis* (*Kozlowskiaspis*) appears to be monotypic and for the time being the emended diagnosis of the subgenus will suffice as an emended diagnosis of the type species *K.* (*K.*) *superna*.

TYPE SPECIMENS AND MATERIAL EXAMINED: The holotype and four paratypes are deposited in the collections of the Czechoslovakian Geological Survey, Prague, numbered as LB20–LB24. We have not reexamined these specimens for this study. We have examined a total of 19 cephala, 11 thoraxes or portions thereof, 11 pygidia, and one hypostoma, distributed as follows: from Padilla, seven cephala, two thoraxes, and one pygidium in the NMNH Braniša Collection, and including one reasonably complete specimen; five cephala, two thoraxes, and three pygidia, Braniša Collection, AMNH; three cephala, three thoraxes, three

pygidia, and one hypostoma, Smith Collection, AMNH. From Otorongo: three cephala, two thoraxes, and two pygidia (including one reasonably complete specimen) Smith Collection, AMNH. From Tarabuquillo, one cephalon, two thoraxes and two pygidia (again, with one reasonably complete specimen), NMNH Braniša Collection. All specimens are from the Lower Icla Formation, and all localities are in the Chuquisaca Department, Bolivia.

REMARKS: These specimens are all preserved as internal molds with only a single poorly preserved external mold available. Thus most of the details concerning cuticular "ornament" remain unknown, and inasmuch as all observable features have been expressed in the generic and subgeneric diagnoses, we have elected not to present a detailed description of *K.* (*K.*) *superna*.
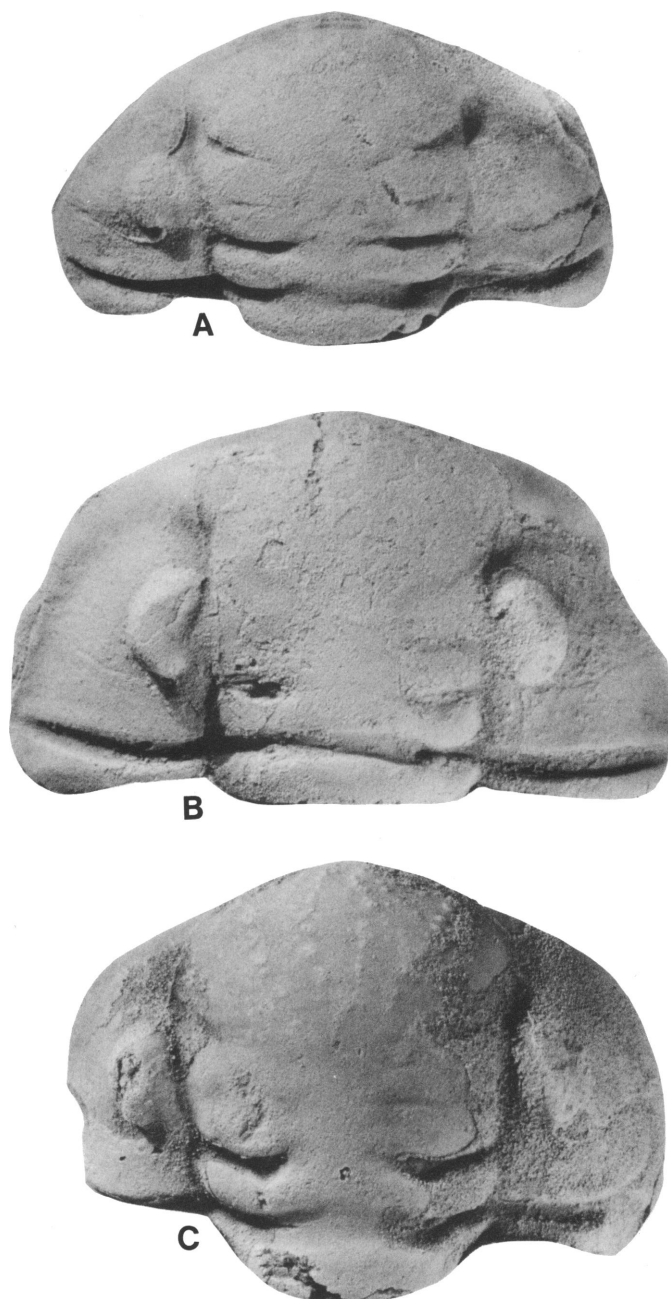
FIG. 29. Comparative figure illustrating close resemblance in overall cephalic conformation and glabellar furrow pattern among three species allocated (on other criteria) to three separate genera. All three specimens from the Icla Fm., Padilla, Bolivia, approximately from the same horizon (Padilla +7, Braniša NMNH locality designation), thus quasi-contemporaneous and possibly sympatric. A. Dorsal view of internal mold of cephalon of undescribed species similar to *Calmonia*. NMNH 245642, ×3. B. Dorsal view of internal mold of cephalon of *Kozlowskiaspis* (*Kozlowskiaspis*) *superna*, NMNH 245643, ×3. C. Dorsal view of internal mold of cephalon of ?*Acastoides verneuili*, NMNH 245644, ×3. Note pattern of auxiliary impression system on anterior glabellar lobe.

The generic and subgeneric diagnoses amplify, and to some extent, correct the diagnosis of *Kozlowskiaspis* given by Braniša and Vaněk (1973). (In their paper the generic diagnosis of *Kozlowskiaspis* stood as the diagnosis of *K. superna*.) In particular, the anterior border, said to be missing in the original description, is present as a thin, bladelike, steeply inclined structure. Thus even in dorsal view the glabella does not quite attain the anterior margin of the cephalon. Also, the glabellar furrows are rather more distinctly incised than originally reported, and the pygidium is nearly isopygous or just slightly longer than the sagittal length of the cephalon (macropygous), but certainly not twice as long as the cephalon as originally maintained (Braniša and Vaněk, 1973, p. 100). Finally, our counts of pygidial axial rings and pleura on the material presently at hand are slightly lower than those originally reported.

While we no longer support the contention (Braniša and Vaněk, 1973, p. 100) that *Kozlowskiaspis* is closely related to ?*Acastoides*, nevertheless we figure (fig. 29A–C) three cephala, one each of *K. (K.) superna,* ?*Acastoides,* cf. ?*A. verneuili,* and an undescribed rather primitive species of a taxon similar to *Calmonia*; all three are internal molds from the Icla Formation at Padilla. Superficially these specimens appear quite similar. However, ?*Acastoides* is readily differentiated by its higher vaulting and more inflated glabella, the course of the facial sutures and axial furrows (the anterior glabellar lobe is never transected by the facial suture in this genus), and genal morphology. Although the distal tips of the thoracic pleura are spined in ?*Acastoides,* the pygidium of this genus is posteriorly rounded and micropygous—totally unlike the situation in *Kozlowskiaspis*. The undescribed species (fig. 29A) herein considered closely related to *Calmonia,* is more highly arched than *Kozlowskiaspis superna,* the glabella is not transected by the facial suture, and the cephalic doublure is quite different (i.e., like normal *Calmonia* morphology), but otherwise these two apparently sympatric species are very similar

indeed (we have been unable to associate a pygidium with the *Calmonia*-like cephalon of fig. 29A).

KOZLOWSKIASPIS (ROMANOPS), NEW SUBGENUS

TYPE SPECIES: *Kozlowskiaspis (Romanops) borealis,* new species; referred species: *Kozlowskiaspis (Romanops) australis,* new species.

ETYMOLOGY: The subgeneric name *Romanops* is a compound based on the first name of Roman Kozlowski, early student of Devonian trilobites and other fossils from Bolivia, whose last name already inspired the generic name, and ops, a conventional suffix of trilobite generic names.

DIAGNOSIS: Cephalon subtriangular, not as broad as in nominate subgenus (length/width ratio approximately .50), somewhat more highly arched and strongly reminiscent of species of *Metacryphaeus*. Anterior border inclined posterolaterally from the midline at an exsagittal angle of approximately 20°. Shouldering pronounced, but break in slope producing shouldered effect commencing in front of visual surface. Anterior and lateral cephalic borders well developed, flat, bladelike, not reflected downward anteriorly as in *K. (Kozlowskiaspis)*; anterior border a subacuminate point at midline. Lateral and anterior border furrows distinct. Axial furrows diverging at an angle of approximately 80° anterior to eye, with anterior glabellar lobe relatively less wide than in *K. (Kozlowskiaspis)*. Genae more steeply sloping and less broad than in nominate subgenus. Anterior cephalic doublure spatulate (triangular), projecting as a ventral process, and quite flat.

Pygidium with 13 or fewer axial rings; ring furrows well incised. Axis not reaching posterior margin; posterior margin less highly emarginate than in nominate subgenus. Eight pleura present; pleural furrows well incised except near pygidial border. Interpleural furrows typically visible throughout length of pleural field. Pygidial margin and ventral doublure less broad than in *K. (Kozlow-*
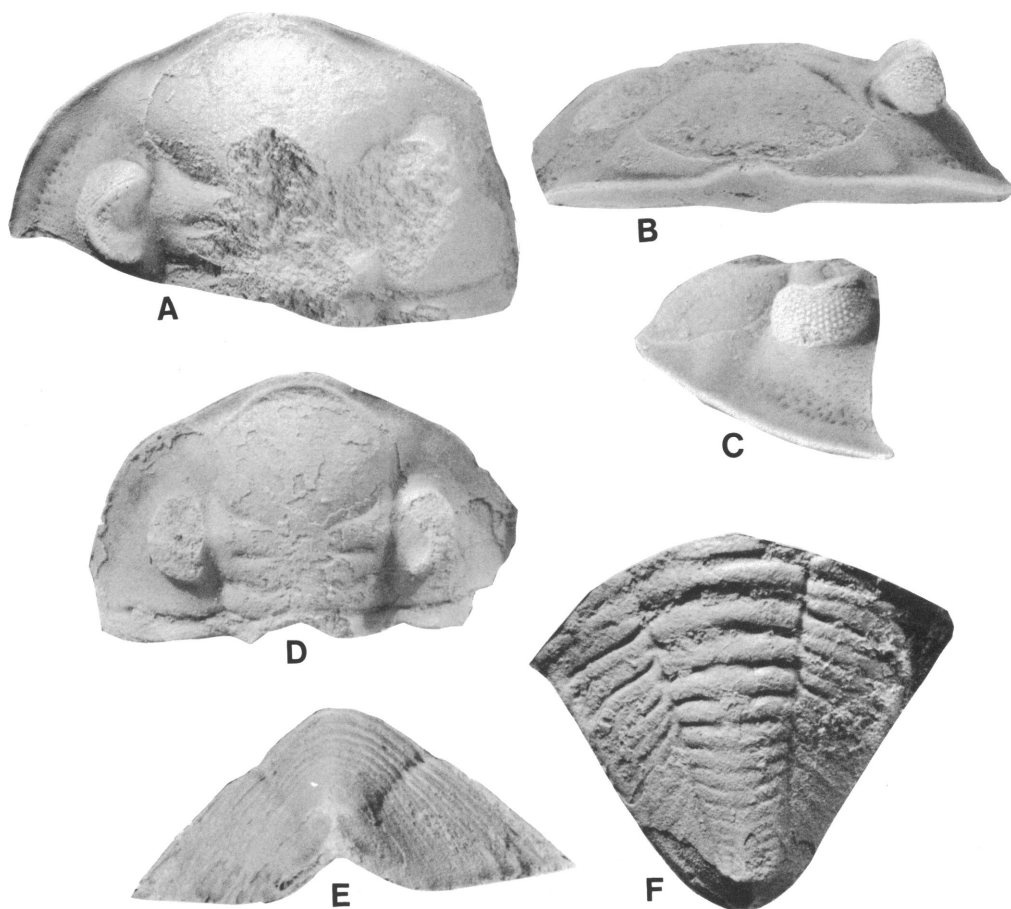
FIG. 30. *Kozlowskiaspis (Romanops) borealis. Scaphiocoelia* Zone, Lower Belén Fm. A–C. Dorsal, frontal, and left lateral views of partial cephalon with cuticle intact. Holotype, AMNH 36715 (Braniša Coll.), ×3. Colchani, Bolivia. D. Dorsal view of internal mold of cephalon. Paratype, AMNH 36716 (Braniša Coll.), ×3. Tikani, Bolivia. E, F. Posterior and dorsal views of internal mold of pygidium. Paratype, NMNH 245645. Belén, Bolivia, ×3.

skiaspis); two minute nodes present on pygidial margin adjacent to anterior two pairs of pleura.

REMARKS: The above diagnosis summarizes the major differences between the younger *Kozlowskiaspis superna* and the two species we refer to *Kozlowskiaspis* from the *Scaphiocoelia* Zone. Features that unite all three species, prompting our referral of the *Scaphiocoelia* Zone species to *Kozlowskiaspis,* include especially the similarities in ce-

phalic doublure morphology (not identical, as we have noted above, but unlike *Metacryphaeus,* a genus to which we originally considered referring these two *Scaphiocoelia* Zone species), genal morphology, depth and course of glabellar furrows—particularly glabellar furrows 3p, great distal expansion of the anterolateral corners of the anterior glabellar lobe (with concomitant transection of the glabella by the facial sutures), near identity of the thoraxes (albeit shared with
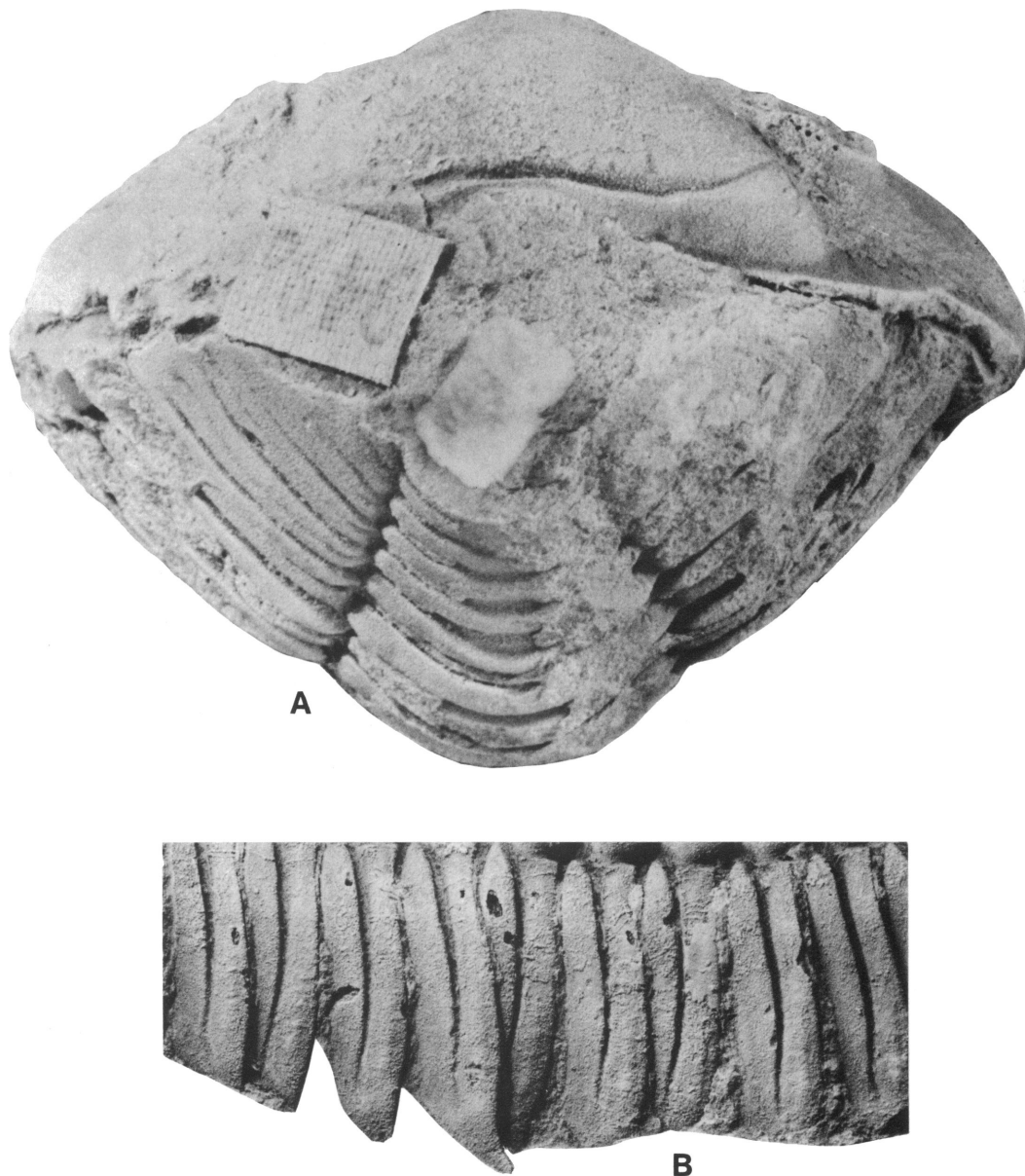
FIG. 31. *Kozlowskiaspis* (*Romanops*) *borealis*. *Scaphiocoelia* Zone, Lower Belén Fm. A. Frontal view of external (natural) cast of nearly complete, enrolled individual. Paratype, NMNH 245646, ×4. Belén, Bolivia. B. Left lateral view of natural cast of thoracic segments 2–10. AMNH 36718 (Braniša Coll.), ×3. Belén region, precise horizon and locality unknown.

Deltacephalaspis and *Metacryphaeus* to some degree), and, not least importantly, the close correspondence of the pygidia, which are unlike all other calmoniid pygidia known to us with the mild exception of *Deltacephalaspis* (see discussion following emended diagnosis of *Kozlowskiaspis* above for criteria for separating the pygidia of these two

genera). These features all debar referral of the two *Scaphiocoelia* Zone species to either *Metacryphaeus* or *Deltacephalaspis*.

All three species of *Kozlowskiaspis* retain a number of characteristics of the *Calmonia* group of calmoniids. However, we regard these as plesiomorphic retentions, and cite overall cephalic conformation, depth of incision of the glabellar furrows, and the fact that, in one of the *Scaphiocoelia* Zone species, the eyes are larger, set slightly out away from the axial furrows, and the slight but definite development of distinctive palpebral morphology typical of *Metacryphaeus* and its closest related genera. It is noteworthy that the youngest species—*K.* (*K.*) *superna*—retains more primitive features (as well as develops a number of distinctive autapomorphies), whereas the older species more clearly indicate the probable affinity of *Kozlowskiaspis* with *Metacryphaeus*. This issue will be dealt with in greater detail in a forthcoming analysis of calmoniid intergeneric relationships. The two *Scaphiocoelia* Zone species of *K.* (*Romanops*) show varying degrees of similarity with *K.* (*K.*) *superna*. These relative similarities and differences are assessed following diagnoses of these two species.

Kozlowskiaspis (Romanops) borealis, new species
Figures 2M; 30; 31

TYPE SPECIMENS: All material referred to this species is from the *Scaphiocoelia* Zone, Lower Belén Formation, in the La Paz-Belén-Sicasica region, northern Bolivia. Holotype: portion of cephalon, Colchani, AMNH 36715; paratype cephalon, Tikani, AMNH 36716; paratype enrolled specimen, Belén, NMNH 245646; paratype, nearly complete specimen, Tikani, AMNH 36717; paratype pygidium and portion of thorax, Belén, NMNH 245645. All specimens collected by Leonardo Braniša.

ADDITIONAL REFERRED SPECIMENS: AMNH Smith Collection: a single cephalon from Tikani (marked as "Estacion bombeo Sica Sica"), and a cephalon and pygidium from Colchani; AMNH Braniša Collection:

a cephalon and thorax from Belén; three cephala, two thoraxes and three pygidia from Tikani, and two cephala and a thorax from Colchani. In addition, a well preserved thorax and pygidium from the Belén region, precise locality unknown, is present in the AMNH Braniša Collection (AMNH 36718). Braniša Collection, NMNH, one thorax from Belén.

ETYMOLOGY: *Borealis,* meaning northern, referring to the occurrence of this species only in northern outcrops of the *Scaphiocoelia* Zone in Bolivia.

DIAGNOSIS: A species of *K.* (*Romanops*) with a bluntly pointed, short anterior median cephalic process formed solely by the anterior border. Facial sutures transecting anterior glabellar lobe high up on glabellar surface and running along anterior slope of glabella just distal to a thick, prominent anterior glabellar ridge, bounded proximally by a deep anterior glabellar furrow. Anterior glabellar lobe moderately highly inflated anteriorly.

Eyes large (Large Eye Index .40–.42), with posterior margin set off moderately far from axial furrows; visual surface with 28–30 dorsoventral files, and a maximum of 10 lenses per file. Palpebral lobe narrow, flat, crescentic, elevated to height of visual surface, with impressions (muscle insertion sites?) developed as visceral pads just proximal to dorsal margin of visual surface. Palpebral area steeply inclined ventroproximally, set off from palpebral lobe by sharp break in slope. Glabellar furrows 3p not reaching axial furrows, but ridge between distal terminus of 3p furrow and axial furrow very low, creating a *de facto* complete posterolateral isolation of anterior glabellar lobe from glabellar lobe 3p.

Pygidium with 13 axial rings and terminal piece generally developed.

REMARKS: See discussion following diagnosis of *K.* (*R.*) *australis* below.

Kozlowskiaspis (Romanops) australis, new species
Figures 2N; 23B; 32

TYPE SPECIMENS: All type material from the *Scaphiocoelia* Zone of the Gamoneda
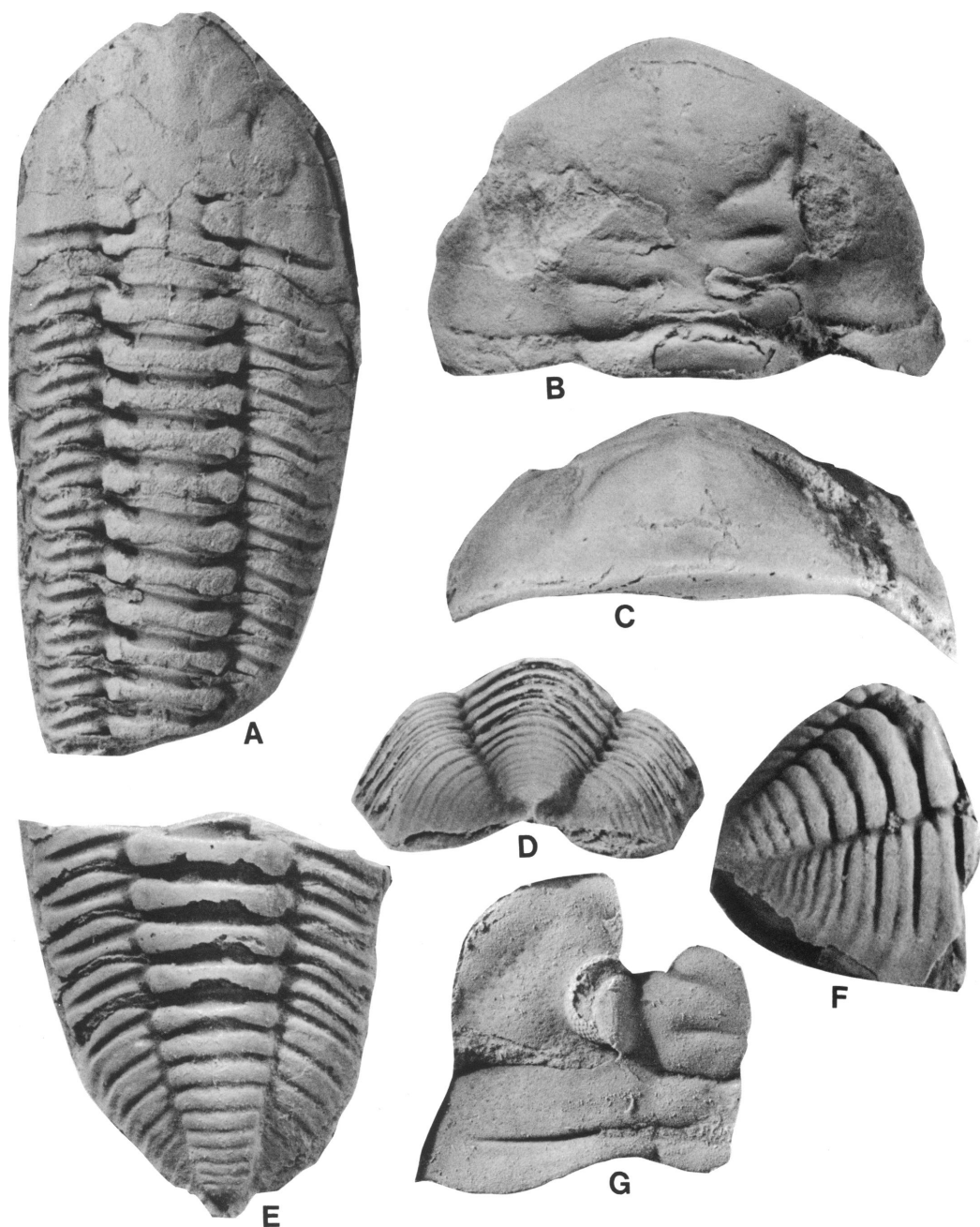
FIG. 32. *Kozlowskiaspis* (*Romanops*) *australis*. *Scaphiocoelia* Zone, Gamoneda Fm. A. Dorsal view of internal mold of cephalon and major portion of thorax. Paratype, NMNH 245647, ×3. Curuyo, Bolivia. B, C. Jarcas, Bolivia. Dorsal and frontal views of internal mold of cephalon. Holotype, NMNH 245630, ×3. (See fig. 23B for view of latex cast of external mold of this specimen.) D, E, G. Curuyo, Bolivia. Dorsal and posterior views (×3) of internal mold of thorax and pygidium, associated in same slab with external mold of portion of cephalon (shown as dorsal view of latex cast, G), ×4. Paratype, NMNH 245648 (latex cast AMNH 36719). F. Oblique right lateral view of internal mold of pygidium. Paratype, NMNH 245649, ×4. Curuyo, Bolivia.

Formation, Tarija Department, Bolivia. Holotype, an internal and partial external mold of a cephalon, Jarcas, NMNH 245630; paratype, internal mold of a cephalon lacking eyes, and a thorax, Curuyo, NMNH 245647. Paratype, external mold of portion of cephalon and associated internal mold of a pygidium and posterior portion of a thorax, Curuyo, NMNH 245648; paratype pygidium (internal mold), Curuyo, NMNH 245649. All type material collected by Leonardo Braniša.

ADDITIONAL REFERRED SPECIMENS: A thorax and pygidium from the Gamoneda Formation (*Scaphiocoelia* Zone), Curuyo; a cephalon lacking eyes from the *Scaphiocoelia* Zone at Presto El Peral. Both specimens in NMNH Braniša Collection.

ETYMOLOGY: *Australis,* meaning southern, referring to the occurrence of this species only in southern outcrops of the *Scaphiocoelia* Zone in Bolivia.

DIAGNOSIS: A species of *K.* (*Romanops*) with smaller (rudimentary) and less prominently pointed anterior median cephalic process. Facial suture transecting a relatively minor portion of anterior glabellar lobe, not associated with an anterior glabellar ridge or furrow. Anterior glabellar lobe flatter, less steeply inclined anteriorly than in *K.* (*R.*) *borealis*. Eyes small (Large Eye Index .29), with posterior margin of visual surface set in close to axial furrow, and with palpebral lobe set off from gently inclined palpebral area by slight break in slope. Eyes with approximately 23 dorsoventral files, with a maximum of six lenses per file. Glabellar furrows 3p distinctly not reaching axial furrows. Pygidium with 10 or fewer axial rings plus terminal piece.

REMARKS: Only character states which truly differentiate the two species have been included in the above diagnoses, and need

not be belabored here. The separation of the *Scaphiocoelia* Zone species assigned to *K.* (*Romanops*) into two morphologically discrete taxa, one each from the northern and southern areas of outcrop, is a by now familiar pattern, paralleling the case in *Deltacephalaspis* (*Deltacephalaspis*) and the geographic variation discussed for *Bainella* (*Belenops*) *insolita* and *Phacopina convexa*.

Kozlowskiaspis (*Romanops*) *australis* is the more conservative (plesiomorphic) of the two species in that it more closely resembles contemporary species of the *Calmonia* complex, as well as the younger *K.* (*Kozlowskiaspis*) *superna*; *K.* (*R.*) *borealis* resembles *K.* (*K.*) *superna* more than does *K.* (*R.*) *australis* only in having a relatively higher placement of the facial suture over the anterolateral corner of the glabella. In *all* other features—including eye morphology—cited in the diagnosis of *K.* (*R.*) *borealis,* that species deviates from typical *Calmonia* group character states, and from *K.* (*Kozlowskiaspis*) *superna,* sharing instead its similarities with *Metacryphaeus*.

There are several species in the *Scaphiocoelia* Zone that, on the basis of cranidial morphology, may be confused with the species of *K.* (*Romanops*). *Phacopina convexa* is best distinguished by its much lighter incision of the glabellar furrows (particularly 2p and 3p), the straighter course of its glabellar furrows 3p, its steeper slope of the anterior region of the glabella, higher cephalic arching, and its more dense covering of microgranulation, which is more commonly preserved on individual specimens. *Kozlowskiaspis* (*Romanops*) also closely resembles *Deltacephalaspis* (*Prestalia*), but is readily distinguished again by the greater depth of incision of the glabellar furrows (in *Romanops*), its lack of larger tubercles, and especially, the presence in *Prestalia* of a dis-
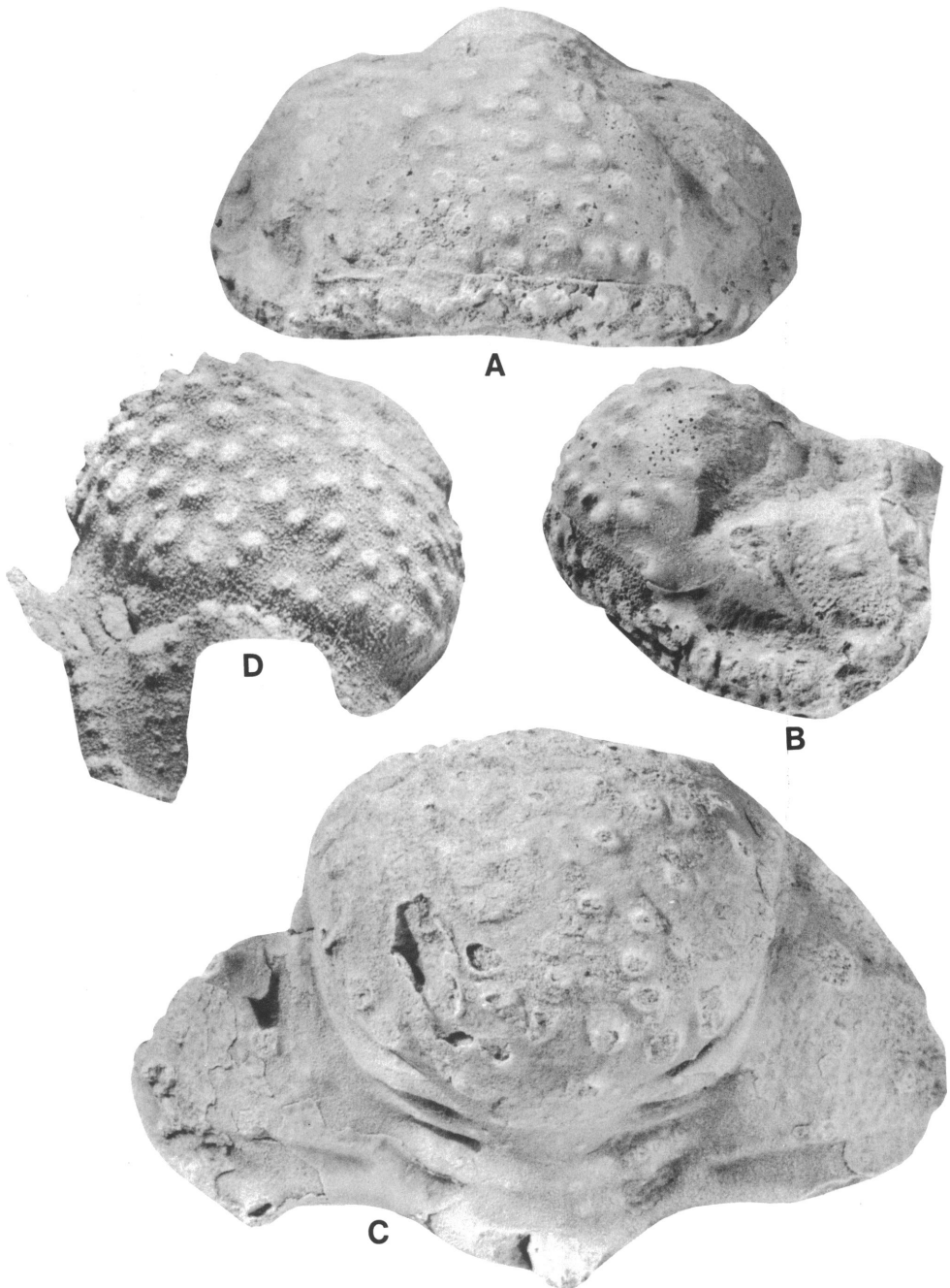
FIG. 33. A–C. *Parabouleia calmonensis*. *Scaphiocoelia* Zone, Lower Belén Fm. A, B. Colchani, Bolivia. Frontal and left lateral views of internal mold of cephalon, ×3. AMNH 36744 (Braniša Coll.). C. Oblique dorsal view of internal mold of cephalon, showing left eye stalk. Tikani, Bolivia (=Estacion Bombeo Sica Sica). AMNH 36745 (Smith Coll.), ×3. D. *Bouleia sphaericeps*. Right lateral view of internal mold of cranidium. Icla Fm., Padilla, Bolivia. AMNH 36746 (Smith Coll.), ×3.

tinctly parabolic course of the anterior branch of the facial suture anterior to the glabella, with the concomitant development of a distinctive, triangular median preglabellar field between the anterior glabellar lobe and the facial suture. Genal and pygidial morphology, of course, quickly set species of *Romanops* off from these and all other calmoniids of the *Scaphiocoelia* Zone, with the single exception of the pygidial similarities between *Kozlowskiaspis* and *Deltacephalaspis* discussed above.

PARABOULEIA ELDREDGE, 1972

Parabouleia Eldredge, 1972a, p. 147.

TYPE SPECIES: *Parabouleia calmonensis* Eldredge, 1972a, by original designation and by monotypy.

REVISED DESCRIPTION: The cephalon of *Parabouleia* has a highly inflated anterior glabellar lobe. Glabellar lobes 3p are inclined anterodorsally and merged with the anterior glabellar lobe to form the posterior wall of the composite glabellar lobe. The entire cephalon is highly arched in standard orientation; in dorsal view, the cephalic outline is roughly equilaterally triangular and is not shouldered. The anterior margin is gently rounded. In lateral view, the anterior region of the anterior glabellar lobe is steeply inclined dorsally, becoming recurved abruptly opposite the eye stalk and steeply inclined posteroventrally throughout the remainder of the glabella. The eye stalk and occipital ring are elevated above the posterior glabellar surface, but do not attain the height of the anterior glabellar lobe.

The axial furrows are moderately deeply incised, diverging at an angle of approximately 60° from the occipital ring through glabellar furrows 2p, and becoming slightly more shallow and somewhat laterally convex opposite lobes 3p, then sharply inclined ventrally and merging with the lateral border furrows. No axial furrow pit is developed. Glabellar furrows 3p are deeply incised, sharply curved, with a short proximal section roughly transverse, located close to the axial furrows. The distal sections of glabellar furrows 3p are sharply reflected anterolaterally, be-

coming subparallel to, but not confluent with, the axial furrows. Glabellar furrows 2p are short, transverse, and developed as apodemes viscerally; they do not reach the axial furrows. Glabellar furrows 1p are likewise transverse; they are developed as deep apodemes, widest (exsag.) proximally, and extending slightly closer to the glabellar midline than glabellar furrows 2p, communicating with the axial furrows. Glabellar lobes 1p and 2p are depressed and flat distally; the median area of glabellar lobes 1p and 2p is slightly elevated above the distal regions forming a distinct median lobe. The occipital furrow is developed as short, nearly transverse apodemes distally, becoming shallow and slightly convex anteriorly in the median region. The occipital ring is a thickened ridge distally, elevated above the distal regions of glabellar lobes 1p and 2p, and highly arched medially, bearing three prominent anteroposteriorly flattened spines.

The posterior border is a prominent ridge, arched (in posterior view) and slightly inclined posterodistally, bearing an irregular series of four or five spines. The genal angle is poorly known; it is apparently bluntly rounded, and bears a short genal spine. (The precise inclination and size of the genal spine are not determinable on the basis of presently available material.) The lateral border is gently curved anteromedially, with a pronounced double row of radiating spines inclined dorsally at a low angle. The lateral border merges smoothly with the anterior border, and is developed as a broadly rounded prominent callus bearing several irregular rows of radiating spines. The anterior border is just barely visible in dorsal view in standard orientation. The anterior and lateral borders are not sharply set off from the recurved doublure—i.e., the cephalic doublure is recurved dorsally, bearing a radiating row of ventrally projecting spines around the entire anterior and lateral cephalic border. The lateral border spines are separated from the lateral doublure spines by a broad, shallow furrow. The lateral border furrow is broad and moderately deep, producing a dishing effect, and is continuous with the axial furrow anteriorly. The anterior border furrow
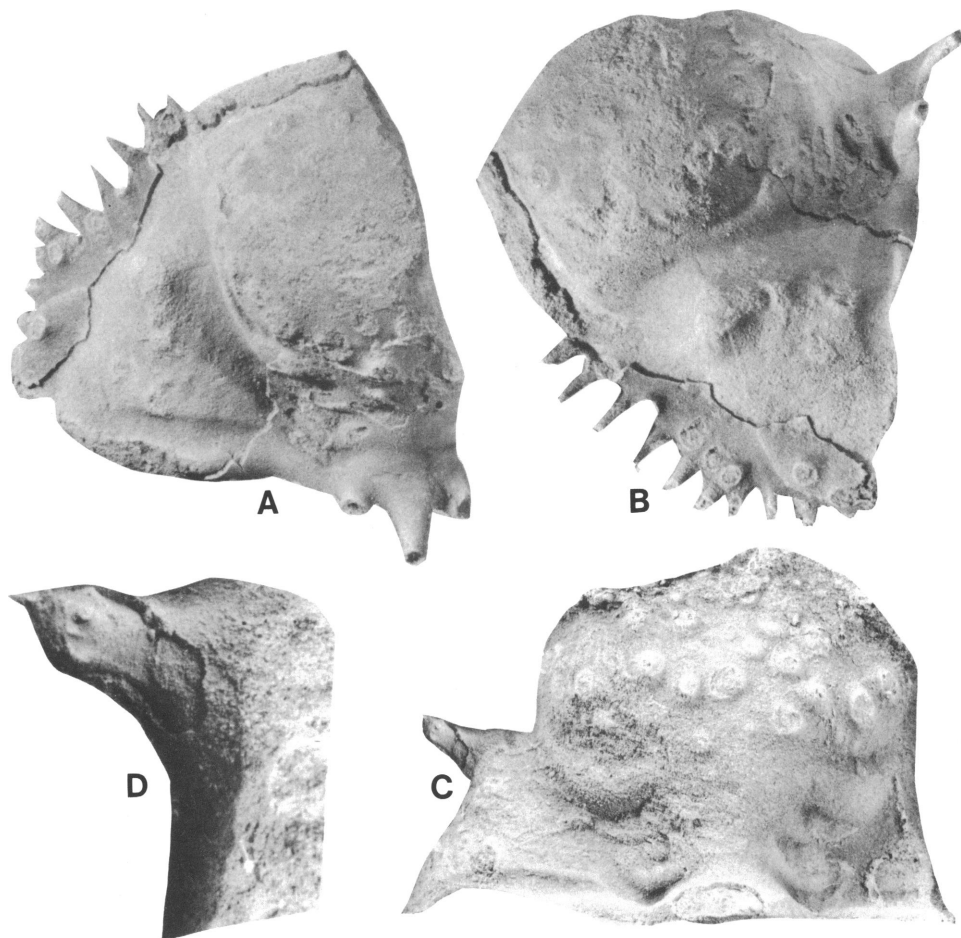
FIG. 34. *Parabouleia calmonensis. Scaphiocoelia* Zone, Lower Belén Fm. A, B. Dorsal (×2.5) and left lateral (×3) views of internal mold of cephalon. Tikani, Bolivia. AMNH 36747 (Braniša Coll.). C. Dorsal view of latex cast of external mold of cephalon, showing left eye stalk, ×3. Colchani, Bolivia. AMNH 36748 (Braniša Coll.). D. Closeup of eye stalk of AMNH 36748. ×12.

is inconspicuous, bearing the anterior branch of the facial suture.

The fixigena is nearly flat, with no palpebral area developed; it becomes steeply inclined ventrolaterally posterior to the eye stalk. The fixigena bears three prominent spines anterior to the posterior border furrow, including a single prominent spine posteroproximal to the eye stalk, and two spines posterodistally, near the genal angle, just proximal to the lateral border furrow. The librigena is small and nearly vertically inclined proximal to the lateral border furrow.

The eye complex is reduced to a single large spine ("eye stalk"), set well off from the axial furrows, inclined dorsolaterally (in posterior view) at an angle of approximately 45°, and anterolaterally (in dorsal view) at an angle of approximately 35°. The eye stalk is 3 mm. long in the only complete specimen (sagittal length of cephalon: 24 mm.; maximum width of cephalon: 37 mm.). The distal surface of the eye stalk is known only in broken specimens, and no lenses have thus far been observed. The eye stalk is thickened near its top, bearing a circlet of small radiat-

ing spines. The dorsal surface of the eye stalk is small and apparently flat (thus making "standard orientation" difficult to achieve, but considered to be with the dorsal surface of the two stalks oriented in a horizontal plane).

The facial suture transects approximately the distal one-third of the eye stalk. The anterior branch of the facial suture runs up the anterolateral face of the stalk; the posterior branch runs directly down the entire posterolateral region of the eye stalk, then runs obliquely posterolaterally across the gena, becoming sharply reflected posteriorly upon reaching the lateral cephalic border, and remaining proximal to the dorsal series of lateral cephalic border spines to the genal angle. The facial suture is thus gonatoparian or slightly opisthoparian. The anterior branch of the facial suture runs anteroproximally, traversing the lateral cephalic border furrow (near the point of juncture of the lateral border furrow with the axial furrow) and thence smoothly curved around the anterior cephalic margin. The facial suture is apparently functional in holaspids.

In ventral view, the median area of the cephalic doublure is depressed, flat, and roughly triangular, bounded anterolaterally by a row of doublure spines. The median doublure spine is set in slightly posteriorly to the main row. The hypostomal suture is gently curved and slightly convex anteriorly. The hypostoma is short and wide, apparently not reaching the posterior margin of the dorsal cephalic surface. The central body tapers slightly, and is broadly rounded posteriorly, set off from the flat and rather narrow lateral and posterior border by a distinct, narrow furrow. The central body is inflated in the posteromedian region slightly above (i.e., in ventral view) the level of the hypostomal suture; the central body slopes steeply laterally, and less steeply to the posterior margin. The anterior wings, incompletely known, are broad, thin, and reflected with the visceral surface inclined anteroproximally. The posterior wings, also poorly known, are situated just posterior to the anterior wing and are inclined dorsally. The hypostomal border has two minute spinules (localized thicken-

ings of the hypostomal border) in the posterolateral area. Maculae have not been observed.

The auxiliary impression system is faintly preserved as dark markings on some casts, consisting of several diverging rows of impressions emanating from the linear posterior median impression, and running over the curved glabellar surface close to the anterior branch of the facial suture in the acastid manner. The visceral surface of the hypostoma bears a dense pattern of impressions on the central body. The anterior glabellar lobe is covered with an irregular array of large spines. A single spine is present on glabellar lobe 3p; smaller tubercles are occasionally present on the median glabellar area (opposite lobes 1p–3p) and on glabellar lobes 1p and 2p. The remainder of the cephalon is smooth, i.e., devoid of granulation. The entire fixigena and the portion of the librigena proximal to the lateral border furrow is covered with small dimples. The entire dorsal cuticle is riddled with minute pores.

The axial rings of the thorax are semicircular in profile, and are arched high above. the pleura, with each axial ring bearing two anteroposteriorly compressed spines, one on each side, just off the midline. The ring furrows are broad and shallow; the articulating half-rings are about as long (sag.) as the axial rings. The pleura are transverse and horizontal proximally becoming steeply reflected ventrally and inclined posterolaterally in the distal portion. The pleural furrows are narrow proximally, arising near the anterior margin of the pleuron just distal to the axial furrow, and running obliquely posterolaterally across the pleuron, becoming broader at the point of pleural inflection, and terminating about three-fourths the distance down the flexed, distal portion of the pleuron. Three large pleural spines are developed in a row on the posterior moiety of each pleuron, starting with the point of pleural inflection and continuing down the distal pleural slope. The distal tips of the pleura are developed into two spines separated by a shallow indentation; the posterior spine of the pleural tip is reflected posteriorly and is seemingly continuous with the row of three

spines on the posterior moiety of the pleuron. The anterior spine on the pleural tip is more ventral in position, shorter, and seemingly an extension of the pleural doublure.

The pygidium is micropygous, roughly one-half the length of the cephalon, semicircular to faintly triangular, and is moderately arched in posterior view. The axis is strongly arched, consisting of eight or nine rings plus a terminal piece. The axis is bluntly rounded posteriorly, and is separated from the pygidial margin by a short posterior pleural field. Eight or nine pleura are present, with interpleural furrows (rather than the usual pleural furrows) being the more deeply incised. The interpleural furrows are broad and deep, and are developed into a broad pit at the distal terminus of each furrow, adjacent to the pygidial margin. The distal terminus of the pleural furrow is posteroproximal to this pit on the interpleural furrow. The posterior moiety of the pleuron is developed as a pronounced ridge bearing three spines on the anterior pleura, and two on the more posterior pleura. At the pygidial margin, terminal spines project dorsolaterally, presumably homologous with the posterior dorsal spines on the pleural tips of the thorax. The pygidial margin is roughly vertical below and between the distal pygidial spines. The pygidial doublure has not been observed.

REMARKS: The preceding revised description of *Parabouleia* considerably augments, but does not conflict with, the original description (Eldredge, 1972a, p. 147 ff.) which was based on the single specimen then available (NMNH 169673). The revised description is based on reexamination of the holotype plus an additional 51 specimens (detailed under the species *P. calmonensis* below), all from the *Scaphiocoelia* Zone of the Lower Belén Formation of the La Paz-Belén-Sicasica area of northern Bolivia.

Eldredge (1972a) has discussed the affinities of *Parabouleia* with *Bouleia* and *Metacryphaeus,* and in the Introduction to this study we have briefly discussed the anomalous situation with which *Parabouleia* confronts us: now appreciating its lower stratigraphic position so that its "intermediate" or "primitive" features (especially those of the glabella) conform with its actual older age vis à vis *Bouleia dagincourti* (Ulrich) and *Bouleia (=Dereimsia) sphaericeps* (Kozlowski), the highly derived "eye stalk" immediately eliminates *Parabouleia* from direct ancestry of *Bouleia.* Eldredge (1972a, p. 147) claimed that possession of three pairs of cephalic apodemes is a primitive feature; however, in view of the general absence of this feature in most other, including coeval and older, acastids and calmoniids, possession of three pairs of cephalic apodemes should probably also be considered an apomorphic, rather than a plesiomorphic, condition.

Parabouleia cannot be readily confused with any other calmoniid genus; basic criteria for differentiating *Parabouleia* from *Bouleia* are given in Eldredge (1972a), but a more detailed comparison of certain anatomical features between this genus and the two recognized species of *Bouleia* seems warranted. *Bouleia sphaericeps* continues to be known solely from cranidia (e.g., fig. 33D), despite the availability of additional specimens (in the AMNH Braniša and Smith collections) beyond the NMNH Braniša material cited in Eldredge (1972a). Again, though Eldredge (1972a) considered *B. sphaericeps* to be the more derived species of *Bouleia* (on the basis of glabellar morphology, a conclusion still valid), with its obviously functional facial sutures, the fact that the anterior glabellar lobe is more protuberant anteriorly in *B. dagincourti,* in contrast with the more "bun-shaped" posterior inflation of this lobe in *Parabouleia* and in *B. sphaericeps,* and its rather narrow spine bases, *B. sphaericeps* conforms more closely to the condition in *Parabouleia* than to *B. dagincourti.* Whether these conditions are to be considered primitive or derived is thus moot.

The auxiliary impression system, vaguely discernible in some specimens of *Parabouleia calmonensis,* and described above as "modified acastid,"—i.e., radiating rows of impressions over a highly curved surface—is now also known to be developed in similar form on some AMNH specimens of *B. dagincourti,* perhaps the final necessary piece of
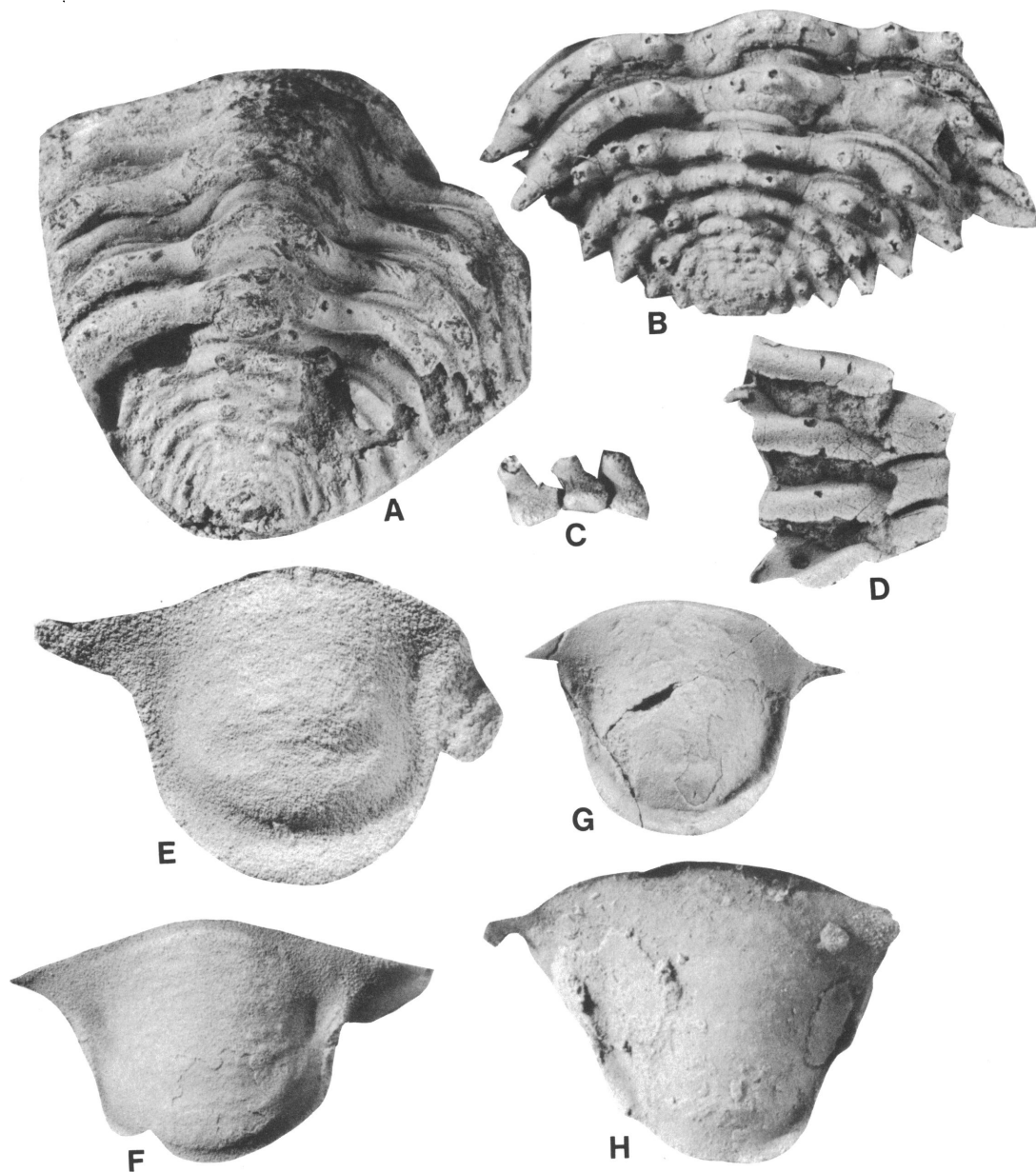
FIG. 35. A, B. Comparison of thorax and pygidium of *Parabouleia calmonensis* (A) and *Bouleia dagincourti* (B). A. *P. calmonensis, Scaphiocoelia* Zone, Lower Belén Fm., Colchani, Bolivia. AMNH 36720, ×3. B. *B. dagincourti,* Chacoma, Bolivia, AMNH 36721, ×3. C, D. *B. dagincourti.* Lateral and ventral views of latex cast of external mold of pleural tips of right thoracic segments 5–7. Upper Belén Fm., *cornutus* Zone, Pujravi, Bolivia. AMNH 36722 (Smith Coll.), ×4. E–H. Comparison of hypostomes of *Bouleia dagincourti* and *Parabouleia calmonensis.* E, F. External views (×3) of internal molds of two hypostomes of *B. dagincourti,* Chacoma, Bolivia (precise horizon unknown). Braniša Coll. E. AMNH 36723. F. AMNH 36724. G, H. External views of two hypostomes of *P. calmonensis.* G. Tikani, Bolivia. External mold, ×3. AMNH 36743. H. Colchani, Bolivia. Latex cast of external mold. AMNH 36720 (same specimen as in fig. 35A), ×4.

data confirming the conclusion (Eldredge, 1972a) that *Bouleia* has calmoniid, rather than phacopid *sensu stricto,* affinities.

Distribution of cuticular spines is very similar in these two genera. However, in *B. dagincourti,* there is but a single row of spines along the lateral cephalic border, positioned well off the actual margin. This single row continues, without multiplication, just below the facial suture around the anterior margin of the cephalon. This condition is in sharp contrast to the multiple rows of spines described above in *Parabouleia.* Also, the anterior cephalic margin of *Parabouleia* is more inflated and less sharply set off from the anterior glabellar lobe than in *B. dagincourti.* (The states of these characters are of course unknown in *B. sphaericeps.*)

Spines are more numerous and arranged differently on glabellar lobes 1p–3p, on the occipital ring, and on the fixigena in the two genera. Of particular importance are the three large spines on the occipital ring of *Parabouleia,* in contrast to the three to five smaller spines in *Bouleia,* presence of only two spines on the axial rings of the thorax in *Parabouleia,* and presence of spines on the proximal (as well as distal) portion of the posterior moiety of the thoracic pleura of *Bouleia.* The distal tips of the pleura of *Bouleia* have more pronounced posteroventral spines (fig. 35C, D); as in *Parabouleia,* presence of a pair of spines on the pleural tips apparently serves as an interlocking device on enrollment.

The pygidium of *B. dagincourti* has never been adequately described from well-preserved material. We here figure (fig. 35B) a pygidium of *B. dagincourti* (AMNH 36721, Braniša Collection) from Chacoma, Bolivia, precise horizon unknown. The pygidium of *B. dagincourti* is relatively shorter, broader, and more distinctly rounded posteriorly than in *Parabouleia,* and the axis is more depressed, with seven discernible rings, three spines per ring, and, most significantly, a posterior margin that blends imperceptibly into the posterior pleural field, in contrast with the higher axis with its bluntly rounded terminus well set off from the posterior pleural field in *Parabouleia.* In *Bouleia dagin-*

courti, there are but six pleura; as in *Parabouleia,* the interpleural furrows are deeply incised, but, in contrast with *Parabouleia,* the pleural furrows are present only on the first pleuron. Dominance of interpleural furrows over pleural furrows is highly unusual in phacopid (*sensu lato*) trilobites, and a further indication of the close relationship between these two genera. Eldredge (1972a, p. 143) noted that marginal pygidial spines were lacking in all *Bouleia* specimens hitherto described or figured; the well-preserved specimen illustrated herein (fig. 35B) shows a well-developed series of spines developed at the margin at the end of each pygidial pleuron. The spines radiate and project slightly dorsodistally. Apparently upon enrollment these spines interdigitate with the anteroventrally projecting radiating row of spines along the anterior border of *B. dagincourti,* serving either as an interlocking device (see discussion in Eldredge, 1972a, and Clarkson, 1969, on *Leonaspis*) or as a means of producing a series of slits for the passage of water currents—as recently suggested by Campbell (1977) for some Dalmanitidae, or possibly for both reasons. The use of the double row of spines on the pleural tips (fig. 35C, D) as an interlocking device may be seen on a specimen of *B. dagincourti* (Eldredge, 1972a, text-fig. 1C), where the posterodorsal spines of the anterior four thoracic pleura project out from under the posterolateral corner of the right librigena, while the anteroventral, more broad and blunt spines remain hidden as they abut the cephalic doublure.

Finally, the hypostoma of *B. dagincourti,* while very similar to that of *Parabouleia* described above, is somewhat broader and not as convex as in *Parabouleia* (fig. 35). The maculae are situated at the posterior base of the anterior wing in *Bouleia*; the posterior margin is broader and more gently rounded, and, as in *Parabouleia,* there are two minute spinules on each side of the posterolateral border. In *Bouleia,* impressions (interpreted as sites of muscle insertion) are developed as scars in a dense pattern, predominantly in the anterocentral part of the central body. Similar impressions, but developed as pads,

(positive relief on the visceral surface) are less well developed on hypostomata of *Parabouleia*.

Parabouleia calmonensis Eldredge, 1972
Figures 33A–C; 34; 35A, G, H

Bouleia dagincourti: Wolfart, 1968 (pars), pl. 5, fig. 4 and possibly fig. 5 *only*.
Parabouleia calmonensis Eldredge, 1972a, p. 147, text-fig. 5A–C.

REVISED DESCRIPTION: As this genus is monotypic, the revised generic description above may stand as the specific description.

TYPE SPECIMEN: Holotype NMNH 169673, *Scaphiocoelia* Zone, Rurrenabaque, Bolivia. See Eldredge, 1972a, p. 147, text-fig. 5A–C for illustrations of this specimen.

ADDITIONAL MATERIAL EXAMINED: All material is from the *Scaphiocoelia* Zone of the Lower Belén Formation, northern Bolivia. From Tikani (Estacion bombeo Sica Sica of Smith): AMNH Braniša Collection, 12 cephala, two hypostomata, three thoraxes and one pygidium, or portions thereof; AMNH Smith Collection, eight cephala, one hypostoma, four thoraxes, and one pygidium; Colchani: AMNH Braniša Collection, eight cephala, one hypostoma, three thoraxes, and one pygidium, including one reasonably complete enrolled individual; AMNH Smith Collection, one thorax; Belén: AMNH Braniša Collection, three cephala; NMNH Braniša Collection, one thorax and associated pygidium.

REMARKS: This species is common in the *Scaphiocoelia* Zone of the Lower Belén Formation in northern Bolivia. As such, it is the only calmoniid genus of the *Scaphiocoelia* Zone restricted to the northern area of outcrop, as it is unknown in the east-central region (Presto, Padilla, Icla) and southern region (Gamoneda Formation of the Tarija Department). The only taxon in the *Scaphiocoelia* Zone fauna with which *Parabouleia calmonensis* may possibly be confused is *Tarijactinoides jarcasensis* Suárez Soruco, diagnosed below. In this case, confusion ensues only if fragmentary specimens are under consideration; see Remarks following diag-

nosis of *Tarijactinoides* for criteria for distinguishing these two taxa.

TARIJACTINOIDES SUÁREZ SORUCO, 1971

Branisaia Villarroel, 1968 (unpublished manuscript—*nomen nudum*).
Tarijactinoides Suárez Soruco, 1971, p. 53.
Bolivianaspis Braniša and Vaněk, 1973, p. 99.

TYPE SPECIES: *Tarijactinoides jarcasensis* Suárez Soruco, by original designation.

REVISED DESCRIPTION: (Based almost entirely on internal molds.) Species of the genus *Tarijactinoides* are rather large calmoniids with a relatively great anterior arch (with a slight anterior "droop"), and distinct shouldering. The axial furrows are lightly to moderately deeply incised, straight, and diverge at an exsagittal angle of approximately 50°–60°. The axial furrows are shallow between the occipital ring and the posterior border, and become deeper and inclined anterodorsally opposite glabellar lobes 1p and 2p; they then become horizontal and shallow opposite glabellar lobe 3p, and are thence reflected steeply anteroventrally, remaining shallow, and bear a minute circular axial furrow pit just distal to the terminus of glabellar furrow 3p. The axial furrows become indistinct anteriorly, and merge with the shallow lateral cephalic border furrow.

The anterior glabellar lobe is protuberant, and ovate to semicircular; the anterior cephalic border is not visible in dorsal view in standard orientation. In lateral view, the anterior region of the anterior glabellar lobe is vertical, thence reflected posterodorsally, culminating in a median glabellar spine, thence sloping posteroventrally. The anterior glabellar lobe is thus elevated strongly above the remainder of the glabella. The median glabellar spine is stout, broad-based, and directed vertically and slightly anteriorly, insofar as known. The anterior glabellar lobe has a distinct globular median lobe producing a sinuous anterolateral border to the anterior glabellar lobe, and arising at the large posterior median impression; laterally, this median lobe is bounded by shallow furrows radiating anterolaterally, coincident with the outer rows of the auxiliary impres-

sion system. The median lobe of the anterior glabellar lobe is bounded anteriorly by the facial suture; its maximum width (at the facial suture) is approximately 50 percent the maximum width of the entire anterior glabellar lobe.

The anterior branch of the facial suture runs anteriorly and just slightly distally from the visual surface, traversing the axial furrow distal to the axial furrow pit, and running along the lateral and median area of the glabella along a distinct anterior glabellar ridge, bounded proximally by a broad and, usually, rather deep anterior glabellar furrow. The facial suture transects a relatively minor section of the anterior glabellar lobe. The course of the anterior branch of the facial suture is smoothly parabolic around the anterior glabellar lobe; the facial suture is not visible in dorsal view, and no preglabellar field is developed.

Glabellar furrows 3p are moderately deep and broad, nearly straight (inclined anterolaterally at an exsagittal angle of approximately 11°), and deflected anteriorly just proximal to the axial furrows. Glabellar furrows 3p are separated from the axial furrows by a low, thin (tr.) ridge. The anterior glabellar lobe is effectively isolated from the remainder of the glabella by a faint, shallow medial continuation of the 3p furrows. Glabellar furrows 2p are short, transverse, and developed into ellipsoidal (in dorsal profile) apodemes not in communication with the axial furrows. Glabellar furrows 2p are connected by a shallow medial furrow (slightly convex anteriorly). Glabellar furrows 1p are developed as short transverse apodemal invaginations distally, communicating with the axial furrows, and connected medially by a very shallow, anteriorly convex "intercalating" furrow. The occipital furrow is likewise developed as small transverse apodemes distally, is continuous medially, and is broad and moderately deeply incised and convex anteriorly. Thus all glabellar lobes are disconnected medially, and bear faint median nodes; in lateral view, the median glabellar surface is developed as ridges (corresponding to lobes) all in the same horizontal plane, separated by furrows. The occipital ring (according to Suárez Soruco, 1971, p. 54) bears a large median spine.

The posterior cephalic border is transverse and thin proximally; it is produced into a large, thick "metafixigenal" spine projecting dorsoposteriorly, causing a posteriad deflection of the border in dorsal view; distal to the spine, the border is reflected transversely ventrodistally, becoming thinner and curved anterodistally to the genal angle. The genal angle is approximately opposite the midpoint of the occipital furrow. The posterior border furrow is broad, moderately deeply incised, and transverse. The genae have "short, but strong, genal spines" (Suárez Soruco, 1971, p. 54). The lateral border is developed as a thin ridge smoothly curved from the genal angle to the anterolateral corner of the glabella, thence is reflected somewhat anteriorly (producing a shouldered effect), merging with the thin anterior border. The lateral border furrow is broad and shallow, apparently continuous with both the posterior border furrow and with the anterior border furrow. The anterior border furrow is very shallow and confined to the anterolateral region of the anterior glabellar lobe, "pinching out" between the anterior border and the anterior glabellar ridge at the midline. The anteromedian region of the doublure is developed as an essentially flat, triangular field, inclined anterodorsally at an angle of approximately 30° in lateral view, and becoming smoothly reflected dorsolaterally so that the margins of the doublure, anterior border ridge, and anterolateral surface of the glabella lie in a single smoothly curved surface. The doublure is produced into a distinct, short, blunt and anteroventrally projecting process in some species. The doublure is reflected against the dorsal cuticle posterolaterally, with the ventral cephalic margin developed as a thin, bladelike ridge. The hypostomal suture is distinctly convex anteriorly. The hypostoma itself is unknown.

The librigenae are very narrow in dorsal view, sloping steeply from the lateral border furrow. The fixigenae are more gently sloping posterolaterally, posterior and lateral to the eye. The eye socle is apparently short and vertical. The eye is small (Large Eye

Index .24–.28), with both the anterior and posterior margins of the eye set well off from the axial furrow. The posterior margin of the eye is opposite glabellar furrow 2p; the anterior margin is opposite the distal terminus of glabellar furrow 3p. The visual surface is very poorly known. Palpebral morphology is complex, with a thin curved ridge developed just proximal to the dorsal margin of the visual surface; this ridge is produced into a large spine on the posterior margin (serially homologous with the "metafixigenal spine"?). The remainder of the palpebral lobe is reniform, sloping proximally and separated from the flatter palpebral area proper by a palpebral furrow and a distinct break in slope.

The posterior branch of the facial suture is recurved anteriorly opposite the posterior region of the visual surface, thence recurved across the genal surface to the cephalic margin. The facial sutures were apparently functional in holaspids.

The cephalic ornament is poorly known; it is apparently microgranular. Faint dimpling has been observed on both the fixigena and librigena. The auxiliary impression system is of the acastid pattern (fig. 2P), with a deep, circular posterior median impression (developed as a pad viscerally); the outer row of impressions is developed as pads or dark markings just distal to the furrow defining the median lobe of the anterior glabellar lobe. The proximal row diverges at a lower angle, running on either side of the median cephalic spine, and extending anteriorly down to the facial suture.

The thorax is incompletely known (from type species only); median (and apparently large) axial spines, somewhat compressed anteroposteriorly, are present. The half-rings are about as long (sag.) as the axial rings. The axis is arched high above the pleural field; the axial furrows are broad and shallow. The pleura are horizontal proximally, and bear a large spine on the posterior moiety at the point of inflection to the steeply sloping distal surface. The pleural furrows are well incised and inclined just slightly posterodistally. The pleural tips taper to ventrolaterally flat spines, insofar as they are

known. The thorax apparently is ornamented with small, densely packed granules.

The pygidium is essentially triangular and micropygous. The axis is arched well above the pleural field, with eight axial rings plus a terminal piece. The ring furrows are sinuous, especially posteriorly, and run slightly anteroproximally from the axial furrow (bearing apodemes in the anterior five or six furrows), thence swinging sharply posteriorly to the axial midline. Each axial ring bears an axial spine or node. The posterior terminal piece is essentially flat, sloping to the pleural field, and set off from the pleura by the posterior continuation of the axial furrows. The pleural field is flat and inclined dorsodistally in the proximal region to the point of inflection, thence sharply reflected vertically down to the pygidial margin. Seven pairs of pleura are present, separated by the nearly confluent pleural and interpleural furrows. The interpleural furrows are deeper and broader than the pleural furrows. The anterior moiety of each pleuron (except the most anterior pleuron) is nearly totally obsolescent. The furrows deepen to the point of inflection, thence become shallower approaching the pygidial margin. The pleura and furrows become progressively inclined more posteriorly, posterior along the pleural field. A large, stout pleural spine is developed at the point of inflection of the pleuron, directed dorsolaterally in a radiating array, and presumably serially homologous with the palpebral, "metafixigenal," and thoracic pleural spines. The margin of the pygidium is entire and slightly emarginate posteriorly (in posterior view). Pygidial ornament is apparently microgranular.

REMARKS: This revised description augments to some degree the original excellent generic diagnosis and specific description given by Suárez Soruco (1971). We differ from Suárez Soruco (1971, p. 54) only in the observation that glabellar furrows 3p do not, in fact, quite reach the axial furrows, as there is a depressed ridge between the distal terminus of glabellar furrow 3p and the axial furrow. However, the great inflation of the anterior glabellar lobe and the relatively deep incision of glabellar furrow 3p result in a *de*

facto isolation of the anterior glabellar lobe. Our only other difference with Suárez Soruco's treatment of this taxon is the minor difference in counts of the axial rings of the pygidium—eight in our material, while Suárez Soruco (1971, p. 55) reports only seven.

Braniša and Vaněk (1973) described *Bolivianaspis scrutator,* new genus and species, from the Gamoneda Formation at Sella-Jarcas (=Jarcas locality usage of this paper)—the same provenance as the holotype of *Tarijactinoides jarcasensis* Suárez Soruco. *Bolivianaspis scrutator* is manifestly a junior synonym of *Tarijactinoides jarcasensis*. The present emended diagnosis of *Tarijactinoides* is greatly expanded over that given by Braniša and Vaněk (1973, p. 99) for *Bolivianaspis*. Two discrepancies emerge between the present emended diagnosis and Braniša and Vaněk's treatment of *Bolivianaspis*: Braniša and Vaněk (1973, p. 99) reported that the "glabella does not exceed anterior border of cephalon. On frontal lobe of glabella, close to posterior margin, is a stout, backwards directed spine"; however, the anterior surface of the glabella is vertical and if anything protrudes slightly beyond the anterior cephalic margin, which is, in any case, not visible in dorsal view (in standard orientation). Furthermore, while specimens are incomplete, and variation is not inconceivable, the median spine on the anterior glabellar lobe is directed nearly vertically and perhaps slightly anteriorly in specimens presently available to us, and not posteriorly as reported by Braniša and Vaněk.

We are in complete agreement with Suárez Soruco's (1971, p. 54) conclusion that *Tarijactinoides* is closely related to ("un genéro afin a") *Cryphaeoides*. [Braniša and Vaněk (1973, p. 99) claim a close relationship between *Bolivianaspis* (=*Tarijactinoides*) and *Malvinella* Wolfart—an assertion not buttressed by argumentation or specific reference to shared morphological features, and which appears wholly without substance.] However, *Tarijactinoides* is even more closely related to the slightly younger genus *Probolops* from the lower part of the Icla Formation at Padilla (see section on *Schizostylus* for further remarks on *Probolops glabellirostris*). Shared-derived features include the curious median lobe of the anterior glabellar lobe, a median spine on the anterior glabellar lobe, presence of pronounced spines on the posterior margin of the palpebral lobe, on the posterior cephalic border ("metafixigenal") spine, and on the posterior moiety of each thoracic pleuron at the point of inflection, and very similar conformation of the glabella, including shallow medial continuation of glabellar furrows 1p, 2p, and 3p and presence of apodemes in the 2p furrows. Some of these features are also shared by *Cryphaeoides* as well as by two as yet undescribed genera, delineating a "*Probolops* group" discussed briefly in the Introduction to this study.

Among *Scaphiocoelia* Zone taxa, *Tarijactinoides* resembles only *Parabouleia*. The differences between these taxa in such fundamental details as the eyes, distribution of spines all over the cuticular surface, and shape and other morphological aspects of the pygidium, preclude any chance of confusion and we need not reiterate criteria for distinguishing the two. However, the points of similarity are worthy of mention for the possible implications of phylogenetic relationship. In both genera, glabellar furrows 2p are produced viscerally into apodemes—a rare feature in calmoniids; further, the anterior glabellar lobe is highly inflated in both genera, though set off from the remainder of the glabella in *Tarijactinoides,* whereas in *Parabouleia* glabellar lobe 3p remains closely associated with the anterior glabellar lobe. Likewise, the facial sutures appear to be functional in the holaspid stage of species of both genera, and, in their pygidia, the interpleural furrows are more deeply incised than the pleural furrows—again, an unusual feature for phacopid and dalmanitid trilobites in general. These observations suggest the possibility of a phylogenetic link between the "*Probolops* group" and the "*Metacryphaeus* group" to which we (see Introduction) have for the time being allocated *Parabouleia* and *Bouleia*.

Finally, the geographic variation exhibited by *Tarijactinoides* within the *Scaphiocoelia* Zone of Bolivia—variation which prompts
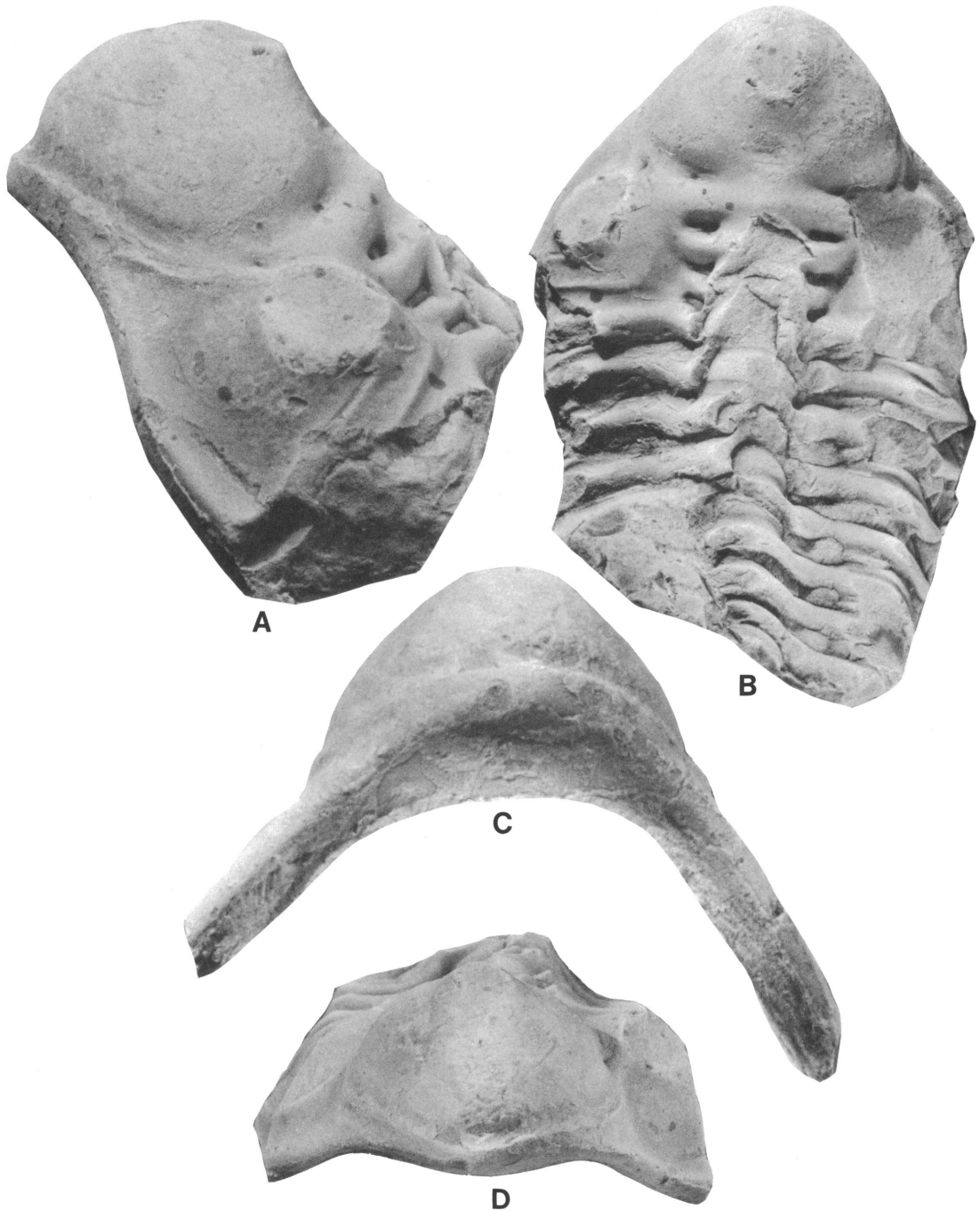
FIG. 36. *Tarijactinoides jarcasensis*. *Scaphiocoelia* Zone, Gamoneda Fm. Tarija Dept., Bolivia. NMNH 245650. Internal mold of cephalon and articulated portion of thorax. A. Oblique left lateral view of cephalon, ×3. B. Dorsal view of entire specimen, ×2. C. Ventral view of cephalon, ×3. D. Frontal view of cephalon, ×2.
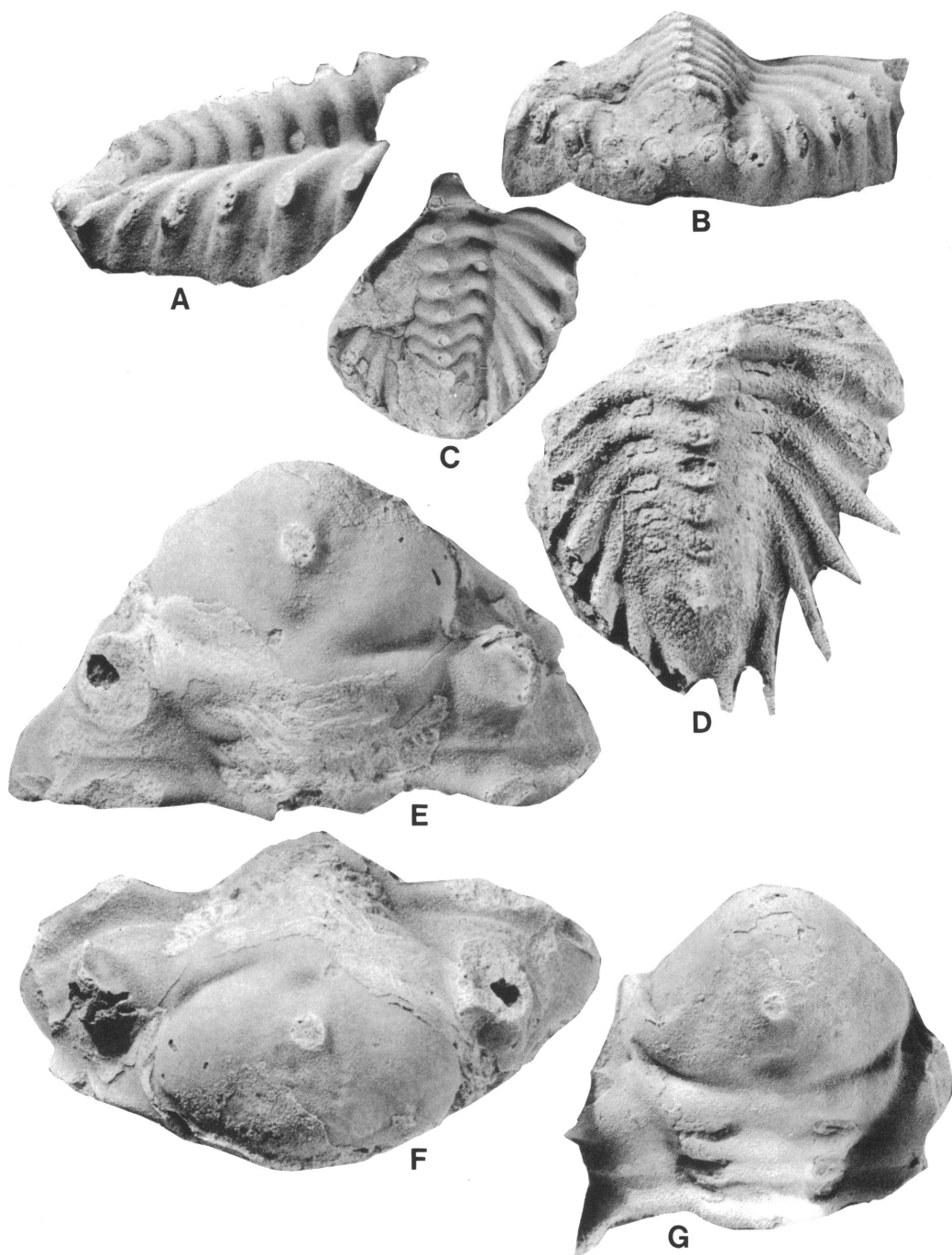
Fig. 37. *Tarijactinoides* spp. A–C, G. *T. jarcasensis, Scaphiocoelia* Zone, Gamoneda Fm., Tarija Dept., Bolivia. A–C. Right lateral (×3), posterior (×3), and dorsal (×2) views of latex cast of external mold of pygidium. NMNH 245651 (latex cast AMNH 36749). D–F. *Tarijactinoides tikanensis. Scaphiocoelia* Zone, Lower Belén Fm., Tikani, Bolivia. D. Dorsal view of internal mold of pygidium. Paratype, AMNH 36750 (Braniša Coll.), ×3. E, F. Dorsal and oblique frontal views of natural cast of cephalon, ×2. Paratype, AMNH 36751 (Smith Coll.). G. *T. jarcasensis* (on same block as specimen A–C). Dorsal view of internal mold of cephalon, NMNH 245652, ×2.

our recognition of two species below, in the familiar pattern of one species in the northern La Paz region, and another in the southern Tarija area—merits attention as it appears related to the distribution of *Parabouleia calmonensis*. *Tarijactinoides tikanensis*, new species, from the north is much flatter and broader than its sister species *T. jarcasensis* to the south, and as such is more classically "dalmanitid" in aspect. In contrast, *T. jarcasensis* is more highly arched and narrower, and the anterior glabellar lobe is much more highly inflated and globular (further differences between these two species are included in their diagnoses below). Therefore, *Tarijactinoides jarcasensis* approaches *Parabouleia calmonensis* in overall conformation much more than does *T. tikanensis*. *Parabouleia calmonensis* is sympatric with *T. tikanensis*, but to our knowledge does not occur in the Tarija Department—the only calmoniid genus (aside from two indeterminate genera described below) of the *Scaphiocoelia* Zone restricted to only one of the three major areas of outcrop. Such a pattern suggests the possibility of some form of ecological character displacement (i.e., between the sympatric species to the north) or mutual exlusion (i.e., of *Parabouleia* in the south), but such contentions are notoriously difficult to test and are not pursued further here.

Tarijactinoides jarcasensis,
Suárez Soruco
Figures 36; 37A–C, G

Branisaia branisi Villarroel, 1968, p. 62, fig. 33 (unpublished manuscript—*nomen nudum*).
Tarijactinoides jarcasensis Suárez Soruco, 1971, p. 54, pl. 1, figs. 1–7; pl. 2, figs. 1–3.
Bolivianaspis scrutator Braniša and Vaněk, 1973, p. 99, pl. 4, 3–7.

TYPE SPECIMENS: Geological Survey of Bolivia LPI 1558 (cephalon) and LPI 1955 (pygidium), Gamoneda Formation, Jarcas, Tarija, Bolivia.

MATERIAL EXAMINED: NMNH Braniša Collection: one cranidium associated with a pygidium, one damaged cephalon with portion of thorax, and an additional section of thorax, Gamoneda Formation, Tarija Department, precise locality unrecorded. Two pygidia (one being a part and counterpart) locality Mi-2, Gamoneda Formation, Tarija. Two portions of external molds of pygidia and a portion of a cephalon, Presto El Peral. AMNH Braniša Collection: one external mold of a cephalon, two partial pygidia, and a partial thorax, Gamoneda Formation, Curuyo. Four pieces with fragments of thoracic segments, Gamoneda Formation, Jarcas.

EMENDED DIAGNOSIS: Cephalon highly arched and relatively narrow (length/width ratio ~2/3); librigenae steeply sloping distally. Axial furrows diverging at an exsagittal angle of approximately 50°. Anterior glabellar lobe narrow, globular, highly inflated above level of posterior glabellar region. Length/width ratio of anterior glabellar lobe .64–.69. Median lobe of anterior glabellar lobe distinct, but set off from lateral areas by only slight break in slope. Median glabellar spine located approximately 60 percent distance posterior along anterior glabellar lobe. Anterior branch of facial suture hardly transecting anterolateral corners of anterior glabellar lobe. Anterior glabellar furrow (proximal to facial suture) broad and quite deep. Anterior cephalic border thick medially, produced into short, blunt process projecting anteroventrally, not visible in dorsal view. All other features as for genus.

REMARKS: The above emended diagnosis gives *differentia* between *T. jarcasensis* and *T. tikanensis* only. Additional remarks follow the diagnosis of *T. tikanensis* below.
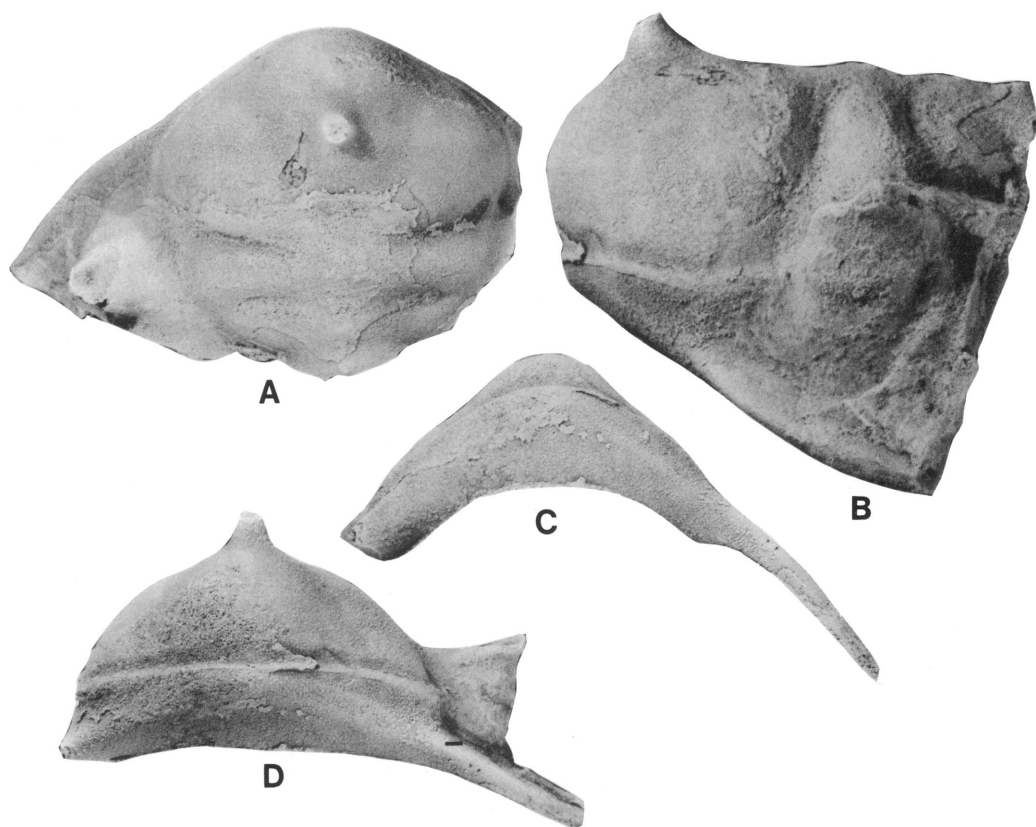
FIG. 38. *Tarijactinoides tikanensis*. *Scaphiocoelia* Zone, Lower Belén Fm., Tikani, Bolivia. A–D. Dorsal (×2), left lateral (×3), ventral (×2) and frontal (×2) views of natural cast of cephalon. Holotype, AMNH 36752 (Braniša Coll.).

Tarijactinoides tikanensis, new species
Figures 2P; 37D–F; 38

TYPE SPECIMENS AND MATERIAL EXAMINED: All specimens are from the *Scaphiocoelia* Zone, Lower Belén Formation. Holotype, AMNH 36752, a cephalon with posterior and right genal regions missing; Braniša Collection, Tikani (=Estacion Bombeo Sica Sica of AMNH Smith Collection), La Paz Department. Paratypes, AMNH 36751, Smith Collection, a nearly complete cephalon with eyes and genae damaged, and a pygidium, AMNH 36750, Braniša Collection, both from Tikani. In addition, we have examined a portion of a cephalon and a pygidium, AMNH Braniša Collection, Tikani, and a portion of a cephalon from Colchani,

La Paz Department, AMNH Smith Collection.

ETYMOLOGY: The species name is based on Tikani, the locality in the La Paz Department that has produced most of the specimens known to us.

DIAGNOSIS: Cephalon moderately arched and relatively broad (length/width ratio approximately .60). Genae moderately sloping, dished. Axial furrows diverging at an exsagittal angle of approximately 60°. Anterior glabellar lobe relatively broad, ovate, with only median lobe of anterior glabellar lobe elevated above posterior glabellar surface. Length/width ratio of anterior glabellar lobe .56–.62. Median lobe of anterior glabellar lobe set off from lateral area by shallow furrow and distinct break in slope. Median gla-
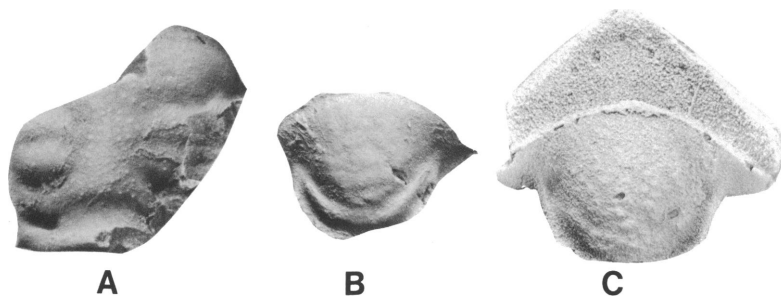
FIG. 39. A. Calmoniid gen. and sp. indet. A. *Scaphiocoelia* Zone, Presto el Peral, Bolivia. Dorsal view of internal mold of cephalon. NMNH 245653, ×3. B. Calmoniid gen. and sp. indet. B. *Scaphiocoelia* Zone, Gamoneda Fm., Curuyo, Bolivia. External view of internal mold of hypostome, ×3. AMNH 36753 (Braniša Coll.). C. *Malvinella haugi.* Upper Belén Fm., *cornutus* Zone, Pujravi, Bolivia. External view of internal mold of hypostome articulated with cephalon, ×3. AMNH 36754 (Smith Coll.).

bellar spine located only 40 percent back along length of anterior glabellar lobe. Anterior branch of facial suture transecting extreme anterolateral corner of anterior glabellar lobe; anterior glabellar furrow narrow and rather shallow. Anterior cephalic border nearly obsolescent medially, indistinctly merging with doublure ventrally, and not produced into anterior process. Thorax unknown; remainder of features as for genus.

REMARKS: Both *T. jarcasensis* and *T. tikanensis* are rare elements of the *Scaphiocoelia* Zone fauna. Unlike the geographic variation exhibited by other taxa discussed in this study, these species differ primarily in basic proportions of the cephalon, though larger samples would undoubtedly reveal additional points of difference between them.

CALMONIID GENUS AND SPECIES INDETERMINATE A
Figure 39A

MATERIAL EXAMINED: A partial cephalon, internal mold, from the *Scaphiocoelia* Zone, Presto El Peral, NMNH 245653, Braniša Collection.

DESCRIPTION: The anterior glabellar lobe is steeply inclined anterolaterally, and moderately inflated. The anterior branch of the facial suture transects the anterolateral corner of the glabella about midway up the slope of the anterolateral face of the glabella. There is no axial furrow pit. Glabellar fur-

rows 3p are broad and moderately deeply incised, slightly sinuous, and not communicating with the axial furrows. Glabellar furrows 2p are broad and less deeply incised, and transverse. Glabellar lobes 2p and 3p are rather bulbous (i.e., arched), only slightly depressed below the median glabellar surface; the entire median surface of the glabella extends continuously from the central region of the anterior glabellar lobe to the occipital furrow, lying in a single horizontal plane (though with the eyes absent, standard orientation can only be approximated). There is a slight indication of longitudinal glabellar furrows connecting the proximal termini of glabellar furrows 1p and 3p (cf. many Pterygometopidae). Glabellar lobes 1p are smaller than lobes 2p and 3p, and significantly depressed distally below the distal height of lobes 2p and 3p. Glabellar furrows 1p are short apodeme-bearing incisions inclined slightly posterodistally. The occipital furrow is broad and shallow medially, with deep distal apodemal invaginations oriented anterodistally. The occipital ring is elevated to the median height of the glabella and is without spines. The librigena is steeply sloping from the eye socle to the lateral cephalic border; the lateral border furrow is nearly obsolescent. Small tubercles occur sporadically over the anterior glabellar lobe and median area of the posterior glabellar region.

REMARKS: This single fragmentary cephalon presents a combination of character

states sufficiently unique to prohibit reference to any previously described taxon, and to warrant special attention. Only the posterior region of the glabella plus the occipital ring, the right third of the anterior glabellar lobe, the anterior region of the librigena, and the posterior region of the doublure on the right side are preserved.

Among calmoniid taxa of the *Scaphiocoelia* Zone, this specimen most closely resembles *Schizostylus* (*Curuyella*) *granulata,* but cannot be referred to that taxon because of the conformation of glabellar lobes 1p–3p, and the absence of both an anterior glabellar ridge and a distinct lateral border furrow.

Reduction in size, and depression of the distal portion of glabellar lobe 1p, whereas glabellar lobes 2p and 3p are inflated to the same height and closely associated with one another, and the development of longitudinal glabellar furrows connecting the proximal tips of glabellar furrows 1p and 3p, are characteristic of the genus *Malvinella* (plus a closely related genus yet to be described) alone among all known calmoniids. Presence of tubercles, though not as critical a feature, also agrees with this assessment. However, both *Malvinella* and the undescribed closely related genus have a well-developed anterior glabellar ridge associated with the anterior branch of the facial suture, as well as a deep axial furrow pit. In view of the extremely limited material, we can only tentatively conclude that the partial cephalon from Presto El Peral represents a new genus perhaps most closely related to the younger genus *Malvinella* among all calmoniids described to date.

CALMONIID GENUS AND SPECIES INDETERMINATE B
Figure 39B

MATERIAL EXAMINED: A single, moderately well-preserved internal mold of an hypostoma from the *Scaphiocoelia* Zone of the Gamoneda Formation at Curuyo (AMNH 36753, Braniša Collection) is available to us. The specimen is not directly associated with any other identifiable trilobite remains.

DESCRIPTION: As preserved, the hyposto-

ma is short and broad and roughly triangular; however, the posterior margin is not preserved. The anterior margin is smoothly and distinctly convexly curved. The central body extends straight back from the anterior margin, i.e., is not inflated appreciably below the plane of the hypostomal suture. The lateral surface of the central body is strongly curved dorsally, and more gently curved posteriorly. A deep, broad furrow, arising at the posterior margin of the anterior wing and confluent with the hypostomal border furrow, runs posteroproximally, becoming obsolescent near the midline. The faint maculae occupy the distal extremities of this central body furrow. The hypostomal border furrow is deep and broad and smoothly curved around the posterior margin of the central body. Thus, a prominent ridge is developed between the central body furrow and the border furrow. The hypostomal border is a thin ridge laterally, and is not preserved posteriorly. The anterior wing is sharply recurved dorsally, its visceral surface facing anteriorly. The posterior wing is vertical and faces laterally.

REMARKS: Hypostomata are by no means rare in the Devonian rocks of Bolivia; however, hypostomes have been definitely assigned thus far only to *Metacryphaeus* (two distinct types, affording further indication that this genus, currently with by far the most evidently valid species of any Malvino-Kaffric genus, is in need of revision), *Kozlowskiaspis* (*Kozlowskiaspis*), *Malvinella, Bouleia, Parabouleia, Vogesina,* and ?*Acastoides* among the calmoniids. Non-calmoniid genera from the Bolivian Devonian for which the hypostoma is known include *Phacops* (*Viaphacops*), *Francovichia, Fenestraspis,* and *Acanthopyge*.

The present specimen is apparently of calmoniid affinity, on the basis of its general short, broad shape and the expression of the rather peculiar central body furrows running obliquely posteroproximally along the posterior region of the central body. Another large hypostoma also from the Gamoneda Formation, which possesses an even deeper and posteromedianly continuous central body furrow, is tentatively allocated to *Ga-*

monedaspis Braniša and Vaněk (one of the two dalmanitids of the *Scaphiocoelia* Zone fauna); this specimen will be described in a future study. The hypostoma of *Parabouleia* is rather similar to this specimen, but lacks the distinctive central body furrows. The only other Bolivian Devonian taxa known to us which possess such furrows are some species of *Metacryphaeus* and *Malvinella haugi*. The hypostoma of *Malvinella,* in particular, is similar in shape to the present specimen, though in the one *Malvinella* hypostoma available to us (fig. 39C) the central

body furrows are rather less strongly developed than on this *Scaphiocoelia* Zone specimen. Thus, this single specimen may indicate the presence of another member of the *Metacryphaeus* group of calmoniids (which includes *Malvinella*—see the Introduction to this study) as yet unrepresented by other specimens in presently available collections. It is noteworthy that the two specimens we have described as indeterminate calmoniid genera A and B both call to mind the genus *Malvinella* more than any other known calmoniid taxon.

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