SYSTEMATICS ON *VIAPHACOPS* MAXIMOVA, 1972 FROM BOLIVIA AND PALEOBIOGEOGRAPHY OF THE SUBFAMILY PHACOPINAE HAWLE & CORDA, 1847 FOR THE LOWER AND MIDDLE DEVONIAN, WITH A PARTICULAR EMPHASIS ON THE GENUS *PACIPHACOPS* MAXIMOVA, 1972

by

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Abstract

SYSTEMATICS ON *VIAPHACOPS* MAXIMOVA, 1972 FROM BOLIVIA AND PALEOBIOGEOGRAPHY OF THE SUBFAMILY PHACOPINAE HAWLE & CORDA, 1847 FOR THE LOWER AND MIDDLE DEVONIAN

by

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The Subfamily Phacopinae Hawle & Corda, 1847 occurs stratigraphically from the Upper Ordovician to the end of the Devonian, spanning an approximately 85 million year interval. Its global distribution allowed extensive studies and a number of monographs have been published since the mid-1800s. The first chapter analyzes *Viaphacops* Maximova, 1972 which is one of the genera occurring in the Lower to Middle Devonian. New material from Bolivia enabled three new species (*Viaphacops spinoedgecombei*, *V. newelli*, and *V. pirovanoi*) and two in open nomenclature to be described here, in addition to the four described previously. With the examination of these species, the generic diagnosis of *Viaphacops* is revised. Cladistic analysis was conducted for the Bolivian *Viaphacops* together with 8 North American species to test their monophyletic relationship. It is found that two geographically separate groups *Viaphacops,* those from North America and those from the Malvinokaffric Realm in Bolivia, are non-monophyletic (Bolivian species either being a basal grade or nesting in otherwise North American clades), and that the difference in environmental settings for these regions did not seem to have affected the developmental constraints of the species. The second chapter treats the phacopid biogeography for the Lower and Middle Devonian, and follows the model of rugose coral biogeography of Pedder and Oliver (1990). More than 300 species belonging to 32 established genera were analyzed. Otsuka, Dice, and Jaccard Coefficient faunal similarity indices at the generic level were used for the 15 phacopid biogeographic units. Together with an area cladogram of *Paciphacops*, Maximova, 1972, strong connection was established between southeastern Australia and Bolivia-Argentina by the circumpolar circulation within southern Panthalassa. The position of Kazakhstan is still unresolved, however, both Otsuka Coefficients and the *Paciphacops* area cladogram show its connection with Australia and South America.

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CHAPTER 1. REVISION OF BOLIVIAN *VIAPHACOPS* MAXIMOVA, 1972 (DEVONIAN, TRILOBITA), AND ITS PHYLOGENETIC AND GEOGRAPHIC RELATIONSHIP WITH NORTH AMERICAN *VIAPHACOPS*

ABSTRACT—The Lower-Middle Devonian phacopid trilobite *Viaphacops* Maximova, 1972 is a quasi-cosmopolitan species occurring in eastern Kazakhstan and southern Siberia (Old World Realm), eastern North America (Eastern North America Realm), and the Andean Bolivia (Malvinokaffric Realm). Its occurrence in Bolivia has been studied over a century. Abundant specimens from such classic localities as Belén, Pujravi, and Icla, with new localities of Totora-Aiquile and Tolamayu, enabled three new species (*Viaphacops spinoedgecombei* n. sp., *V. newelli* n. sp., and *V. pirovanoi* n. sp.) and two in open nomenclature (*V.* cf. *orurensis* and *V.* cf. *chavelai*) to be described here. The five previously established species *V. multicinctus, V. kozlowskii*, *V. spatiosus*, and *V. orurensis* by Pek and Vaněk (1991) and *V. salteri* (Kozlowski, 1923) were examined and *V. spatiosus* was reassigned to *Paciphacops*. A total of 9 *Viaphacops* species from Bolivia were cladistically analyzed with 8 North American species. The result indicates that although most of the Bolivian taxa were placed at basal clades, the significant environmental differences between these regions as evidenced by sedimentary composition does not seem to affect the morphological developmental rates.

INTRODUCTION

PHACOPID TRILOBITES now recognized as members of *Viaphacops* Maximova, 1972 from the Lower and Middle Devonian strata of the Bolivian Andes have been in the literature for more than a century (Salter, 1861; Ulrich, 1893; Kayser, 1897; Knod, 1908; Groth, 1912; Bonarelli, 1921; Kozlowski, 1923; Swartz, 1925; Ahlfeld and Branìša, 1960; Fricke *et al*., 1964; Branìša, 1965; Wolfart, 1968; Eldredge and Ormiston, 1979; Pek and Vaněk, 1991). The most recent work on the systematics of these species is that of Pek and Vaněk (1991), in which they recognized and described three new species, *Viaphacops multicinctus, V. kozlowskii, V. spatiosus*, in addition to *V. orurensis* (Bonarelli, 1921) *sensu* Pek and Vaněk (1991).

The very first mention of Bolivian phacopid trilobites in the literature is Salter (1861), "On the fossils of the High Andes (Bolivia), collected by David Forbes." In this paper Salter briefly described a specimen from a locality near Oruro, and assigned it to *Phacops latifrons* (Bronn, 1825), which he remarked is a common Devonian species in Europe.

Bonarelli (1921) recognized the figure in Salter's (Pl. 4, fig. 8, 1861) as representing a species distinct from *Phacops latifrons* (Bronn, 1825) and erected *Phacops orurensis*. However in his paper, no figure, description, nor type specimens for this species were reported. Two years later, Kozlowski (1923) erected another species, *Phacops salteri*, for the same Bolivian "*Phacops latifrons*" without the knowledge of Bonarelli's work.

Some authors accepted Bonarelli's *P. orurensis* (Ahlfeld and Braniša, 1960; Fricke *et al*., 1964; Braniša, 1965), but Swartz (1925) referred to Kozlowski's *salteri*. Wolfart (1968) revised Kozlowski's work on the Devonian trilobites from Bolivia. In his paper he validated Kozlowski's *salteri* by choosing a lectotype for it from a figure illustrated in Kozlowski (1923, pl. 6,fig. 2).

Pek and Vaněk (1991) prioritized Bonarelli's *orurensis*, acknowledging the fact that he was "the first to distinguish…the taxonomical and nomenclatorical (*sic*) independence of his species" (p. 83) from *Phacops latifrons*. They selected the specimen figured by Salter (1861, pl. fig. 8) as the holotype by monotypy, and referred to Wolfart's description (1968, p. 63) for the species.

A close examination reveals that the holotype of *orurensis* (Pek and Vaněk, 1991) and the lectotype of *salteri* (Wolfart, 1968) are not conspecific, and both species are herein treated as valid, separate species. Based on the illustrated figures from the above-mentioned authors and more than 500 specimens housed at the American Museum of Natural History (AMNH), the National Museum of Natural History, Smithsonian Institution (USNM), the Museo de Historia Natural de Cochabamba, Bolivia (MHNC), and the Australian Museum, Australia (AMF), a revision of *Viaphacops* from Bolivia became possible. Three more new species together with two in open nomenclature (*V*. cf. *orurensis*, *V. spinoedgecombei*, *V. newelli*, *V. pirovanoi* and *V*. cf. *chavelai*) are recognized and their systematic description is given herein.

VIAPHACOPS MAXIMOVA, 1972

In her paper in 1972, Maximova erected a new genus, *Paciphacops* and two new subgenera, *Paciphacops* and *Viaphacops*, that occur in the strata of Lower and Middle Devonian of Kazakhstan, Altay and Eastern North America. She distinguished *Paciphacops* (including the two subgenera) from *Phacops* by its reduced preoccipital lobe (or medial L1), which in *Viaphacops* is "fully reduced" (p. 78). *Paciphacops* also has genal spines developed to some degree.

Maximova's phylogenetic scheme for *Paciphacops* and *Viaphacops* suggests the unidirectional evolutionary trends from the Silurian *Ananaspis* Campbell, 1969 to *Paciphacops*, and from *Paciphacops* to *Viaphacops*. The trends she noted are: 1) development of vincular furrow, 2) reduction of the preoccipital lobe, 3) elevation of the eyes, 4) angular genal angle, and 5) the formation of genal spines. According to her, *Viaphacops* completely lost its preoccipital lobe and it is therefore depressed. Also it has a deeper vincular furrow, shorter and less segmented pygidium, and coarser ornament on the glabella.

Validity of genus Viaphacops. – After Maximova's publication on *Paciphacops* and *Viaphacops* (1972), many accepted their establishment as subgenera of *Paciphacops* (Chlupáč, 1977; Campbell, 1977; Pek and Vaněk, 1991). Some even acknowledged them at a generic level (Holloway, 1980; Eldredge, 1985; Ramsköld and Werdelin, 1991; Linsley, 1994; Carvalho and Moody, 2000). Eldredge (1973) revised North American *Paciphacops* and *Viaphacops*, but preferred to refer them as *Phacops logani* group and *Phacops cristata* group, respectively, but later elevated them to a generic level (Eldredge and Ormiston, 1979). After establishing a Silurian phacopid *Ananaspis* Campbell, 1967, Campbell (1977), while reconstructing a phylogenetic relationship of these taxa and other Lower Devonian phacopine trilobites, revised the diagnosis of *Paciphacops* and *Viaphacops*, but kept their status at the subgeneric level. Chlupáč (1977) rejected Maximova's *Viaphacops*, arguing that its diagnostic features such as the complete reduction of preoccipital ring, narrow occipital ring, convex margin of the vincular furrow, shorter and less segmented pygidium and coarser tuberculation would not differentiate *Phacops logani* (type species of *Paciphacops*) and *P. cristata* (type species of *Viaphacops*) groups (p. 67). He accepted *Paciphacops* and noted that its medially reduced preoccipital ring is usually developed as a narrow band on the external mould, but as a concave depression on the internal mould. The latter feature is often confused with the diagnostic character of *Viaphacops*. Holloway (1980), on the other hand, rejected the validity of *Paciphacops* and synonymized it with *Ananaspis*, but accepted the generic status of *Viaphacops*. With abundant material from Bolivia, together with published works on *Viaphacops* from elsewhere, it became possible to reevaluate its generic status here. The revised diagnosis of the species is given in the following section.

Distribution of Viaphacops Maximova, 1972. – *Viaphacops* Maximova, 1972 is a quasi-cosmopolitan (*sensu* Eldredge and Ormiston, 1979) taxon. It occurs in the Lower to Middle Devonian strata in southern Peru and the Andes of Bolivia (Belén and Sica Sica Formations and their equivalents; Salter, 1861; Ulrich, 1893; Kayser, 1897; Knod, 1908; Groth, 1912; Bonarelli, 1921; Kozlowski, 1923; Swartz, 1925; Newell, 1949; Ahlfeld and Braniša, 1960; Fricke *et al.*, 1964; Braniša, 1965; Wolfart, 1968; Eldredge and Ormiston, 1979; Pek and Vaněk, 1991) of the Malvinokaffric

Realm, North America (Little Saline Limestone of Missouri, Frisco and Bois d'Arc Formations of Oklahoma, Schoharie and Onondaga Formations and their equivalents of the other Appalachian region; Hall and Clarke, 1888; Stewart, 1922; Tansay, 1922; Eldredge, 1973; Campbell, 1977; Linsley, 1994), Columbia (Floresta Formation; Caster, 1939), and Venezuela (Cano del Oeste Formation; Carvalho and Moody, 2000) of the Appalachian Realm (Eldredge and Ormiston, 1979), which is also referred to as the Eastern Americas Realm by Boucot and others (Boucot and Gray, 1979 and 1983; Boucot, 1988; Meyerhoff *et al.*, 1996), Central Kazakhstan (Sardzhal, Kazakh, Besoba, and Aidarla horizons) and the Rudny Altai region (Eifelian) of the Old World Realm (Maximova, 1960, 1967, and 1972).

In all the marine realms where *Viaphacops* occurs, coeval species of *Paciphacops* can also be found (Iwasaki, 2001). In North America, Campbell (1977) reported coeval species of *Paciphacops* and *Viaphacops* in the Frisco Formation of Oklahoma (Lower Devonian). In Kazakhstan, *Paciphacops angulatus* (Maximova, 1968), which Maximova (1978) then assigned to her new genus, *Angulophacops*, occurs with *Viaphacops praepipa* Maximova, 1968 in the Sardzhal horizon. Pek and Vaněk (1991) reported a new species of *Viaphacops, V. spatiosus,* from Sella Jarcas, Bolivia (Gamoneda Formation). However, a close examination of the type specimen (NM – S 2100 at the National Museum, Prague) reveals that this species belongs to *Paciphacops* in having a sagittally broad, low occipital ring, and well-defined preoccipital ring (i.e., medial L1). From the same formation in the nearby locality of Cerro Picacho, a single specimen which is assigned here to *Viaphacops* was found (AMNH 45512). Because of the poor preservation, identification of this specimen beyond generic level is difficult, however, it is tentatively identified as *V*. cf. *orurensis* (Bonarelli, 1921) because of overall similar appearance. Both species are from the Gamoneda Formation. The stratigraphic overlap between *Paciphacops* and *Viaphacops* in these regions may indicate a possible direct relationship. With the absence of other phacopine species in these formations, it could be suggested that *Viaphacops* might have been derived from *Paciphacops*.

Stratigraphic range of Viaphacops in Bolivia and implication of sea level change. – The first geological occurrence of *Viaphacops* within South America is *V*. cf. *orurensis* and is reported from the *Scaphiocoelia* zone of the Gamoneda Formation, in Tarija Department in the southern Bolivia (Fig. 1). Above this zone, there is no record of *Viaphacops* in the Tarija region (see Fig 2).

Viaphacops newelli n. sp. and *V. pirovanoi* n. sp. and *V. salteri* (Kozlowski, 1923) appear next in beds of the Lower Member of the Belén Formation, in the Belén area of northern Bolivia. They continue to appear in the Upper Belén Formation in the same region. In the late Emsian, or the lowest beds of the Upper Belén Formation (also Upper Icla Formation), six species occur in northern and central Bolivia. In the north, three species emerge: *V. kozlowskii* Pek and Vaněk, 1991, *V. multicinctus* Pek and Vaněk, 1991, and *V. spinoedgecombei* n. sp. *V. salteri* (Kozlowski, 1923) appears in the central Bolivia, together with *V.* cf. *chavelai* (Baldis and Longobucco, 1977) and *V. spinoedgecombei*. Only *V. spinoedgecombei* continues to occur into the Givetian in both regions. *Viaphacops orurensis* (Bonarelli, 1921) may have appeared sometime in the Upper Belén Formation, but is most common in the Sica Sica Formation in northern Bolivia. *Viaphacops newelli* occurs in the Upper and Lower

Belén Formations in northern Bolivia and in the Cabanillas Formation (Givetian), southern Peru. This formation is an equivalent of Sica Sica Formation and is considered to be a part of Bolivia (Newell, 1949; Lieberman, 1993), or belongs to the Bolivia-Peru basin (Isaacson and Díaz Martínez, 1995; Sempere, 1995; Grader *et al.*, 2007).

Both Isaacson (1975) and Melo (1988) interpreted that the transgression moved from southern Bolivia towards southern Peru. From their figures (Isaacson, 1975, figs. 3 and 4; Melo, 1988, figs. 4-7), it would be assumed that the bathymetry in Gamoneda and Icla regions was similar and possibly deeper subtidal when the *Scaphiocoelia* zone was formed, supporting the idea of Eldredge and Braniša (1980) that these regions were biogeographically closely related. With the exception of *Viaphacops* cf. *orurensis* of the *Scaphiocoelia* zone in Gamoneda, *Viaphacops* occurs above this zone in Icla and Belén areas only, shifting the biogeographic relationship from south-central to central-north. The subtidal zone moved into southern Peru and northward into the Givetian, making the sea level of southern Bolivia shallower. Lefebvre and Rachebœuf (2007), based on their finding of deep-water echinoderms, also report that the upper part of the Icla Formation (Emsian into Eifelian, central Bolivia) reflects deeper subtidal environment, supporting Issacson's view.

The faunal association of Bolivian *Viaphacops* with deeper water species such as *Austronoplia steubeli* (Brachiopoda), *Gamonetes anteloi* (Brachiopoda), in the Icla and Belén Formations (Isaacson, 1975) and *Conularia* sp. (Conularida) and *Australospirifer* (Brachiopoda) in the Cabanillas Formation, Jarajache, Peru (Douglas, 1920; Newell, 1949; Braniša, 1965) indicates that it was dwelling in the subtidal zone, or perhaps on the slope. Inferring from Mikulic (1981), phacopids, as well as dalmanitids, were non reef-building species that often appeared as migrants on the fringe of carbonate buildup. Although the absence of carbonates in Bolivia discounts this, it could be considered that they lived on the periphery of a slope, towards the open ocean, and this might explain their widespread distribution (Whittington, 1997). Habitat tracking is common among phacopids as well as dalmanitids (Chlupáč, 1983; Sandford and Holloway, 2006). It seems *Viaphacops* also tracked the preferred habitat towards deepening Peru (Iwasaki, 2002).

North American and Bolivian Viaphacops species and their environment. – *Viaphacops* Maximova, 1972 is quasi-cosmopolitan and is found in the carbonate-rich rocks in North America and Kazakhstan, and in siltstone and/or mudstone in Bolivia. The rocks from the latter region contain no carbonate. This lithological difference indicates a difference in depositional environment. The presence of carbonate often indicates a coral reef environment, which is often warm, shallow, and clear water. On the other hand, siltstone or shale can be deposited in muddy, murky water. Paleomaps of the Devonian reconstructed by various authors (Boucot and Gray, 1983; Dalziel *et al*., 1994; Eldredge and Ormiston, 1979; Poncet, 1990; Scotese and McKerrow, 1990; Van der Voo, 1988) tend to place Eastern North America within 30 degrees latitudes, which is tropical, and Bolivia higher than 30 degrees latitude south. Although the Malvinokaffric Realm is distinguished by its cold water fauna, Bolivia and Peru were peripheral to it and belonged to what Meyerhoff *et al*. (1996) termed as “intercalating zone,” which received both colder currents from the

Malvinokaffric and warmer water from Eastern North American Realms, enabling warmer water fauna of Eastern North America to settle there (Boucot *et al*., 1980).

One of the striking differences between North American and Bolivian *Viaphacops* species is their eye morphology. Bolivian species possess higher number of dorsoventral files (average of 16-17, ranging 15-18, some 19), while North American species have fewer (average of 14, ranging 13-16, some 12). Accordingly, the number of lenses per file for the Bolivian species is 7 to 8, while that of North American species is 5 to 6 (Iwasaki, 2004; Table 1). In addition, the North American taxa exhibit a strong convexity of the visual surface, making it globular in many species, but the Bolivian species have a dorsoventrally flat visual surface. The summary of relationship between depositional environment and eye morphology is in Table 2. Struve (1970) also noticed two different eye morphology types among the Devonian Eifel trilobites, "low-eyed" species with small number of lenses and "tall-eyed" species with numerous lenses. He concluded that the former were common in limy sediments, indicative of near-reef shallow water environment, and the latter in sediments of deeper or turbid water environments. Chlupáč (1977: 139) also notes environmental influences on the eye morphology.

Eldredge (1972: 104) reports the similar correlation between lithology type and number of lenses per file for *Phacops rana* group, which is now recognized as *Eldredgeops* Struve, 1990. The majority of *Eldredgeops crassituberculata* specimens were found predominantly in limestone (see Eldredge, 1972: Table 7). This species has 18 dorsoventral files, with 6 lenses per file. *Eldredgeops milleri*, on the other hand, occurs in shale (see Eldredge, 1972: Table 7). It also has 18 dorsoventral files, but the number of lenses counts more; 8 to 9 per file. Again, those occurring in shale have more lenses than those in carbonate environment (Iwasaki, 2004; Table 3).

This observation contradicts many cases in which inhabiting a dark, muddy environment leads to the loss or reduction of eyes in phacopids (e.g. Crônier, 2003; Crônier and Feist, 1997; Feist and Clarkson, 1989; Sandford, 2000). Chlupáč (1977: 145-146), however, reported the occurrence of both large-eyed and blind or reduced-eyed phacopids in shale facies in the Barrandian area. He interpreted that the difference in the phacopid eyes was due to the different mode of life, which is substrate dependent. Whittington (1997: 132) also suggests that adaptations to an endo-benthic (or burrowing) life are the likely cause of blindness in trilobites. Chatterton *et al*. (2006: 10) give an example of a Devonian Moroccan trilobite *Erbenochile* to explain the development of large eyes in deep water. Together with Chlupáč's interpretation above, it would be concluded that large eyes could have developed in deep water alongside species that have experienced the loss of eyes. Chlupáč (1977: 147) further notes that some genera such as *Phacopidella* and *Denckmannites* of the Silurian belong to a branch characterized by a reduction of eyes. This last remark needs to be tested at some point.

Morphologically, North American taxa exhibit some apomorphic characters like the tendency to form wavy ridges on doublure and the loss of granules on glabella. Among the Bolivian taxa, the retention of the primitive condition is commonly observed. Just like its predecessor, *Paciphacops*, many of the Bolivian *Viaphacops* species possess granules on the vincular furrow, and most of the time granules on the doublure are not fused together completely, but rather they become smaller in dimension and are arranged in rows along the margin (Figs. 19.5, 19.6, 21.1 –21.5). The granules on the frontal wall of the glabella are a common feature among the Bolivian taxa, as well as among the *Paciphacops* species, and this character is also observed in the *Viaphacops* species from the Frisco Formation described by Campbell (1977), but not in the other species in younger beds from North America.

SYSTEMATICS

Family PHACOPIDAE Hawle and Corda, 1847

Subfamily Phacopinae Hawle and Corda, 1847

Genus VIAPHACOPS Maximova, 1972

Phacops cristata Hall and Clarke, 1888, p. 14, pl. 6, figs. 1-13, 16-29, pl. 8A, figs. 1-4

Phacops cristata var. *pipa* Hall and Clarke, 1888~~,~~ p. 18, pl. 8A, figs. 5-8.

Viaphacops Maximova, 1972, pp. 78-80.

Type species. – *Phacops cristata* var. *pipa* Hall and Clarke, 1888 (same as *Phacops cristata bombifrons* Hall, 1861; see Eldredge, 1973, p. 315). Onondaga Fm., NY.

Other species. – *Phacops cristata bombifrons* Hall, 1861; *Phacops cristata* cf. *bombifrons* Hall, 1861; *Phacops canadensis* Stumm, 1954; *Phacops chavelai* Baldis and Longobucco, 1977; *Viaphacops* cf. *chavelai* (Baldis and Longobucco, 1977); *Phacops cristata* Hall and Clarke, 1888; *Phacops* cf. *cristata* var. *pipa* Hall and

Clarke, 1888; *Phacops* cf. *altaicus* Tschernyshew, 1892; *Phacops dentatus* Maximova, 1968; *Phacops* ex gr. *cristata* Hall and Clarke, 1888; *Phacops gaspensis* Clarke, 1908; *Viaphacops kozlowskii* Pek and Vaněk, 1991; *Viaphacops mongolicus* Maximova, 1974; *Viaphacops multicinctus* Pek and Vaněk, 1991; *Viaphacops* sp. Campbell, 1977; *Phacops nasutus* Stumm, 1954; *Viaphacops newelli* n. sp.; *Phacops oculeus* Maximova, 1960; *Phacops orurensis* Bonarelli, 1921; *Viaphacops* cf. *orurensis* (Bonarelli, 1921); *Viaphacops pirovanoi* n. sp.; *Phacops praepipa* Maximova, 1968; *Phacops pustulatus* Maximova, 1968; *Phacops* aff. *pustulatus* Maximova, 1968; *Phacops salteri* Kozlowski, 1923; *Viaphacops* cf. *salteri* (Kozlowski, 1923); *Viaphacops spinoedgecombei* n. sp.; *Phacops cristata stummi* Eldredge, 1973; *Phacops subcristatus* Khalfin, 1955; *Phacops cristata variabilis* Eldredge, 1973; *Viaphacops venezuelensis* Carvalho and Moody, 2000; *Viaphacops vitrea* Lespérance, 1991.

Revised diagnosis. – Posterior border furrow shallow and wide, becoming shallower and wider into lateral border furrow, making it almost or completely effaced under the visual surface. Postocular platform not well developed, often shorter sagittally than posterior border furrow and only developed posteriorly from the eye and not laterally. Occipital furrow shallow to obsolescent, almost or entirely absorbed into the depressed, or weakly developed preoccipital lobe. In lateral view, preoccipital lobe or glabellar lobe L1 (intercalating ring) lower than the composite lobe, appearing depressed. Distal nodes of preoccipital lobe or L1 small, usually smaller than those of thoracic rings. Occipital ring and thoracic axial rings become taller and narrower sagittally in some species (*spinoedgecombei* n. sp., some *orurensis, salteri, multicinctus, canadensis*). Development of thoracic axial spines and spiny tubercles observed (*spinoedgecombei* n. sp., some *orurensis, stummi, cristata*, some *variabilis*, some *bombifrons*). Gena withdrawn posteriorly, often into short spines (*salteri*, *multicinctus, kozlowskii, orurensis*, *spinoedgecombei* n. sp., *nasutus*, *cristata, canadensis, bombifrons*, some *gaspensis*, some *variabilis*). Development of subtriangular glabellar anterior margin commonly observed. Eyes located forward and outward, towards the anterolateral cephalic margin. Granules on glabella, when present, reduced to the frontal wall and the anterolateral corners, on and between tubercles. Glabellar tubercles of 2 to 3 size classes, become slightly denser and smaller in dimension anteriorly. Large tubercles often superimposed by granules into rosette figure. Lateral nodes of thoracic rings usually small, and sometimes indistinct, but fairly developed. Pygidial axis has a terminal piece which merges into the posterior pleural field without furrow.

Occurrence. – Lower to Middle Devonian. Central Kazakhstan, Mongolian Altai, Rudny Altai (southern Siberia), Inner Mongolia (Zhusilengharhan area), Eastern North America, Oklahoma, Venezuela, Colombia, Bolivia and Peru.

Discussion. – Diagnostic characters cited above, such as the development of narrower and taller occipital ring and thoracic rings, and the appearance of genal spines, do not necessarily apply to every species of *Viaphacops*. These features rather appear in the *Viaphacops* groups for the first time in the phylogenetic lineage of *Ananaspis-Paciphacops-Viaphacops*. Both occipital and axial rings of *Paciphacops* are much wider sagittally and lower, with distinct distal nodes. While some authors recognize *Viaphacops* as a separate genus from *Paciphacops* (e.g., Eldredge, 1985; Ramsköld and Werdelin, 1991; Linsley, 1994), other authors (Chlupáč, 1977; Campbell, 1977) disagree, especially with Maximova's diagnostic character on the reduction of preoccipital lobe, and thus assign this species to a subgenus of *Paciphacops*; however, when compared with *Paciphacops, Viaphacops* does have less distinct preoccipital lobe due to the weakly incised, shallow occipital furrow and the small distal nodes of preoccipital lobe (or distal L1). This character is not obvious in dorsal view, but is apparent in lateral view, and the depression of the preoccipital lobe can be easily observed. Other characters, especially the distribution pattern of granules on cephalic doublure and on hypostoma, are similar to that of *Paciphacops*, except that some *Viaphacops* species, particularly those from North America, strongly show the development of wavy ridges laterally (*stummi*, *bombifrons*) or entirely (some *cristata*). The species from Bolivia show the reduction of the size of granules posterolaterally (*multicinctus*, *kozlowskii*, *spinoedgecombei* n. sp), and sometimes form thin, weak wavy ridges along the margin of vincular furrow and hypostomal suture (*newelli* n. sp., *pirovanoi* n. sp., some *multicinctus*, some *kozlowskii*, some *spinoedgecombei* n. sp.), but not much deformation of granules occurs. A postocular platform is not developed well like in *Phacops* or *Paciphacops*, and only slightly appears right behind the eye, except some *pirovanoi*, which shows a deeper lateral border furrow going around under the eye. The posterior border furrow often disappears into the wider and much shallower lateral border furrow which merges into the eye stem area.

VIAPHACOPS SPINOEDGECOMBEI new species

Figures 3, 4, 21.1 – 21.3

Phacops orurensis Bonarelli. Ahlfeld and Braniša, 1960, pl. 6, figs. 1-3.

Phacops orurensis Bonarelli var. *B*. Braniša, 1965, pl. 19, figs. 6-9, 11.

Phacops salteri Kozlowski. Wolfart, 1968, pl. 4, fig. 1.

Diagnosis. – Pentagonal glabella covered with knobby, well-pronounced tubercles. Occipital ring tall, subtriangular and narrower dorsally, ornamented with three to four knobby tubercles. Thoracic rings having three to four spiny tubercles medially, with the lateral ones being more prominent. Pygidial axis tuberculated as well. Visual surface with generally 17 dorsoventral files, a maximum of 6 lenses per file and the average of 81.70 (ranging from 76 to 91) lenses.

Description. – The anterior margin of glabella is subtriangular; glabella pentagonal in dorsal view. Genae are withdrawn posterolaterally, curving slightly inward at the genal angles. Genal spines are developed at the tips of genal angles, extending posterodorsally from the lateral view. The glabella is moderately inflated; in lateral view, the preoccipital lobe (glabellar lobe L1) is depressed, and the medial L1 is steeply raised toward the glabellar furrows S2, from which the curvature of the glabella becomes gently inclining anteriorly to the frontal wall. The glabellar furrows S2 and S3 are shallow and narrow, but distinct. The medial glabellar lobe L1 is inconspicuously separated from the weakly developed, rather wide occipital furrow posteriorly, and bounded by medially weakened, or more often reduced, glabellar furrows S1 anteriorly. In most specimens examined, the medial glabellar lobe L1 is incorporated into the composite glabellar lobe anteriorly. Granulation on the external mold is observed on the frontal wall and the anterolateral corners of the glabella, on and between tubercles (Fig. 3.4). Rosette pattern on tubercles is developed on those granulated areas only, such that the granules are covering those areas regardless of presence or absence of tubercles. Tubercles are of two sizes, with the smaller ones interspaced between the larger, more knobby-looking, conical ones. These tubercles are more densely distributed anteriorly where they become slightly smaller. The overall the density of glabellar tubercles is moderate to dense.

The visual surfaces are strongly arched anteroposteriorly from the dorsal view, with the anterior margin reaching to the glabellar axial furrows, from which the palpebral furrows diverge very slightly from each other. Dorsoventral files of 17, occasionally 18, with the observed range of 76 to 91 (mean = 81.70) lenses are counted on the visual surface. The maximum number of lenses per file is six. The eye stem under visual surface is tall, unornamented, and gently merged into the wide, shallow and indistinct cephalic lateral border furrow. Some specimens with weak tuberculation on the palpebral areas are observed, and granulation is also observed on the lateral margin of the palpebral lobe, just above the visual surface.

The cephalic doublure is ornamented with granules that become smaller and more densely distributed posterolaterally, where they become weakly fused together, but not connected well enough to form wavy ridges. Granules are also dispersed to the well-developed vincular furrow. The doublure is long sagittally, with hypostomal suture positioned slightly posterior from the anterior corner of the eye. Hypostomal suture is almost straight. Hypostoma is unknown.

The occipital ring is tall and becomes narrower dorsally into three knobby tubercles, the middle one of which is taller, so as to form a subtriangular arch. The thoracic axial rings are tall and narrow dorsally, like the occipital ring, but topped with three or usually four spiny tubercles medially. The lateral ones of these tubercles are more prominently developed than the rest in between. The tubercles are spiny, almost look like true spines, but they are rather bluntly rounded off on top, not extending to form spiny points.

The pygidial pleural furrows are shallow, but very distinctly appearing on the anterior four pairs of pleural ribs, and weakly incised on the rest of the pleura on the external mold. The pygidium is composed of a total of 5 to 6 pairs of pleural ribs, with the anterior four pairs conspicuously bearing wide interpleural furrows. The pygidium is short and wide, having a round posterior margin. The axis narrows posteriorly, formed of 7 axial rings and a terminal piece which is bluntly absorbed into the posterior pleural field. The axial rings are ornamented with a few tubercles medially, with the lateral ones appearing more distinct than others in between.

Etymology. – This species is named for Dr. Greg Edgecombe, whose contribution to Bolivian paleontology is enormous. *Spino* refers to the spiny tubercles this species exhibits.

Type. – Holotype, MHNC 0565, one cephalon from Kochis, Cochabamba Department. Paratypes, MHNC 7482, AMF 99349, 99356, AMNH, 45511, 45513 – 45515, 45576, 45577, 46256, 45658, 46259, 46601, 46602, 63465. USNM 539689 – 539697, 539699.

Occurrence. – Upper Member of the Belén Formation (Emsian – Eifelian) in Pujravi (Wolfart) and Jacha Chili (Braniša) of the La Paz Department, the Sica Sica Formation (Givetian) in Chacoma, Belén, Chiarumani, Colchani, Cahuanota, Pisakaviña of the same department, the Huamampampa Formation (Givetian) in Presto (USNM locality 20039 and 20040) and Cha-kjeri (USNM locality 17909) of Chuquisaca Department, and the Upper Member of the Icla Formation (Emsian - Eifelian) in Kochis, Totora-Aiquile region of Cochabamba Department.

Discussion. – This species is distinguished from the closely resembling *V. orurensis* by its coarse, conical tubercles on the glabella and the peculiarly developed spine-like tubercles on the occipital ring and tall thoracic rings. *V. multicinctus* also possesses tall, narrowing thoracic rings, but does not develop these spine-like tubercles; *V. multicinctus* instead has small tubercles on them. The glabellar features of *V. spinoedgecombei* n. sp. are different from *V. multicinctus* for the latter species develops a strongly inflated glabella and its tubercles are less pronounced. *V. spinoedgecombei* also develops tubercles on the pygidial axis.

VIAPHACOPS NEWELLI new species

Figures 5, 6, 21.6

Phacops orurensis Bonarelli var. *A*. Braniša, 1965, figs. 1, 3-5, 16.

Phacops orurensis Bonarelli. Braniša, 1965, pl. 19, fig. 17.

Phacops salteri Kozlowski. Wolfart, 1968, pl. 4, fig. 4.

Diagnosis. – The entire glabella ornamented with tubercles of a "rosette" pattern. Genae generally moderately inflated, covered with small tubercles and granules which spread onto both cephalic lateral margins and posterior border. Genae round and devoid of spines or node. Occipital ring low and wide, flattened dorsally where fine, small tubercles and granules developed. Visual surface very tall, with 17 to 18 dorsoventral files, a maximum of 6 to 7 lenses per file, and an average of 89.09 lenses, ranging from 78 to 102 lenses. The height of visual surface having an average ratio of 0.88 to the length. Granules and small tubercles covering the round and low thoracic rings and posterior ramus of the thoracic pleura. Convex surface of pygidium granulated and ornamented with these small tubercles. Large species, cephalon width ranging from 26.0 mm to 55.7 mm, and the length from 19.2 mm to 32.9 mm.

Description. – Cephalic anterior margin is generally round, but in some specimens weakly to fairly subtriangular. The entire glabella is covered with somewhat large and low tubercles on which granules are superimposed to form a "rosette" pattern. Tubercles are more or less uniform in size, more densely distributed anteriorly, and become moderately spaced posteriorly. Those located anteriorly tend to become slightly smaller. Granules are also present on the frontal wall and anterolateral corners of the glabella, on and between the tubercles (Fig. 21.6).

The glabella is moderately inflated; in frontal view, it is dorsally flattened to inconspicuously round. The glabellar lobe L1 is continuous from the occipital furrow, depressed to slightly inflated, indented laterally by weakly developed glabellar furrows S1, which are medially reduced, and incorporated into the composite glabellar lobe anteriorly, usually ornamented with two tubercles. The glabellar furrows S2 and S3 are relatively strongly grooved. Genae are extending posterolaterally, forming into round genal angles without spines, but covered with granules and small tubercles. The genae are commonly inflated well enough to be seen from the ventral view.

On some well-preserved specimens, the granules continue spreading from the posterior cephalic margin into genal angle, then along the cephalic lateral margins where they form into wavy ridges (AMNH 45476). Their occurrence is terminated at the bottom of the eye stem.

Cephalic posterior border furrow on the internal mold is wide, distinct, and incorporated into the wide, rather indistinct lateral borer furrow. Both palpebral lobe and palpebral area are covered with granules, and on the palpebral areas weak tuberculation is also developed. The occipital ring is low, wide, and somewhat flattened dorsally, covered with both granules and fine, small tubercles. Dispersion of the fine tubercles is observed distally on the posterior border, and becomes somewhat massive on the genae. The posterior border is granulated as well.

The visual surface contains 17 to 18 dorsoventral files, with a maximum of 6, sometimes 7, lenses per file, and has an average of 89.00 lenses (observed range: 78 - 102). The visual surface is tall, with the average height to length ratio of 0.88. Granulation occurs on top of the visual surface to the entire surface of the palpebral lobe, but not on the sclera of the visual surface. Slight granulation on bottom of the visual surface is also observed. Eye stem is somewhat low, devoid of ornament, and merging into the lateral border furrow.

Cephalic doublure is densely ornamented with granules that become finer along the margins, and sometimes these finer granules form weak wavy ridges.

Granulation is observed on the wide, but rather shallow vincular furrow as well. Hypostomal suture is almost straight to slightly arched anteriorly. Hypostoma is unknown.

Thoracic rings appear low and round dorsally, covered with a mass of small tubercles which are also developed on the posterior ramus of the pleura. Granulation is also visible on the tuberculated areas on the thorax on the external mold.

Pygidium is short and wide. Posterior pygidial margin forms a semicircular outline. The axis is low and wide, made up of 8 axial rings and a terminal piece. The posterior half of the axis progressively becomes lower and the terminal piece is almost merging into the posterior pleural field. Pleural furrows are somewhat distinctly developed on the anterior two pairs of pleural ribs. A total of 7 pairs of ribs is observed on the pleural field, with the posteriormost ribs becoming very inconspicuous. On convex surface of both pygidial axis and pleura, granulation and a mass of small tubercles occur. The granulation can be seen only on the external mold.

Etymology. – After the late Dr. Norman Newell who collected specimens of this new species from Imarucos or Jarajache, Peru in the 1940s.

Type. – Holotype, AMNH 45475, internal mold of a cephalon from Pujravi, La Paz Dept. Paratypes, AMNH 26368/1, almost complete specimen from Jarajache, Peru, AMNH 45476 – 45480, 45572 – 45575, 46245 – 46249, 53020 – 53022, 63464. USNM 539685 – 539688, 539698.

Occurrence. – Lower and Upper Members of the Belén Formation (?Emsian – Eifelian) in Belén , Huaychani, Chacoma, Pujravi, Patacamaya, Cahuanota, Colchani, Maskachili (Wolfart), Hisakachili (Braniša) of the La Paz Department. Cabanillas Formation of Jarajache, Peru (Newell).

Discussion. – This species differs from *V. pirovanoi* for its large "rosette" patterned tubercles on the glabella. Both *V. newelli* and *V. pirovanoi* develop small tubercles on thoracic rings and pleura, as well as on their pygidia; tuberculation is more massive on *V. newelli* on those areas. Also, tubercles that occur on the palpebral areas, genae, occipital ring, cephalic border, as well as on the thorax and pygidium of *V. pirovanoi* are rather conical and centrally depressed, the same as the glabellar tubercles; whereas the corresponding areas of *V. newelli* are ornamented with fine tubercles which are different from its granulated glabellar tubercles. Nearly the entire convex surface of *V. newelli* is covered with fine granules, which is one of its characteristics. The inflation of the glabella is somewhat similar to that of *V. multicinctus*, but the latter has smaller tubercles with no granulation. The visual surface of *V. newelli* is remarkably high, with the height to width ratio of 0.88 while the other species have a ratio of around 0.50 and 0.66 for *V. pirovanoi.*

VIAPHACOPS PIROVANOI new species

Figures 7, 8, 20.3

Phacops orurensis Bonarelli var. *A*. Braniša, 1965, pl. 19, fig. 19.

Phacops salteri Kozlowski. Wolfart, 1968, pl. 5, fig. 1.

Diagnosis. – Ornamentation on almost the entire convex surface with small, well-defined and conical, centrally depressed or perforated tubercles. Posterior cephalic border furrow deep for genus. Cephalic lateral border furrow well developed. Pygidium elongated sagittally, strongly segmented with nine pairs of pleural ribs. No genal spines present; genae inflated. Vincular furrow anteromedially shallower. Visual surface with 17 to 18 dorsoventral files, the average of 104.00 lenses, ranging from 96 to 111 lenses, and a maximum of 7 lenses per file. Small species, with the cephalic width ranging from 22.2 mm to 29.0 mm, and the length from 13.7 mm to 16.7 mm.

Description. – Round cephalic anterior margin. Glabella very inflated. Glabellar furrows S2 and S3 distinct, but S1 obsolescent to very weakly incised laterally, reduced medially. The medial glabellar lobe L1 usually depressed to weakly developed, but continuous from the wide occipital furrow posteriorly, and absorbed into the composite glabellar lobe anteriorly. Cephalic posterior border furrow deep for genus. No genal spine present. Genae and posterior border ornamented with sparsely distributed, small, generally centrally perforated tubercles. Glabella also covered with these tubercles of two sizes. These small, prominent tubercles are rather densely distributed; only sparsely anteriorly. Occipital ring low and stout, rather flattened dorsally, ornamented with 30 or so such tubercles on top. Palpebral areas also ornamented with these tubercles, fewer than 10 on the palpebral area and about 15 on the palpebral lobe observed (Fig. 20.3).

Hypostomal suture slightly arched anteriorly. Vincular furrow shallower anteromedially. Sparse tuberculation on the anterior margin of the vincular furrow observed.

Thoracic rings very low, with flattened dorsal surface ornamented with about 18 centrally perforated tubercles. Pleura with a line of tubercles, which, in some cases, are enlarged on the posterior band of the pleura (Figs. 8.9 – 8.11).

Pygidium with a rather angular posterior margin, elongated sagittally, composed of 9 pairs of pleural ribs, 8 to 9 axial rings and a terminal piece. Convex surface of the pygidium covered with small perforated tubercles, as a mass on the axial rings and as a row on the pleura. Pygidial axis fairly wide, terminating somewhat sharply and away from the posterior pleural field. Pleural furrows very deep for genus.

Etymology. – Named after Sr. Giuseppe Pirovano who has been working for development in the Aiquile region, Cochabamba Department, by the Roman Catholic diocese, and who discovered the locality not of this species, but *V. spinoedgecombei*, in Tolamayu, Cochabamba Department.

Type. – Holotype, AMNH 45486, internal mold of a cephalon with right side intact. From Belén, La Paz Department. Paratypes, AMNH 45484 – 45488, 53019, 53023, 53024, USNM 508382-508386.

Occurrence. – Lower and Upper Members (?Emsian – Eifelian) of the Belén Formation in Chacoma, Belén , Maskachili (Wolfart), and Hisakachili (Braniša) of the La Paz Department.

Discussion. – Centrally perforated small tubercles are observed on most of the convex surface of the specimens analyzed. This species closely resembles *V. newelli* for some characters, such as the low, tuberculated occipital ring and thoracic rings. But one of the major differences between these species can be found in the morphology of the pygidium. *V. pirovanoi* has a sagittally elongated, well-segmented pygidium, whereas that of *newelli* is short and wide, less segmented. Other similarities and differences between these species are discussed in the section of *V. newelli*.

One extraordinary specimen (USNM 508384) from the locality of Belén, La Paz Department has 19 dorsoventral files and 121 lenses on the right visual surface (a maximum of 8 lenses per file).

VIAPHACOPS ORURENSIS (Bonarelli, 1921)

Figures 9 – 11, 20.1, 20.2

Phacops latifrons Bronn. Salter, 1861, pl. 4, fig. 8.

Phacops salteri Kozlowski, 1923, pl. 6, figs. 3-5.

Phacops cf. *P. logani birdsongensis* Delo. Braniša, 1965, pl. 19, fig. 2.

Phacops salteri Kozlowski. Wolfart, 1968, pl. 3, figs. 3, 4.

Revised diagnosis. – Variations in the shape of occipital ring and thoracic rings, from low and dorsally round to tall and triangular. Median node often developed on some triangular occipital ring. Visual surface with 15 to 16 dorsoventral files, with a maximum of 5, sometimes 6, lenses per file, and the average of 63.64 (observed range: 59-70) lenses. Small, short genal spine often present. Palpebral area ornamented with non-granulated tubercles. Glabella relatively flat in the standard orientation, covered with small tubercles of moderate density. Cephalon with broad, semicircular anterior margin. Pygidium very short and broad, having very narrow axis. Ornamentation absent on the thorax and the pygidium, except for some thoracic rings.

Description. – Glabellar furrows S1 generally conspicuous distally, in some cases faintly developed medially. Glabellar furrows S2 and S3 commonly developed, some distinct as dark marks and in some cases thinly incised. The frontal wall and anterolateral corners of glabella granulated. Small, distinct glabellar tubercles developed in two sizes, with a moderate density throughout the glabella. Medial glabellar lobe L1 weakly developed, often ornamented with two or three tubercles.

Variation in the occipital ring and thoracic ring observed. There are basically three patterns: low and dorsally round (Figs. 10.7 – 10.10); tall and triangular (Figs. 9.8 – 9.11; Figs. 10.1 – 10.6); and tall and triangular, bearing a median node (Figs. 9.1 – 9.4, 10.11 – 10.13, 11.5 – 11.9). Some of the specimens exhibit intermediate morphology between these patterns and therefore separating them out into different groups would be difficult.

Hypostomal suture straight to inconspicuously concave medially. Short and wide hypostoma with a rather pointy, subtriangular posterior margin observed. Vincular furrow slightly narrow posterolaterally. Cephalic doublure covered with granules entirely, and some wavy ridges developed near hypostomal suture.

The axis of the pygidium slightly narrowing posteriorly, containing 7 axial rings and a terminal piece. The terminal piece weakly separated from the posterior pleural field. The pleural field composed of 6 pairs of ribs, bearing narrow but distinct pleural furrows on the external mold. Interpleural furrows very inconspicuous on both molds.

Type. – Cephalon figured by Pek and Vaněk (1991) on pl. 7, fig. 5.

Assigned specimens. – AMNH 45472, 45489 – 45492, 45494 – 45501, 45503, 46255 – 46257, 57800, 57801, 57803, 63455, 63456, 63463, 63466.

Occurrence. – Sica Sica Formation (Givetian) in Ayo Ayo, Belén , Pujravi, Chacoma, Pisakaviña, and Patacamaya of the La Paz Department. Oruro, Oruro Dept., Upper Icla Fm.

Discussion. – The validity of this species name is discussed in the introduction. This species has fewer dorsoventral files than the other species, the feature which can be considered to be derived (cf. Eldredge, 1973). Unlike other species of Bolivian *Viaphacops*, this is the only one exhibiting variations in character on the occipital and thoracic rings.

VIAPHACOPS cf. ORURENSIS (Bonarelli, 1923)

Figure 12

Assigned specimen. – AMNH 45512, internal mold with a counterpart of an almost complete, slightly enrolled specimen from Cerro Picacho, Tarija Dept. Gamoneda Fm.

Occurrence. – Cerro Picacho, Tarija Dept. Gamoneda Fm.

Discussion. – The morphology of the pygidium and the overall similarity of the cephalon indicate that this specimen may belong to *V. orurensis* from the Sica Sica Formation of the La Paz area. However, this specimen and *V. orurensis* have a considerably wide geologic distance (Pragian to Givetian, about 18 million years difference) and geographic distance, conglomerating this specimen into *V. orurensis* is questionable. Hopefully, more specimens will be available from this locality or formation for further investigation. Few details are known for this specimen due to the deformation and poor preservational condition. However, because the medial glabellar lobe L1 is depressed from the lateral view (Fig. 12.3), its assignment to *Viaphacops* must be valid.

One of the characters which differentiates this species from *Viaphacops orurensis* is that it has tuberculated occipital ring and thoracic rings (Figs. 12.5 and 12.6). However, because of the variation expressed in this morphology, from low and unornamented to high and sometimes with a node in *V. orurensis*, one cannot confidently assign this species to it until other characters are found. Other noticeable characters include glabellar tubercles that are more prominent and more densely distributed than those on *V. orurensis*. Just as in *V. orurensis*, palpebral areas are tuberculated on external mold.

VIAPHACOPS MULTICINCTUS Pek and Vaněk, 1991

Figures 13, 14, 21.4

Phacops salteri Kozlowski. Wolfart, 1968, pl. 4, fig. 5.

Phacops (*Viaphacops*) *multicinctus* Pek and Vaněk, 1991, p. 81, pl. 7, figs. 1-4.

Revised diagnosis. – *Viaphacops* with a strongly inflated glabella. A visual surface with 17 dorsoventral files, a maximum of 5 to 6 lenses per file, and average of 74.75 lenses. Small tubercles of more or less uniform size developed on the glabella. The occipital ring tall and narrow, ornamented with some small tubercles dorsally. Short, slightly stout genal spines present. Thoracic rings somewhat "ribbed" by three to four small tubercles dorsally. Pygidial axis short and broad, terminated clearly from the posterior pleural field. Pleural field flattened.

Description. – Anterior margin of cephalon semicircular to subtriangular. Glabellar furrows S2 and S3 generally inconspicuous. Tubercles on the glabella small and prominent, in two sizes. Granulation observed on the frontal wall and the anterolateral corners of the glabella. The rest of the glabella devoid of granulation. The occipital ring tall and narrow, but its dorsal surface slightly thickened by some non-granulated tubercles. Thoracic rings as well ornamented with small tubercles in a row on the dorsal surface, with each tubercle appearing rather indistinctly, and this in effect, making the ring look "ribbed" (Figs. 14.1 – 14.7, 14.10 – 14.12).

Anterior band of thoracic pleura granulated on external mold. The medial glabellar lobe L1 slightly developed, almost continuous from the wide occipital furrow posteriorly, and weakly bounded by medially indistinct glabellar furrows S1, usually ornamented with two tubercles. Hypostomal suture straight to slightly concave postero-medially. Hypostoma elongated sagittally, with the posterior margin having two pointy corners. Granules developed on the hypostoma, but not forming into wavy ridges. Pygidium short and broad, with a semicircular posterior margin. The axis short and broad for genus, made up of 7 axial rings and a terminal piece. Termination of the axis clear, and not reaching to posterior margin. Pleural field low and somewhat flat, consisting of 6 pairs of ribs. No ornament observed on the pygidium.

Type. – Cephalon figured by Pek and Vaněk (1991), pl. 7, figs. 1-3.

Assigned specimens. – AMNH 45252, 45462, 45467 – 45469, 45485, 45493, 45497, 45507, 46250 – 46253, 53025, 57799, AMF 99365, USNM 540771.

Occurrence. – Upper Member of the Belén Formation (Emsian-Eifelian) in Chacoma, Belén, Pujravi (Wolfart), Hisakachili (Braniša) and Chiarumani, all in La Paz Department.

Discussion. – In addition to the bulginess of the glabella discussed by Pek and Vaněk (1991), this species can also be characterized by its pygidial morphology. The pygidia of both *V. newelli* and *V. orurensis* resemble that of *V. multicinctus*, but the pygidial axis of this species is taller than that of *V. newelli* and broader than that of *V. orurensis* and much shorter than either of them. The pygidial pleura are more inclined posteriorly from the dorsal view, when compared with other species. The pleural field of this species is low and flattened while the other species have more angular and raised ones. Thoracic rings and occipital rings are very similar to those of *V. spinoedgecombei*, but those of *V. multicinctus* develop much smaller, less pronounced tubercles that are clustered together.

VIAPHACOPS SALTERI (Kozlowski, 1923)

Figures 15, 16

Phacops salteri 1923, Kozlowski, pp. 54-56, pl. 6, fig. 2.

Phacops salteri Kozlowski. Wolfart, 1968, pp. 63-66, pl. 4, fig. 3.

Phacops (*Viaphacops*) *orurensis* (Bonarelli). Pek and Vaněk, 1991, 30, pp. 82-83, pl. 7, figs. 6-9, pl. 8, figs. 1-6, pl. 9, figs. 1-7, pl. 10, figs. 1-2.

Revised diagnosis. – Glabella weakly pentagonal, covered with low, indistinct tubercles of uniform size. Occipital ring tall and narrow, forming a subtriangular arch, occasionally bearing a median node. Medial glabellar lobe L1 depressed, merged with occipital furrow posteriorly, and absorbed into the composite glabellar lobe anteriorly. Glabellar furrows S2 and S3 generally weakly incised, and sometimes appearing as dark marks on internal mold. Glabellar tubercles indistinct; either small or low, and moderately to sparsely distributed. Palpebral areas unornamented. Genae withdrawn into somewhat stout genal spines for the genus with blunt ends. Thoracic rings tall and narrow, weakly subtriangular. Thorax devoid of ornament. Hypostomal suture straight to slightly concave. Hypostoma granulated on external mold, with a round posterior margin. Pygidium with 7 axial rings, anterior 4 to 5 rings of which are distinctly separated by distinct furrows, and a terminal piece present. Six to 7 pairs of ribs on pleural field. Pygidial axis bluntly incorporated into the posterior pleural field. Visual surface with generally 17 dorsoventral files, the average of 76.48 (observed range from 72 to 84) lenses. Maximum of 5 to 6 lenses per file.

Assigned specimens. – AMNH 45463 – 45466, 45470 – 45473, 46259, 45503 – 46608, 46610, 57798, 63457, 63460 – 63562.

Occurrence. – Lower Member of the Belén Formation in Maskachili (Wolfart) to Upper Member of the Belén Formation in Hisakachili (Pek and Vaněk), Patacamaya (Kozlowski), Chacoma, Pujravi, Belén and Cahuanota of the La Paz Department, and the Icla Formation in Padilla (Pek and Vaněk), Chuquisaca Department.

Discussion. – The occipital ring of this species is tall and narrow, and many of the observed specimens develop a median node instead of knobby tubercles, characteristic of *V. spinoedgecombei*. The difference between *V. salteri* and *V. multicinctus* can be the bulginess of the glabella which is more characteristic of the latter species (cf. Pek and Vaněk, 1991). Also, thoracic rings of *V. multicinctus* are ornamented with some small tubercles and are somewhat "ribbed," but those of *V. salteri* are devoid of any ornament. The pygidium of *V. salteri* has a narrow, tall axis while that of *V. multicinctus* is wide, short and flat. The number of pygidial axial rings is the same (7 plus a terminus) for both, but the segmentation of the axis is more pronounced on *V. multicinctus*. The pleural field is more raised on *V. salteri* than *V. multicinctus*.

VIAPHACOPS cf. CHAVELAI (Baldis and Longobucco, 1977)

Figure 17

Phacops orurensis Bonarelli var. *D*. Braniša, 1965, pl. 19, figs. 13, 14.

Phacops orurensis Bonarelli. Braniša, 1965, pl. 19, fig. 15.

Description. – The glabella with a round anterior margin, moderately inflated, covered with distinct tubercles of uniform size. Glabellar lobe L1 depressed to slightly developed. Glabellar furrows S2 and S3 shallow and wide. Facial suture weakly present. Glabellar tubercles uniform in size, distinct to prominent, and moderately dense.

A visual surface with 17 dorsoventral files, a maximum of 5 lenses per file observed. The anterior file usually with 3, and the posterior one with 2, lenses observed on the visual surface. Both palpebral lobe and area are smooth.

Thoracic rings round dorsally, with the anterior wall sloping gently anteriorly, forming a cup-shaped appearance, with the opening posteriorly. No ornament observed on the thorax. Distal nodes on the thoracic rings are larger (sag.) than those on the occipital ring; lateral nodes on the occipital nodes as large as lateral glabellar lobe L1.

Each pygidial pleural rib distinctly appearing, somewhat raised, and bearing deep pleural furrows. Seven to 8 tall axial rings and 5 or 6 pairs of pleural ribs are counted.

Large species, with the observed cephalic width ranging from 9.21 mm to 44.24 mm, and the cephalic length ranging from 17.11 mm to 27.02 mm.

Assigned specimens. – AMNH 45481 – 45483, from Pílon de Azúcar, Icla, Chuquisaca Department. AMF 99369 from Aiquile, Cochabamba Dept.

Occurrence. – Padilla (Braniša) and Pílon de Azúcar, Icla, of the Chuquisaca Department; Aiquile of the Cochabamba Department. Upper Icla Fm.

Discussion. – Not many details are known for the available four specimens, due to the poor preservational condition. Because of this reason, these specimens are tentatively assigned to *V.* cf. *chavelai*, until more specimens are available for study. The structure of the thoracic rings is unique for genus; they are not tall and narrow nor low and round, but they are somewhat wide and cup-shaped, with the anterior pleural band sloping gently anteriorly. This feature is very similar to *Phacops* *chavelai* Baldis and Longobucco, 1977 from the Chinguillos Group (Givetian-Frasnian) of the northwestern Precordillera, Argentina. However, the lateral nodes of the occipital ring of *P*. *chavelai* are as large as the lateral thoracic axial nodes, and this is different from *V*. cf. *chavelai* of Bolivia.

VIAPHACOPS KOZLOWSKII Pek and Vaněk, 1991

Figures 18, 19, 21.5

Phacops salteri Kozlowski. Wolfart, 1968, pl. 3, fig. 5.

Phacops (*Viaphacops*) *kozlowskii* Pek and Vaněk, 1991, 30, pp. 83-84, pl. 7, figs. 10-16, pl. 8, figs. 7-9, pl. 10, figs. 3, 4.

Description. – Glabella flat, in a pentagonal shape, with its anterior margin strongly extending medially to form a subtriangular cephalic outline. Glabellar tubercles in two sizes, low and flattened, distributed densely. Granulation developed on the frontal wall of the glabella (Fig. 21.5). Visual surface with 15 to 16 dorsoventral files, the average of 57.50 (observed range: 56-61) lenses, and a maximum of 5, sometimes 4, lenses per file. Visual surface long anteroposteriorly and narrow dorsoventrally, averaging the ratio of 0.47 for its height to the length. Occipital ring moderately long sagittally, unornamented. Medial glabellar lobe L1 fairly developed for genus, glabellar furrow S1 weakly developed medially. Some specimens showing fairly grooved occipital furrow, not continuous into the glabellar lobe L1. Thoracic rings somewhat tall, with no ornament. Anterior band of the thoracic pleura granulated (Fig. 19.3). Short and broad pygidium with 8 axial rings and a terminal piece, and 6 or 7 pairs of pleural ribs. Granulated vincular furrow becoming slightly narrower posterolaterally. On cephalic doublure, finer granules connected to form wavy ridges posterolaterally and along hypostomal suture; larger granules covering medially. Hypostoma granulated, wavy ridges not observed.

Type. – Incomplete cephalon figured by Pek and Vaněk (1991) on pl. 8, figs. 7-9.

Assigned specimens. – AMNH 45493, 45504 – 45506, 45508 – 45510, 45514, 45578, 46254, 46254, 53027, 53028.

Occurrence. – Upper and Lower Members of the Belén Formation (Emsian-Eifelian) in Pujravi, Chacoma, Colchani, and Patacamaya (Kozlowski), all in La Paz Department.

Discussion. – The visual surface of this species is long anteroposteriorly, averaging the ratio of 0.47 for its height to the length; other species have over 0.54 ratio, ranging from 0.54 (*V. orurensis*) to 0.88 (*V. newelli*).

CLADISTIC ANALYSIS OF BOLIVIAN AND NORTH AMERICAN *VIAPHACOPS*

Material and character selection. – All nine Bolivian *Viaphacops* species described here were analyzed cladistically to examine their phylogenetic relationship among themselves and with 8 available North American species (*V. cristrata* from Schoharie Fm., NY; *V. bombifrons* from Onondaga Fm., NY; *V. stummi* from Jeffersonville Fm., Indiana; *V. nasutus* from Jeffersonvill Fm., Indiana; *V. canadensis* from “Lower Onondaga limestone,” Ontario; *V. variabilis* from Needmore Fm., Pennsylvania; *V. gaspensis* from Grande Grève, Quebec; and *V.* sp. from Frisco Fm., Oklahoma). Two outgroup species were chosen: *Paciphacops waisfeldae* Edgecombe and Ramsköld, 1994, from central Bolivia (Catavi Fm., early Lochkovian) as it is the only *Paciphacops* currently known from this region, and the type species of *Paciphacops, P. logani* (Hall, 1861) *sensu* Ramsköld and Werdelin (1991) from New Scotland Formation, NY (Lochkovian). Rather than using the character set of Ramsköld and Werdelin (1991), new characters were created. They mainly focused on the Silurian taxa, *Acernaspis* and *Ananaspis*, and therefore their characters are more suitable for these species that show more variability (e.g. dimorphism in *Paciphacops*, Campbell, 1977: 36-37; ventral morphology, Lespérance, 1991: 180).

A total of 37 characters were selected from literature (i.e. Campbell, 1967, 1977; Chlupáč, 1977; Eldredge, 1972, 1973; Maximova, 1972; Ramsköld and Werdelin, 1991) and observation of available specimens (Appendix 1). Of these 26 are from the cephalon (characters 0 to 25), 4 are from the thorax (characters 26 to 29) and 7 are from the pygidium (characters 30 to 36). Of the 26 cephalic characters, binary coding was intentionally applied to quantitative characters as arbitrary grouping of numbers seems unnatural. These are character 10 (width of glabella relative to cephalic width, shown in percentage) and character 23 (large eye index, shown in percentage). Character matrix is given in Table 4.

The phylogenetic importance of number of dorsoventral files in the visual surface was extensively discussed by Eldredge (1972, 1973) for phacopids and including the number of dorsoventral files in the diagnosis became a common practice (e.g. Campbell, 1977; Chlupáč, 1977; Struve, 1976, 1982, 1984, 1985, 1992, 1995). However, as discussed above, the environmental condition was different in

Bolivia from North America, and one might doubt if the ecological differences would have influenced the development of eyes. In general, the North American species have fewer dorsoventral files, from 13 to 14 while 16 to 17 is common among the Bolivian species. This character is excluded in the analysis because of the intraspecific variations.

The maximum number of lenses per eye is also omitted in the analysis. This character is mostly influenced by ontogeny (Crônier and Clarkson, 2001) and therefore is considered to be less important by Chlupáč (1977: 131). However, a total number of lenses can often be included in generic and specific diagnosis (e.g. Chlupáč, 1971, 1972; Eldredge, 1972, 1973). This character also varies among specimens examined for each species and discrete, non-overlapping character states could not be identified.

Methods and results. – A PC program Winclada (Nixon, 1999-2002) was used for parsimonious cladistic analysis. The character matrix (Table. 4) was fed into this program, and NONA (Goloboff, 1999) was chosen to compute the most parsimonious trees. All the characters were set as nonadditive (Fitch), with the character weight of 1.000, and unordered.

An exhaustive search was conducted using Ratchet (Island Hopper) method. The algorithm was set to sample 7 characters (about 20% of the total characters) with 2,000 replications. Two separate analyses were performed. The first one used *Paciphacops waisfeldae* as a root and the most parsimonious tree was found with a tree length of 191, consistency index (=CI) of 39, and retention index (=RI) of 46.

The second analysis was with *P. logani* as a root. The most parsimonious tree was found (tree length = 191, CI = 39, RI = 46) (Figs. 22 and 23).

When *P. waisfeldae* was an outgroup, *P. logani* is included in the ingroup, as a sister to *V. pirovanoi*, that relationship being supported by three characters (14:1, 18:0, 23:1), and when *P. logani* was used as an outgroup, *P. waisfeldae* becomes an ingroup taxon, replacing *P. logani*. The topology above the node supported by characters 4 (height of palpebral area relative to palpebral lobe), 11 (shape of occipital ring), and 25 (palpebral furrow) is the same in both trees. Overall, Bolivian species for the most part are concentrated in the basal part of the cladogram. However, both *V. kozlowskii* and *V. spinoedgecombei* are placed within the North American clades. The first is a sister to *V.* sp. from Oklahoma, united by characters 5 (degree of inflation of medial L1), 8 (appearance of S3), 13 (lateral L1 lobes), and 14 (uniformity of tubercles), and latter is sister to a *V. canadensis*-*V. gaspensis* clade (3: development of postocular platform, and 8: appearance of S3).

The mostly North American clades, including the two Bolivian species indicated above, are supported at the 10th node by characters 3 (development of postocular platform), 4 (height of palpebral lobe and area), 19 (ornaments on doublure), 29 (thoracic axial apodemes), and 34 (termination of pygidial axis posteriorly). The peculiar character mentioned above, character 24 (dorsoventral convexity of visual surface), does not support the node. Another distinct feature of North American taxa, pitted or perforated cephalic border, only supports *V.* sp. as an apomorphy.

The placement of most of the Bolivian taxa at the basal clades could reflect the significant differences in depositional environment between the colder Malvinokaffric Bolivia and warmer Eastern North America as evidenced by the presence/absence of carbonates, and this in turn may imply that the differences in water temperature might have affected the developmental rates of characters (Stehli, Douglas, and Newell, 1969). However, the distribution of the two Bolivian taxa (*V. kozlowskii* and *V. spinoedgecombei*) in the higher nodes among the North American species, rather than clustering with the other Bolivian taxa, may indicate that environmental control was minimal (Edgecombe, personal comm., 2010).

Future work. – It is desirable if all the reported phacopid taxa from Bolivia and northern Argentina will be included in the cladistic analysis. These include *Phacops* (*Viaphacops*) *spatiosus* Pek and Vaněk, 1991 (Gamoneda Fm., southern Bolivia), *Phacops chavelai* Baldis and Longobucco, 1977 (Chinquillos Group, NW Argentina), *Zaplaops zaplensis* Baldis and Blasco, 1976 (Lipéon Fm., NW Argentina; Baldis *et al*., 1976), and *Notophacops lampayensis* Suarez Soruco, 1988 (Cancañiri Fm., central Bolivia). In addition, it is important to find more specimens from the field or museum collections for the species in open nomenclature in this paper, *Viaphacops* cf. *orurensis* and *V*. cf. *chavelai,* to establish their taxonomic status, so as to understand Bolivian *Viaphacops* phylogeny better, and hopefully, from a complete study of these species, the relationship of species distribution in time and space with phylogeny will further contribute to our knowledge of evolutionary processes.

CHAPTER 2. PHACOPID TRILOBITE DISTRIBUTION AND THE PALEOGEOGRAPHY OF THE LOWER AND MIDDLE DEVONIAN

ABSTRACT—Phacopid trilobites of the Lower and Middle Devonian were analyzed quantitatively for their distribution pattern. The result was compared against rugose coral distributions of Pedder and Oliver (1990). Both groups of organisms are widely distributed during that time interval. Based on the trilobite data, 15 regions were set and more than 300 species were analyzed at generic level, using Otsuka, Dice, and Jaccard Coefficient faunal similarity indices. A few points were found: 1) the high provincialism during the Lower Devonian is weakly reflected in the phacopid distribution, and it becomes more widespread in the Middle Devonian, possibly because of the transgression at the end of the Emsian; 2) the circumpolar current of the southern Panthalassa ocean is suspected for the close relationship of southeastern Australia with Bolivia-Argentina of South America and western North America and Canada; 3) Kazakhstan has a close affinity with Australia and Asia, but not with Europe. A Lower Devonian genus *Paciphacops*, which occurs pandemically in North America, Kazakhstan, southeastern Australia, and South America, was selected for constructing an area cladogram to test the regional relationship of these areas calculated in the Coefficients. The problem with the position of Kazakhstan is still unresolved, although the cladogram shows its closeness with Australia and South America, which is congruent with the Coefficient analyses.

INTRODUCTION

PHACOPID TRILOBITES are quite diverse and abundant throughout the Silurian and Devonian, and their occurrence is reported from all over the world. Their widespread distribution provides a key to understanding the paleogeography of this time interval (e.g. Chlupáč, 1975; Kobayashi and Hamada, 1977; Maximova, 1972; Ramsköld and Werdelin, 1991).

According to Chlupáč (1975: 402), a high diversification of phacopid species at the generic level was attained within the Bohemian magnafacies of the European Varisan geosyncline during the Lower Devonian. This paleobiogeographical region belonged to the Rheic Ocean (Stamplfi, *et al*., 2002: Fig. 4; Torsvik and Cocks, 2004: Fig. 5).

The use of widespread taxa for paleogeographic interpretation has been criticized by some authors (e.g. Blieck and Janvier, 1994; Fortey and Cocks, 2003; Marss *et al*., 2007; Rosen, 1978). Their argument stems from the fact that cosmopolitan species do not signal provincial differences. On the other hand, Rong *et al*. (1995) suggest that widely distributed species can be more useful than rare taxa that are only found in a single locality or a closely clustered group of localities. They further note that taxa that are moderately restricted by provinciality but occur in many different localities are biogeographically more informative than either very rare taxa or abundant cosmopolitan species. The phacopid group is relatively controlled environmentally (Chlupáč, 1977) and is thus applied for biogeographic analysis.

Pedder and Oliver (1990) analyzed the distribution pattern of the Devonian rugose corals to test the Devonian paleogeographic models. Their interpretation will be compared against the phacopid distribution.

Procedure. – The list of phacopid species for the Lower and Middle Devonian was compiled from literature and given here in the appendix (Appendix 1). Then the species were categorized into regions defined below. Based on this categorization, the number of shared genera was determined to calculate the faunal similarity index.

A generic-level analysis was applied here because genus is the most commonly used biogeographic unit and is often a more agreeable taxonomic category (Fortey and Cocks, 2003: 252). Determination of genera relied on Jell and Adrain (2003) and Ramsköld and Werdelin (1991) and the list of genera used in the analysis is given in the appendix (Appendix 2).

Stratigraphic range of the genera is provided in table 5. Because it is still problematic to correlate geological formations mentioned in literature and this task is beyond the scope of this study, a robust division of geologic age by epoch (i.e., Lower and Middle Devonian), rather than by age (i.e., from Lochkovian to Givetian) was applied. Since many genera are long-ranged and occur in more than one age unit, this approach may not be too unreasonable.

DIVISION OF GEOGRAPHIC RANGE

Overview of paleogeography. – The recent development of the Paleozoic tectonic evolution was reviewed by Ruban, Al-Husseini, and Iwasaki (2007).

They recognized some problems with the identification of plate tectonic units, especially for the Eurasian plate, and assignment of their present-day regions. For example, Young (1994) identified the Barrandian region as a part of Armorica. Cocks and Torsvik (2002) termed Perunica for this region, which Lees, Fortey, and Cocks (2002) called Bohemia. Şengör, Natal'in, and Burtman (1993) interpreted Paleozoic Kazakhstan not as a single plate as conventionally thought (e.g. Burrett, Long, and Stait, 1990; Filippova, Bush, and Didenko, 2001; Golonka, 2002; Heckel and Witzke, 1979; Scotese and McKerrow, 1990; Scotese, Van der Voo, and Barrett, 1985; Zonenshain, Kuzmin, and Kononov, 1987), but as a series of island arcs termed as Kipchak Arc. Li and Powell (2002: Fig. 1), Torsvik and Cocks (2004: Fig. 3, modified in Ruban, Al-Husseini, and Iwasaki, 2007: Fig. 2), Cocks and Torsvik (2007: Fig. 2) and Yolkin *et al*. (2000: Fig. 4) summarize the tectonic units and their geographic assignment for the Eurasian continent. This interpretation is still controversial (Boucot, 2007; Winkler Prins, 2007; Mosseichik and Ignatiev, 2007; Angiolini, 2007; van Loon, 2007).

Since the main purpose of this chapter is to compare the faunal similarity between the phacopid trilobite regions and not the reconstruction of Devonian paleogeography, the tectonic evolution and determination of terranes are referred to elsewhere (e.g. Ruban, Al-Husseini, and Iwasaki, 2007). Only after the faunal similarity analysis, selected reconstructions will be compared against the result.

Assignment of phacopid regions. – In their paper, Pedder and Oliver (1990) analyzed the Devonian rugose corals from 25 regions labeled from A to Y (Fig. 24; Pedder and Oliver, 1990: Fig. 1). These are:

A. Canadian Arctic Islands

B. Western Canada and neighboring northeastern Alaska

C. Great Basin, Nevada

D. Venezuela and Colombia

E. Michigan and Illinois Basins

F. Appalachian Belt

G. North Africa, including Algeria, Morocco and Spanish Sahara

H. Spain and the Pyrenees

I. Armorica, Montagne Noire, northern Vosges (Saxothuringian plate), Thuringia and Czechoslovakia

J. Britain, northern France, Belgium central Germany (Rhenish Massif) and Poland

K. Northeastern Europe, western Urals and Novaya Zelmya

L. Carnic Alps and southeastern Austria

M. Turkey

N. Northern Zizang (Tibet), northwestern Yunnan and Burma (Shan Plateau)

O. Tien Shan

P. Lake Balkash region, Kazahkstan, and Hoboksar region of northern Xinjang

Q. Altai-Sayan, including the Salair, Kuznetsk Basin, Minusa Depression, Gorniy Altai and Rudniy Altai

R. Taimyr

S. Indigirka River Region

T. Mongolia

U. Qinling Mountains region, central China

V. South China, including the Longmenshan Mountains and part of northern Vietnam

W. Western Australia

X. Eastern Australia

Y. Zhusilengharhan area of western Nei Mongol (Inner Mongolia) and the Erdaogou area of Jilin Province, China

The regional division by Pedder and Oliver (1990) puts together an extensive region across Europe (I: Armorica, Montagne Noire, northern Vosges or Saxothuringian plate, Thuringia [or Harz Mts. in eastern Germany] and Czechoslovakia [Prague area] and J: Britain, northern France, Belgium central Germany or Rhenish Massif Eifel Mts. in western Germany, and Poland). Although the differentiation indicates the division of continental Europe into southern (I) and northern (J) parts, or Hun Gondwanan and Hun Cordilleran Supercontinents (Stampfli and Borel, 2002; Stampfli, Raumer, and Borel, 2002; Stampfli *et al.*, 2001; von Raumer, Stampfli, and Bussy, 2003), respectively. However, this tectonic interpretation is not conventionally accepted in some literature (e.g. Scotese and Mckerrow, 1990) and because the British Isle was considered already a part of Laurentia by the beginning of the Lower Devonian rather than belonging to the Rhenish Massif (e.g. Cocks and Torsvik, 2002; Fortey and Cocks, 2003; Torsvik and

Cocks, 2004), their biogeographic division is reconsidered here and a new set of regions is provided in Table 6 below:

Proposed regions	Phacopid localities	Rugose coral regions (Pedder and Oliver, 1990)
Siberia	Kuznetsk Basin (Kazakhstan), Rudny Altai and northern Xinjang	P
Australia	Victoria and New South Wales	X
North Africa	Spanish Sahara, Zagora, Tafilalt, Bou Tchrafine, Tizi, Tiflet, Rabat, Sidi Ahroun, Oulmes, Ezzhilga (Morocco) and Algeria	G
Kazakhstan	Central Kazakhstan, Mongolian Altai (western Mongolia).	Q
Shan-Thai	Northern and southern Shan States (Burma), Vietnam, Thai-Malay Peninsula	N
Zhusilengharhan	Zhusilengharhan of western Inner Mongolia, northeastern Heilongjiang, eastern Inner Mongolia, and Far East.	Y
Central China	Southern Sichuan	U
South China	Northern Guangxi and southern Yunnan	V
Armorica	Spain, France, southeast Sardinia	H, I
North America	Nevada, Michigan, Appalachian, and Ontario. Oklahoma, NW Territory, Canada	C, E, F, B
South America	Argentina, Bolivia, Colombia, and Venezuela	Z (tentatively)
Baltica	Holy Cross Mts. (Poland)	J
Rhenish	Ardennes (Belgium), Eifel Mts., Rhineland, Harz Mts., Kellerwald Mts., Frankenwald area, Thuringia, Rhenish Mts., W. Sauerland, Attendorn, Gummersbach, Endorf, Dillenburg, Godddelsheim, Rothaargebirger, Wildungen, Ense-Grenzweg, Hohenlimberg, Herscheider Mts., Lahn Mts., Langenaubach, Hangenden, Cürten (Germany)	I
Turkey	Pontides	M
Bohemia	Barrandian, Prague Basin	I

TABLE *6*—Fifteen geographic regions based on phacopid localities. The rugose coral regions of Pedder and Oliver (1990) are referred to on the right column for comparison.

Northwest Territory, Canada (B) is considered to belong to Uralian-Siberian-Canadian subprovince, and Nevada (C) to Cordilleran. However, they were both located within the North American continent, and because the purpose of this work is more concerned towards continental configuration rather than determining biogeographic or environmental separation of species, they are assigned to North America together with the rest of North American localities.

The rugose coral region (I) is divided into Rhenish, Bohemia, and Armorica as Bohemia Massif was located within the Moldanubian zone and Rhenish Slate Mountains within the Rhenohercynian zone (Hüneke, 2006, Fig. 1). Armorica also includes Spain or Iberian Peninsula, following Cocks and Torsvik (2002). Goldring and Langenstrassen (1983) also differentiate Bohemia from the Rhenish region. They interpret the former being the open sea or basin and the latter as shelf environment.

Colombia-Venezuela has Appalachian faunal elements, and biogeographically they belong to Eastern North America (Boucot, 1971, 1988; Boucot and Gray, 1979, 1983; Boucot, Johnson, and Talent, 1969; Boucot, Isaacson, and Laubacher, 1980; Boucot and Blodgett, 2001). However, this region was included in South America together with Bolivia-Argentina because it did not form a separate terrane. Rather than relying on the differentiation of marine realms, or provinces, which can be influenced by oceanic currents and local environment, geographic assignment of these regions are based on tectonic units as the purpose of this study is to evaluate continental configuration for the Devonian. This problem with the usage of provinces was also discussed in Fortey and Cocks (2003: 280). Although Bolivia and northwestern Argentina belong to the Malvinokaffric Realm, they are thus geographically called “South America” (or Z) in this paper. The differentiation of the Colombia-Venezuela from Bolivia-Argentina needs a further evaluation in the future.

Kobayashi and Hamada (1977) recognized 10 trilobite subprovinces for the Lower and Middle Devonian (Kobayashi and Hamada, 1977: Table 8). In their scheme, there is no clear boundary between the subprovinces, and when superimposing the rugose coral regions A to Y of Pedder and Oliver (1990), many subprovinces, especially those in the Eurasian continent, will contain multiple regions (Table 7 below).

Trilobite subprovinces (Kobayashi and Hamada, 1977)	Rugose coral biogeographic regions (Pedder and Oliver, 1990)
Appohimchi	E, F
Rhenish-Bohemian	G, H, I, J, L, M
Uralian-Siberian-Canadian	A, B, K, P, R, S
Kazakhstan-Mongolian-Okhotsk	Q, T, Y
Oriental	N, O, U, V, W
Tasman-New Zealand	X
Cordilleran	C
South American	n/a
Colombian-Amazon	D
South African-Malvinian-West Antarctic	n/a

TABLE *7*—Comparison of the trilobite biogeographic regions of Kobayashi and Hamada (1977) and those of rugose corals of Pedder and Oliver (1990) for the Lower and Middle Devonian. There is no report of rugose coral occurrence in South American and South African-Malvinian-West Antarctic trilobite subprovinces.

The new assignment of regions proposed here is similar to the trilobite subprovinces, with an addition of North Africa, Armorica and Turkey. Cordillera and Colombian-Amazon subprovinces are incorporated into North America and South America, respectively. South African-Malvinian-West Antarctic subprovinces are omitted as there is no phacopid occurrence. Rhenish-Bohemian subprovince is divided into Rhenish and Bohemian regions.

Method. – In their analysis on the Devonian rugose corals, Pedder and Oliver (1990) used Otuska Coefficients to calculate faunal similarity index. Rong, Li, and Kul'kov (1995) examined 9 methods for the calculation of affinity indices and recommended four formulae, Jaccard, Otsuka, Dice, Correlation ratio, and Fager. Their equations are:

$C/(N1 + N2 - C)$ (Jaccard)

$C/(N1N2)^{1/2}$ (Otsuka)

$2C/(N1 + N2)$ (Dice)

$C^2/(N1N2)$ (Correlation ratio)

$C/(N1N2)^{1/2} - 1/[2(N2^{1/2})]$ (Fager)

where N1 is the total number of genera in the first region, N2 is the total number of genera in the second region (where the first region contains fewer genera, i.e. $N1<N2$), and C is the number of genera shared in both regions.

Holland and Bassett (2002) also used Otsuka Coefficients for their Lower Silurian coral fauna distribution, and this practice is followed here for the analysis of the Devonian phacopids. In addition, the Jaccard and Dice Indices are also calculated to evaluate the consistency of Otsuka Coefficients. The Jaccard emphasizes differences (Campbell and Valentine, 1977; Cheetham and Hazel, 1969) and Dice emphasizes the similarity (Cheetham and Hazel, 1969). The Simpson Coefficient also emphasizes similarity, but Raup and Crick (1979: 1225) report some anomalies associated with it and is excluded here.

RESULT

The Otsuka, Dice, and Jaccard Coefficients were calculated in the Microsoft Excel. The result is given in Table 8 for the Lower Devonian, Table 9 for the Middle Devonian. Comparison between the three methods is shown as line graphs in the Appendix 4. It shows the identical pattern between them, but the Jaccard Coefficients score lower than others. This is more evident when the coefficient values are contrasted.

An Otsuka Coefficient value of more than 30 indicates high similarity between the regions (Pedder and Oliver, 1990). In most regions compared, the values marked above this point in the Otsuka and Dice Coefficients. This may reflect the fact that most phacopid genera are cosmopolitan or quasi-cosmopolitan (Holland and Bassett, 2002), despite the high provinciality during the Lower Devonian. However, rather conservative estimate by the Jaccard Coefficients gives much lower scores. When coefficients for the Lower Devonian is compared to those of the Middle Devonian, it is apparent that the Middle Devonian experienced more cosmopolitanism.

Lower Devonian. – Despite the high provincialism in the Lower Devonian (Bailey, 1978; Boucot, 1971, 1988; Meyerhoff, *et al*., 1996; Wei-Hua, 1990) some phacopids such as *Paciphacops* occur globally, showing resistance against environmental variables (Chlupáč, 1977). In the following, summary of each region is given.

Siberia. Three regions score more than 30 in both Otsuka and Dice Coefficients: Kazakhstan, North America, and South America, but only one (North America: 33.33) in Jaccard.

Australia. All coefficients have 2 regions that score more than 30 (North America and Bohemia).

North Africa. A total of 7 regions score more than 30 in both Otsuka and Dice, and 3 regions in Jaccard (Rhenish: 50.00; Turkey: 37.50; Bohemia: 44.44).

Kazakhstan. Three regions (Siberia, North America and South America) have more than 30 in Otsuka and Dice, 2 in Jaccard (North America: 33.33 and South America: 66.67).

Shan-Thai. A total of 6 regions score more than 30 in Otsuka, 5 in Dice, and 2 (South China: 100 and Armorica: 100) in Jaccard.

Zhusilengharhan. Only South America scores more than 30 (31.62) in Otsuka. No region scores more than 30 in Dice and Jaccard.

Central China. No phacopid trilobites reported.

South China. North Africa, North America, Rhenish, and Turkey score more than 30 in Otsuka Coefficients. In Dice, all of them, except for North America score more than 30. All regions scored below 30 in Jaccard.

Armorica. Identical result as in South China.

North America. A total of 10 regions score more than 30 in Otsuka Coefficients, 8 in Dice, and 5 (Siberia: 33.33; Australia: 33.33; Kazakhstan: 33.33; South America: 40.00; Bohemia: 37.50) in Jaccard.

South America. Siberia, Kazakhstan, Zhusilengharhan, and North America score more than 30 in Otsuka Coefficients. Siberia, Kazakhstan, and North America in Dice, and only Kazakhstan and North America in Jaccard.

Baltica. No phacopid data collected.

Rhenish. In both Otsuka and Dice, 7 regions score more than 30, and 3 (North Africa: 50.00; Turkey: 33.33; Bohemia: 40.00) in Jaccard.

Turkey. In both Otsuka and Dice, 7 regions score more than 30, and 3 (North Africa: 37.50; Rhenish: 33.33; Bohemia: 42.86) in Jaccard.

Bohemia. In all Indices, 5 regions (Australia, North Africa, North America, Rhenish, and Turkey) score more than 30.

Middle Devonian. – Transgression at the end of the Emsian (Johnson, Klapper and Sandberg, 1985; Dargan, 2000) may have contributed to the cosmopolitanism in the Middle Devonian.

Siberia. Out of the 14 regions compared against, 10 regions scored coefficients of more than 30 in the Otsuka Indices, 9 in Dice Indices, and only2 (Kazakhstan: 50.00; North America: 40.00) in Jaccard.

Australia. In the Otsuka Coefficients, 10 regions score more than 30, 8 in Dice Indices, and 6 (Zhusilengharhan: 33.33; South China: 50.00; Armorica: 33.33; North America: 33.33; Baltic: 50.00; Turkey: 50.00) in Jaccard.

North Africa. Seven regions score more than 30 in the Otsuka Coefficients, 5 in Dice, and one (Rhenish: 33.33) in Jaccard.

Kazakhstan. Siberia, North America, and South America score more than 30 in both Otsuka and Dice, but in Jaccard, North America scored only 25.00.

Shan-Thai. Siberia, Zhusilengharhan, central China, and Rhenish regions have more than 30 in Otsuka and Dice; only central China in Jaccard (50.00).

Zhusilengharhan. A total of 9 regions score more than 30 in both Otsuka and Dice. Only Australia scores more than 30 in Jaccard.

Central China. Siberia (50.00), Shan-Thai (70.71), and Rhenish (30.15) in Otsuka Coefficients. Siberia (40.00) and Shan-Thai (66.67) in Dice and Shan-Thai (50.00) in Jaccard.

South China. More than 30 in 8 regions in Otsuka, 7 in Dice, and 3 (Australia: 50.00; Baltic: 33.33; Turkey: 33.33) in Jaccard.

Armorica. Both Otsuka and Dice have 9 regions that score more than 30. In Jaccard, only 3 (Australia: 33.33; Baltic: 66.67; Bohemia: 60.00).

North America. Both Otsuka and Dice have 10 regions that score more than 30, but only three in Jaccard (Siberia: 40.00; Australia: 33.33; South America: 33.33).

South America. Siberia, Kazakhstan, and North America score more than 30 in Otsuka and Dice. Kazakhstan (50.00) and North America (33.33) in Jaccard.

Baltica. In both Otsuka and Dice indices, 9 regions score more than 30. In Jaccard, 5 regions (Australia: 50.00; South China; 33.33; Armorica: 66.67; Turkey: 33.33; Bohemia: 40.00) have strong signal with Baltica.

Rhenish. In Otsuka Coefficients, 9 regions score more than 30, 5 in Dice (North Africa: 50.00; Shan-Thai: 30.77; Armorica: 42.86; Baltic: 30.77; Bohemia: 37.50), and one in Jaccard (North Africa: 33.33).

Turkey. In Otsuka Coefficients, 8 regions score more than 30. These regions, except for Bohemia, score more than 30 in Dice. In Jaccard, Australia (50.00), South China (33.33), and Baltic (33.33) have strong affiliation with Turkey.

Bohemia. A total of 7 regions score more than 30 in the Otsuka Coefficients, 5 (Australia: 33.33; North Africa: 42.86; Armorica: 75.00; Baltic: 57.14; Rhenish: 37.50) in Dice and 2 (Armorica: 60.00; Baltic: 40.00) in Jaccard.

DISCUSSION – FAUNAL SIMILARITIES

Pedder and Oliver (*1990*) *rugose coral distribution pattern*: *Lower Devonian*. – Based on the coefficients of the Lower Devonian rugose corals, possible paleocurrents are interpreted in a map (Fig. 25). Here, the probable three major paleocurrents are shown based on the faunal similarity index: one circulating in the Tethys, one going around Australia and Asian terranes, east of the Tethys, and one in the Panthalassa. Eastern North America and North Africa share common species, and bidirectional migration routes can be considered. The peripheral Tethyan Ocean regions have high similarity index (value more than 30) with each other (e.g., I: Armorica; O: Tien-Shan, and V: South China), and such a distribution signal could be explained by placing an ocean current in the Tethys.

The strong association of the Appalachian Belt (F) with North Africa (G) infers that these regions were close enough to permit species to swim across a body of water. There are only weak signals from Europe and this reflects increasing distances between Europe and these regions (Pedder and Oliver, 1990: 270).

Eastern Australia (X) is closely associated with Western Canada (B), Canadian Arctic Islands (A), and Nevada (C) of the eastern Panthalassa. It also has a strong association with Zhusilengharhan (Y) and Tien Shan (O) to its west. Because of its association with these regions, it is agreed that Eastern Australia was located on the western periphery of the Panthalassa and the east (southeast?) of Asian terranes.

Pedder and Oliver (*1990*) *rugose coral distribution pattern*: *Middle Devonian*. – North America (F) continues to have a strong association with North Africa (G). Weak signals from Armorica (I) and Siberia (K) are present. Its communication developed slightly with Baltica (J).

Kazakhstan (P) developed a strong affiliation with the Baltica (J) in the Eifelian. It continues to have strong relationships with Shan-Thai (O) and Siberia (K).

Eastern Australia (X) has no more connection with Kazakhstan (P). Its relationship with Shan-Thai (O) and North America (F) is still strong.

North Africa (G) no longer shares faunas with Shan-Thai (O), but develops a connection with the Baltica (J). It still has a relationship with Kazakhstan (P), Armorica (I), and North America (F).

Phacopid distribution pattern: *Lower Devonian*. – A close look at Table 8 indicates that:

1. Siberia possibly had the Arctic route for species to migrate, and was connected to South America (via Arctic route?).

2. Australia had two migration routes or current routes, one which connects to western North America or eastern Panthalassa, and the other connects to the Tethyan regions.
3. North Africa was on the western Tethyan periphery.
4. Kazakhstan follows the same pattern as Siberia.
5. Shan-Thai was on the eastern Tethys.
6. South China was also on the eastern Tethys.
7. Armorica was on the western Tethys.
8. North America had Arctic current route to connect to the western Tethyan regions such as Bohemia and North Africa, through Canada and Nevada.
9. Rhenish region was on the Tethys and had a weak connection with North America.
10. Turkey was on the western Tethys.
11. Bohemia was also on the western Tethys, but the stronger connection to southeastern Australia suggests it was more towards the eastern Tethys. However, signals from eastern Tethyan terranes are weak.

Figure 26 was constructed to show the Lower Devonian phacopid trilobite regions and possible paleocurrents based on the summary above. The distribution pattern of phacopids agrees with that of rugose corals for the Lower Devonian, and possible presence of both Tethyan and Antarctic circumpolar currents is supported by faunal similarity indices of phacopids. The closeness of southeastern Australia and South America is reported by Dalenz Farjat (2005) who interpreted the presence of a

Bolivian bivalve genus, *Notonucula*, in New Zealand and Antarctica was due to the circumpolar current route developed in the late Silurian which continued into the Lower and Middle Devonian within the southern Panthalassa ocean.

Phacopid distribution pattern: *Middle Devonian*. – Although many phacopid species appear to be rather pandemic in the Lower Devonian, which is often characterized by high provinciality, their distribution is even more widespread in the Middle Devonian. Widespread trend may be the result of transgression at the end of the Emsian reported by Johnson, Klapper, and Sandberg (1985) and Dargan (2000). Baltica and Siberia both opened communications with the rest of the regions in the Middle Devonian, and many regions share common taxa among themselves, except for Kazakhstan and South America.

Based on Table 9, the following is suggested:

1. Siberia had connections with eastern Tethyan or Asiatic regions, and also with North America, possibly by way of Arctic route. Its connection to South America and Australia is strong as well. Very weak signals from western Tethyan regions.
2. Australia develops a stronger affiliation with both western and eastern Tethyan regions.
3. North Africa has stronger signals from the neighboring western Tethyan regions, as well as eastern Tethys areas.
4. Kazakhstan remains unchanged from Lower Devonian, except for the loss of signal from Zhusilengharhan.
5. Shan-Thai connects with both western and eastern Tethys.

6. Zhusilengharhan has connections with both western and eastern Tethys.
7. Central China develops a connection with Siberia and Shan-Thai.
8. South China has more connections with eastern Tethys.
9. Armorica remains to be close to western Tethyan regions, but also develops a connection with eastern Tethys.
10. North America has influence from Siberia via Arctic route and from South America. It also has a connection with Bohemia.
11. South America keeps connection with Kazakhstan and North America.
12. Baltic develops a connection with Australia via western Tethyan regions.
13. Rhenish has a close affiliation with North Africa.
14. Turkey has both western and eastern Tethyan connections.
15. Bohemia still keeps good connection with western Tethys and weakly connected to eastern Tethys.

The lack of connection between Australia and South America, and the development of affiliation of the former with Bohemia concludes that Australia was more influenced by the Tethyan current. The connection of South America with North America and Kazakhstan could be explained by an Arctic route via Siberia into western North America. However, the position of Kazakhstan in Lower as well as Middle Devonian could not be peri-Tethyan as it lacks faunal similarity with the Tethyan regions (Fig. 27).

Rugose coral Lower Devonian and Middle Devonian. – In the Lower Devonian, Eastern Australia shows high faunal similarity index with Kazakhstan, western part of North America (Nevada and western Canada), and Shan-Thai. The similarity of some Lower Devonian tetracoral, rugose, brachiopod, bivalve, and trilobite species between northwestern Canada and southeastern Australia has been remarked and a migration from the latter was suggested by some authors (e.g. Bradshaw, 1998; Dalenz Farjat, 2005; Perry and Chatterton, 1976; Pedder and Oliver, 1990). The proximity of Eastern Australia with Shan-Thai is evident in many paleogeographic reconstructions (Johnson *et al*., 2004: Figs. 7 and 9; Li and Powell, 2002: Figs. 11 and 12; McCarthy *et al*., 2007; Metcalfe, 1999; Young, 1994: Fig. 12.2). Kazakhstan did not have any relationship with Europe in the Lower Devonian. Northeastern America had a communication with North Africa, but only weak signals are reported from Europe. This might indicate that North America was much closer to Gondwana as reported by Dalla Salda, Cingolani, and Varela (1992), Dalla Salda *et al*. (1992), Dalziel, Dalla Salda, and Gahagan (1994), and Dalziel and Dalla Salda (1996). In the Middle Devonian, Eastern Australia lost communication with Kazakhstan. North Africa loses connection with Shan-Thai, but continues to have a relationship with Kazakhstan, Armorica, and North America. The development of interrelatedness between North America and North Africa in the Middle Devonian was reported by Lieberman (1994) and his subsequent works on biogeography.

PACIPHACOPS DISTRIBUTION AND AREA CLADOGRAM

Paciphacops Maximova, 1972 occurs globally from the Upper Silurian into the Lower Devonian. Among phacopid trilobites, it is one of the groups less dependant on facies or environmental changes (Chlupáč, 1977). It was selected here for an area cladogram because of its wide distribution range from the Appalachians (Gaspé Peninsula, New York Pennsylvania, Virginia, and western Tennessee: Eldredge, 1973; Campbell, 1977) to the central North America (Oklahoma: Eldredge, 1973, and Campbell, 1977; Missouri: Tansey, 1922). It is also known from central Kazakhstan (northeast of Lake Balkhash: Maximova, 1968), central Nevada (Haas, 1969; Merriam, 1973), southeastern Australia (Wright and Haas, 1990; Ramsköld and Werdelin, 1991; Ebach, 2002), northwestern Argentina and Bolivia (Edgecombe and Ramsköld, 1994). Peculiarly, it does not occur in Europe. Chlupáč (1977) reports *Paciphacops* sp. I and *P*. sp. II from Bohemia and Moravia, respectively, however, they only superficially resemble *Paciphacops* (e.g. configuration of cephalic outline) and further examination will be necessary to determine their generic assignment.

Material. – Well-established *Paciphacops* species were chosen for the cladistic analysis (Appendix 3). Thirty-two characters of Ramsköld and Werdelin (1991) were used here because the same set of characters was coded for *Paciphacops waisfeldae* and *P*. *argentinus* by Edgecombe and Ramsköld (1994), and *P*. *crawfordae* by Ebach (2002). Two Kazakh species, *Angulophacops saryarkensis* and *Phacops logani balchashensis*, are treated here as *Paciphacops*, despite the ambiguity of their generic assignment (Ramsköld and Werdelin, 1991) and the fact that the latter was identified as *Angulophacops* by Kobayahsi and Hamada (1977). Four *Kainops* taxa are chosen for an outgroup: *K*. *microps*, *K*. *invius*, *K*. *veles*, and *K*. *raymondi*.

Method and Result. – The character matrix is given in Table 10. This set was then analyzed in NONA using Winclada ver. 1.00.08 (Nixon, 1999-2002). Characters were set non-additive (Fitch) and no weighting scheme was applied. Heuristic search for the shortest trees was conducted and two shortest trees were found. Next, Ratchet Island Hopper was used and a total of 7 trees were calculated. The trees from both methods have the tree length of 98, Consistency Index (=CI) of 56, retention index (=RI) of 59.

Out of 32 characters, 7 of them turned out to be uninformative. These are characters 2, 4, 7, 10, 14, 18, and 20. When these characters are deactivated, one tree with 95 steps (CI = 54, RI = 59) was computed in heuristic analysis.

Interpretation of species relationship. – After deactivating uninformative characters, a resolved tree was created by heuristic analysis (Fig. 28). *Kainops* species are placed within the basal clade. *Paciphacops logani balchashensis* is a sister taxon to *Angulophacops saryarkensis*, supporting Kobayashi and Hamada's (1977) identification of this species. *Phacops natlensis* from northwestern Canada may not belong to *Phacops*, but to *Paciphacops*. In the cladogram, it is placed as a sister to yet another species with questionable generic assignment, '*Paciphacops claviger*'. Taxonomic evaluation of these species may be necessary in the future.

These trees were then used for area cladogram by replacing the species names with their localities.

Interpretation of area relationship. – The area cladogram of *Paciphacops* was produced here (Fig. 29) using the cladogram above. The taxon names were replaced with their locality. Within North America, those belong to the Appalachian region is indicated by NA (E), NA (C) for central North America or Oklahoma, NA (W) to include Nevada and southwestern Canada.

According to the tree, eastern Australia and Argentina are closely related, and this is consistent with the distribution pattern of rugose corals (Pedder and Oliver, 1990), bivalves (Bradshaw, 1998; Dalenz Farjat, 2005) and phacopid trilobites (this study). These areas also are indicated to be closer to central Kazakhstan. The western part of North America is close to central and eastern North America. It is considered that the migration route existed in the north from Siberia into the Canadian Arctic region to reach into western Canada (or Northwest Territory, Canada) (Ormiston, 1972), and Nevada through Oklahoma into the Appalachian (Campbell, 1977). Central Bolivia is more related to eastern North America than geographically close Argentina, which is in contrast to the cladistic analysis of *Paciphacops* by Edgecombe and Ramsköld (1994) and Ebach (2002). However, the appearance of the Appalachian species into Bolivia is reported in many literature (e.g. Boucot, 1971, 1988; Boucot and Gray, 1979, 1983; Boucot, Johnson, and Talent, 1969; Boucot, Isaacson, and Laubacher, 1980; Isaacson, 1977; Eldredge and Ormiston, 1979; Laubacher, Boucot, and Gray, 1982; Wolfart, 1968) makes the interpretation difficult.

Position of Kazakhstan. – The relationship of Kazakhstan with the Appalachian, Bolivia, and southeastern Australia is problematic. Although the Appalachian and Bolivia might have been close geographically (e.g. Bahlburg, 1993; Dalziel, Dalla Salda, and Gahagan, 1994) and the connection between Australia and Bolivia could be explained by a circumpolar current route (Dalenz Farjat, 2005), the paleogeographic position of Kazakhstan is not clear, especially longitudinally (see Boucot and Blodgett, 2001; Cocks and Torsvik 2002; Ormiston, 1972; Scotese and

McKerrow, 1990). It is often positioned on the northern periphery of the Tethyan ocean, away from other terranes (see Fig. 24).

According to Chlupáč (1975: 402) and Campbell (1977: 5-9), the similarity of Kazakhstan and North America may have resulted from migration of Kazakhstan species into the Appalachian via Nevada and Oklahoma. The rugose coral evidence by Pedder and Murphy (2004) supports the idea that the migration route was unidirectional, from Kazakhstan to Nevada, then into the Appalachians. Ormiston (1972) suggests a possible seaway in northeast China (North China terrane) connecting Kazakhstan and North America. Maximova (1972) also implies that Kazakhstan belonged to the Pacific paleobiogeographic region. Kobayashi and Hamada (1977) reached the same conclusion.

From the phacopid faunal similarity analysis and *Paciphacops* area cladogram, two hypotheses can be proposed (see Fig. 30). One is to place Kazakhstan as a northern extension of eastern North America and group it together with Siberia and Canadian Arctic. Gourvennec (2000) proposes a counterclockwise migration route of the Upper Silurian spiriferid brachiopods from South China via Kazakhstan into Europe and North America within a tropical belt. The absence of *Paciphacops* in Europe may be explained by unfavorable environmental condition rather than biogeographic separation (McKerrow *et al*., 2000) or competition among phacopids for the available niches (Cox, 1968).

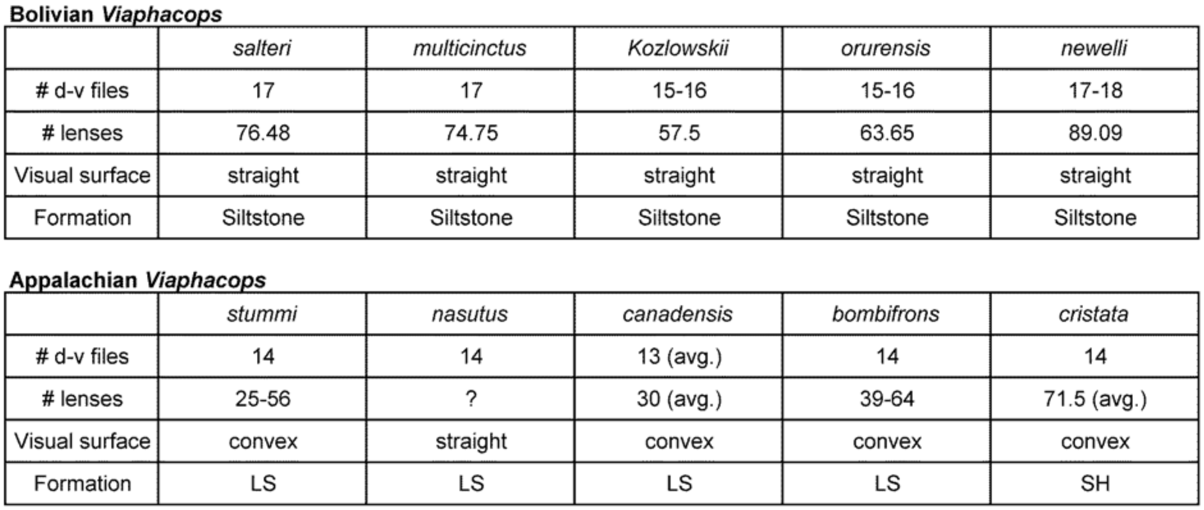
Another hypothesis is to place Kazakhstan towards the Panthalassa (Iwasaki, 2006, 2007; Ruban, Al-Husseini, and Iwasaki, 2007). Şengör, Natal'in, and Burtman (1993) and Şengör and Natal'in (1996) interpret Kazakhstan as a series of island arcs called Kipchak arc, which originated somewhere east of Tethys, and eventually moved closer to the Siberian terrane. This is supposed to be in the middle of the Tethys, but is much closer to some Asian terranes. Some authors made a connection between Kazakhstan and North America by way of Asia on the Panthalassa side (Ormiston, 1972; Maximova, 1972; Kobayahsi and Hamada, 1975, 1977), supporting the second hypothesis. Torsvik and Cocks (2004) acknowledge the significant role the Panthalassic Ocean maintained for the distribution of marine fauna, vertebrates or otherwise, throughout the Paleozoic, a point that has not been stressed enough. According to Pedder and Oliver (1990: 267), long-living teleplanic larvae can theoretically travel a distance double the size of the present-day Atlantic Ocean. The family Phacopida is thought to have had Life-History Strategy II, in which the species spawn as pelagic, then settle on the substrate as benthic larvae and become adult (Chatterton and Speyer, 1997; Crônier, 2007). This means that the distribution of the eggs might have depended on the ocean currents. Lerosey-Aubril and Feist (2005) speculate that an Upper Devonian phacopid species had a developmental strategy to have an extended planktonic period so that it would migrate farther. It is plausible, therefore, that Kazakhstan was located on or closer to Panthalassa for its species to disperse across this vast ocean, probably with some isolated terranes or islands within it (Talent *et al*., 2000: 207). Yet, another view suggests to place Kazakhstan or Kazakhstania together with Laurussia or with some other landmasses into a larger continent (Zharkov, 1988: 424).

CONCLUSION

The existing reconstructions of the Devonian paleogeography, or Paleozoic paleogeography in general, are Tethys-centric and need to be rigorously reviewed. Especially, the position of Kazakhstan is debatable, and the role of Panthalassa for species migration cannot be dismissed. McCarthy *et al*. (2007) offers an alternative view of Gondwana, linking Australia-New Zealand to South America, unlike the conventional maps that separate the two into East and West Gondwana, respectively. Taira (2001: Fig. 13) also offers an alternative view of the world, which places the Pacific as its center. He suggests the evolution of the Pacific rims encompassing Australia, Antarctica, South America, North America, and Asian terranes that include Siberia. Bradshaw (1998) and Hunter and Lomas (2003: Fig. 1) place the map with South Pole as a center, showing how Gondwana as a continent was assembled. It is clear here that eastern Australia is connected to South America, and although the distance is quite far, a current could have run along the coast of eastern Australia-South America, enabling species to migrate.

TABLES AND FIGURES

TABLE *1*—Species-level comparison of *Viaphacops* eye characters and lithology type between Bolivia and the Appalachian. Data for the Bolivian *Viaphacops* excludes *V*. cf. *orurensis* and *V*. cf. *chavelai*. For the Appalachian *Viaphacops*, data were taken from Eldredge (1973). *V*. *stummi* occurs in the Jeffersonville LS, Columbus LS, Bois Blanc and Amherstburg LSs; *V*. *nasutus* in the Jeffersonville LS; *V*. *canadensis* in the "Onondaga" LS; *V*. *bombifrons* in the Onondaga LS and Columbus LS; *V*. *cristata* in the Schoharie Grit/SH; *V*. *variabilis* in the Ragland and Needmore SHs; and *V*. *gaspensis* in the Gaspe LS. *Viaphacops* sp., which occurs in the Frisco Fm., Oklahoma, was excluded from this table.



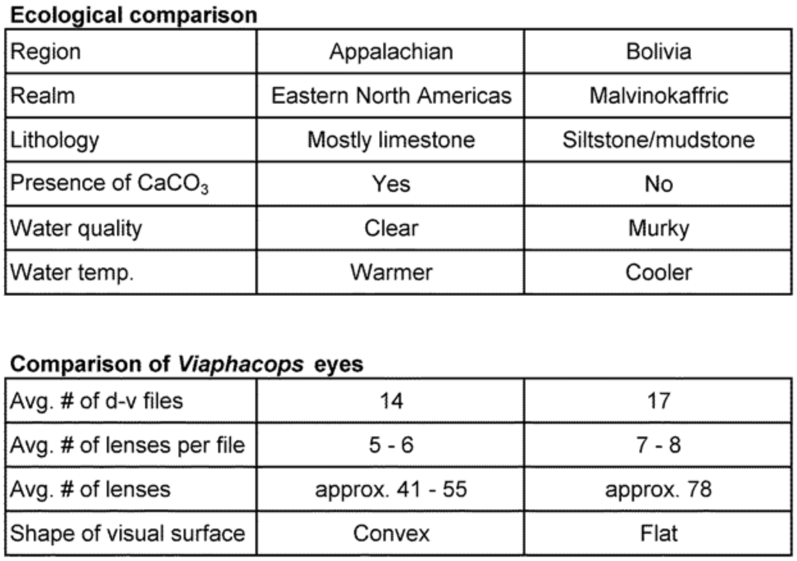
Bolivian *Viaphacops*

	salteri	*multicinctus*	*Kozlowskii*	*orurensis*	*newelli*
# d-v files	17	17	15-16	15-16	17-18
# lenses	76.48	74.75	57.5	63.65	89.09
Visual surface	straight	straight	straight	straight	straight
Formation	Siltstone	Siltstone	Siltstone	Siltstone	Siltstone

Appalachian *Viaphacops*

	stummi	*nasutus*	*canadensis*	*bombifrons*	*cristata*
# d-v files	14	14	13 (avg.)	14	14
# lenses	25-56	?	30 (avg.)	39-64	71.5 (avg.)
Visual surface	convex	straight	convex	convex	convex
Formation	LS	LS	LS	LS	SH

TABLE *2*—Summary of comparison of ecology between the Appalachian and Bolivia, and *Viaphacops* eyes in these areas. The top table is a comparison of ecological condition between the Appalachian and Bolivian regions as evidenced primarily by lithology and presence/absence of $CaCo_3$. The bottom table shows a comparison of eyes between *Viaphacops* of these regions. The Appalachian species, which mostly occurs in a limy deposition, has lesser number of lenses and visual surface tends to be globus.



Ecological comparison

Region	Appalachian	Bolivia
Realm	Eastern North Americas	Malvinokaffric
Lithology	Mostly limestone	Siltstone/mudstone
Presence of $CaCO_3$	Yes	No
Water quality	Clear	Murky
Water temp.	Warmer	Cooler

Comparison of *Viaphacops* eyes

Avg. # of d-v files	14	17
Avg. # of lenses per file	5 - 6	7 - 8
Avg. # of lenses	approx. 41 - 55	approx. 78
Shape of visual surface	Convex	Flat

TABLE *3*—Comparison of eye characters between *Eldredgeops* species (*Phacops rana* group) occurring in different lithology. Both species have 18 dorsoventral files, but *E. crassituberculata*, which occurs mostly in limestone, possesses lesser number of lenses per file than *E. milleri*, which occurs predominantly in shaly deposit. Data taken from Eldredge (1972).

Eldredgeops crassituberculata	***Eldredgeops milleri***
Majority of specimens are found in limestone	Majority of specimens are found in shale
18 dorsoventral files	18 dorsoventral files
6 lenses maximum per file	8 - 9 lenses maximum per file
Predominantly in limestone	Predominantly in shale

TABLE *4*—Character matrix of the *Viaphacops* used in cladistic analysis. A total of 37 characters were coded for 17 ingroup taxa (9 Bolivian taxa; 8 North American taxa) and 2 outgroup taxa (*Paciphacops waisfeldae* from central Bolivia and *P. logani* from New York).

Taxon	**Characters**																		
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Paciphacops waisfeldae Edgecombe & Ramskold, 1994	0	0	0	0	2	0	0	0	1	0	0	0	1	0	2	3	2	2	1
Paciphacops logani (Hall, 1859)	1	1	0	2	1	0	1	2	2	1	0	0	2	1	1	4	2	3	2
Viaphacops cf. *chavelai* (Baldis and Longobucco, 1977)	1	0	0	0	1	2	2	1	1	?	0	2	0	1	2	3	2	2	2
Viaphacops newelli n.sp.	1	0	0	0	2	2	2	1	1	0	0	0	2	2	2	1	2	0	0
Viaphacops pirovanoi n. sp.	0	0	0	0	2	2	2	0	0	0	1	0	2	1	1	3	1	1	2
Viaphacops spinoedgecombei n. sp.	1	1	2	0	1	2	2	2	2	1	0	1	3	1	1	4	2	2	2
Viaphacops kozlowskii Pek and Vanek, 1991	2	1	2	1	0	1	1	0	0	1	0	2	0	2	1	1	1	2	2
Viaphacops multicinctus Pek and Vanek, 1991	1	1	?	0	2	1	1	2	2	0	0	1	2	1	2	3	2	2	2
Viaphacops salteri (Kozlowski, 1923)	2	1	2	0	1	2	2	1	1	0	0	1	1	1	2	1	3	2	1
Viaphacops orurensis (Bonarelli, 1921)	0	1	1	0	1	1	1	1	1	2	1	2	1	1	1	2	2	2	2
Viaphacops cf. *orurensis* (Bonarelli, 1921)	0	1	1	0	1	1	2	2	2	?	1	?	?	1	2	3	1	?	2
Viaphacops cristata (Hall, 1861)	0	1	2	2	0	2	2	2	2	1	1	2	1	2	0	0	0	3	2
Viaphacops bombifrons (Hall, 1861)	1	1	1	2	0	2	2	1	1	?	1	2	1	1	2	3	1	3	1
Viaphacops stummi (Eldredge, 1973)	2	1	2	2	?	2	2	0	1	2	1	0	2	0	2	3	1	3	2
Viaphacops nasutus (Stumm, 1954)	2	1	2	2	?	2	2	1	1	2	0	?	?	?	2	2	2	?	2
Viaphacops canadensis (Stumm, 1954)	0	1	2	0	1	2	2	2	2	2	0	1	0	1	2	2	2	?	1
Viaphacops variabilis (Eldredge, 1973)	1	1	0	2	?	1	2	2	2	2	1	0	0	1	2	2	1	?	?
Viaphacops gaspensis (Clarke, 1908)	0	0	0	0	?	2	2	2	2	2	0	?	?	1	2	2	2	?	0
Viaphacops sp. (Campbell, 1977)	0	1	0	2	0	1	2	0	0	0	1	2	0	2	1	3	1	0	2

	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Paciphacops waisfeldae Edgecombe & Ramskold, 1994	0	2	0	1	0	0	0	0	0	2	0	1	2	1	3	0	1	1
Paciphacops logani (Hall, 1859)	?	?	0	1	1	0	1	1	0	2	0	1	1	0	3	0	0	1
Viaphacops cf. *chavelai* (Baldis and Longobucco, 1977)	?	0	0	4	0	0	0	0	1	1	0	0	1	1	1	0	0	1
Viaphacops newelli n.sp.	?	0	2	5	1	0	1	0	1	0	0	0	0	0	0	0	2	0
Viaphacops pirovanoi n. sp.	1	2	0	3	0	0	0	2	2	2	1	1	2	1	3	0	2	1
Viaphacops spinoedgecombei n. sp.	1	?	0	0	0	0	1	1	0	2	1	1	1	1	2	0	2	2
Viaphacops kozlowskii Pek and Vanek, 1991	?	1	1	2	1	0	1	2	1	2	0	1	2	1	2	0	1	1
Viaphacops multicinctus Pek and Vanek, 1991	3	1	1	2	0	0	2	2	0	2	0	1	2	1	2	0	1	2
Viaphacops salteri (Kozlowski, 1923)	3	1	0	2	1	0	3	0	3	2	0	1	2	1	3	0	2	0
Viaphacops orurensis (Bonarelli, 1921)	?	?	?	?	1	0	1	?	?	2	0	1	2	1	3	0	2	2
Viaphacops cf. *orurensis* (Bonarelli, 1921)	2	1	1	?	0	1	1	0	2	?	?	?	2	?	3	?	1	0
Viaphacops cristata (Hall, 1861)	1	0	1	?	1	0	1	0	0	2	1	1	2	1	2	1	1	0
Viaphacops bombifrons (Hall, 1861)	1	1	0	?	1	2	1	0	2	1	?	0	2	1	3	1	0	1
Viaphacops stummi (Eldredge, 1973)	?	0	1	?	0	1	1	?	?	?	?	?	?	?	?	?	?	?
Viaphacops nasutus (Stumm, 1954)	?	?	?	?	1	2	2	?	0	?	?	0	2	1	3	1	0	1
Viaphacops canadensis (Stumm, 1954)	?	?	?	?	0	1	0	0	3	0	1	1	2	1	3	1	1	0
Viaphacops variabilis (Eldredge, 1973)	?	?	?	?	0	2	1	1	0	?	1	1	2	?	3	?	?	?
Viaphacops gaspensis (Clarke, 1908)	0	1	0	?	1	0	0	0	1	0	0	0	2	1	3	1	1	1
Viaphacops sp. (Campbell, 1977)	?	0	0	?	0	1	1	1	0	2	1	1	2	1	2	1	?	1

TABLE *5*—Stratigraphic range of most of the phacopid genera used in the analysis. For a complete list of phacopid genera and species used in the study, refer to Appendices 2 and 3.

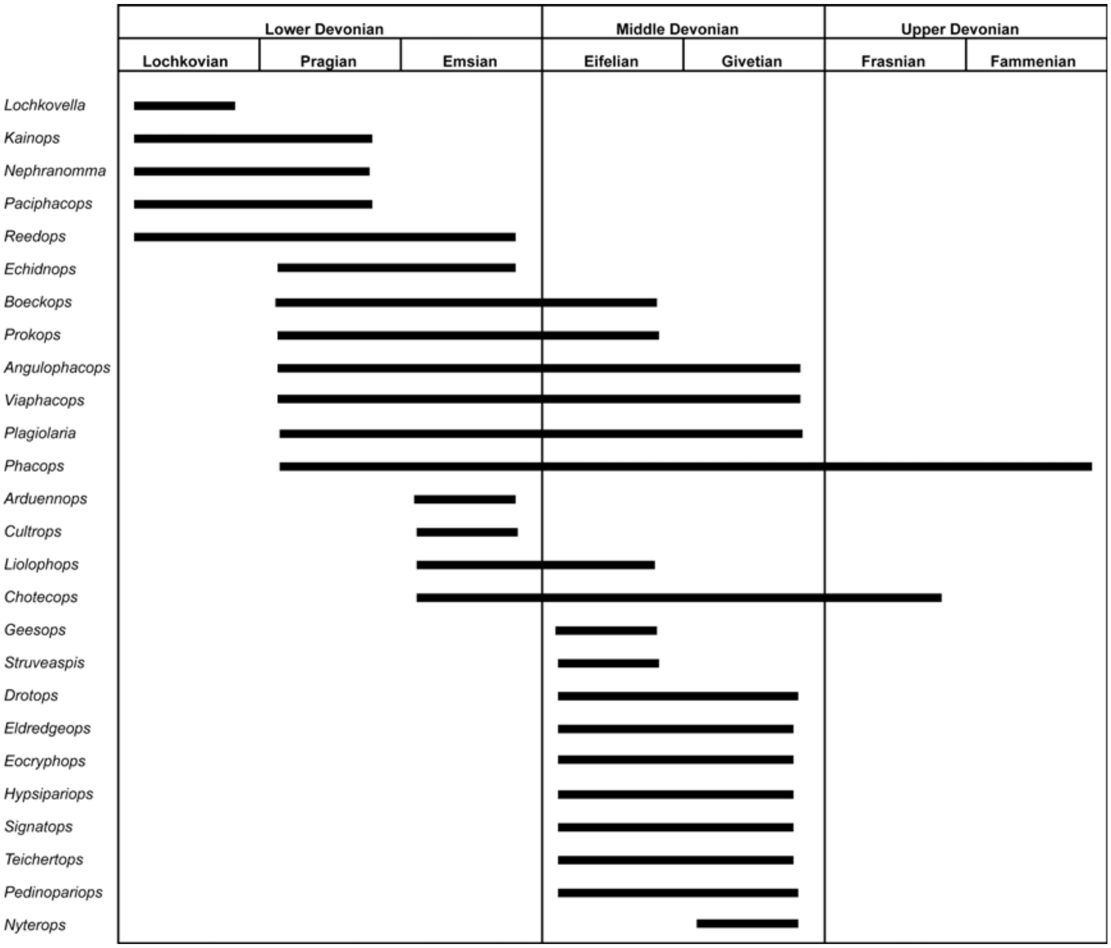

Lower Devonian
Middle Devonian
Upper Devonian
Lochkovian
Pragian
Emsian
Eifelian
Givetian
Frasnian
Fammenian
Lochkovella
Kainops
Nephranomma
Paciphacops
Reedops
Echidnops
Boeckops
Prokops
Angulophacops
Viaphacops
Plagiolaria
Phacops
Arduennops
Cultrops
Liolophops
Chotecops
Geesops
Struveaspis
Drotops
Eldredgeops
Eocryphops
Hypsipariops
Signatops
Teichertops
Pedinopariops
Nyterops

TABLE *8*—Faunal similarity coefficients for the Lower Devonian phacopid regions. The Otsuka (O), Dice (D), and Jaccard (J) coefficients were calculated to compare their results. The index at 30 and above indicates a significant correlation.

Lower Devonian	Siberia			Australia			N. Africa			Kazakhstan			Shan-Thai			Zhusileng			C. China			S. China		
	O	D	J	O	D	J	O	D	J	O	D	J	O	D	J	O	D	J	O	D	J	O	D	J
Siberia	-	-	-	21.82	20.00	11.11	21.82	20.00	11.11	33.33	33.33	20.00	0.00	0.00	0.00	0.00	0.00	0.00	-	0.00	0.00	0.00	0.00	0.00
Australia	21.82	20.00	11.11	-	-	-	28.57	28.57	16.67	21.82	20.00	11.11	26.73	22.22	12.50	0.00	0.00	0.00	-	0.00	0.00	26.73	22.22	12.50
N. Africa	21.82	20.00	11.11	28.57	28.57	16.67	-	-	-	0.00	0.00	0.00	53.45	44.44	28.57	16.90	16.67	9.09	-	0.00	0.00	53.45	44.44	28.57
Kazakhstan	33.33	33.33	20.00	21.82	20.00	11.11	0.00	0.00	0.00	-	-	-	0.00	0.00	0.00	25.82	25.00	14.29	-	0.00	0.00	0.00	0.00	0.00
Shan-Thai	0.00	0.00	0.00	26.73	22.22	12.50	53.45	44.44	28.57	0.00	0.00	0.00	-	-	-	0.00	0.00	0.00	-	0.00	0.00	100	100	100
Zhusileng	0.00	0.00	0.00	0.00	0.00	0.00	16.90	16.67	9.09	25.82	25.00	14.29	0.00	0.00	0.00	-	-	-	-	0.00	0.00	0.00	0.00	0.00
C. China	-	0.00	0.00	-	0.00	0.00	-	0.00	0.00	-	0.00	0.00	-	0.00	0.00	-	0.00	0.00	-	-	-	-	0.00	0.00
S. China	0.00	0.00	0.00	26.73	22.22	12.50	53.45	44.44	28.57	0.00	0.00	0.00	100	100	100	0.00	0.00	0.00	-	0.00	0.00	-	-	-
Armorica	0.00	0.00	0.00	26.73	22.22	12.50	53.45	44.44	28.57	0.00	0.00	0.00	100	100	100	0.00	0.00	0.00	-	0.00	0.00	100	100	100
N. America	51.64	50.00	33.33	50.71	50.00	33.33	33.81	33.33	20.00	51.64	50.00	33.33	31.62	28.57	16.67	20.00	20.00	11.11	-	0.00	0.00	31.62	28.57	16.67
S. America	40.82	40.00	25.00	26.73	22.22	12.50	0.00	0.00	0.00	81.65	80.00	66.67	0.00	0.00	0.00	31.62	28.57	16.67	-	0.00	0.00	0.00	0.00	0.00
Baltic	-	0.00	0.00	-	0.00	0.00	-	0.00	0.00	-	0.00	0.00	-	0.00	0.00	-	0.00	0.00	-	-	-	-	0.00	0.00
Rhenish	20.41	18.18	10.00	26.73	26.67	15.38	66.82	66.67	50.00	0.00	0.00	0.00	50.00	40.00	25.00	15.81	15.38	8.33	-	0.00	0.00	50.00	40.00	25.00
Turkey	28.87	28.57	16.67	18.90	18.18	10.00	56.69	54.55	37.50	0.00	0.00	0.00	35.36	33.33	20.00	22.36	22.22	12.50	-	0.00	0.00	35.36	33.33	20.00
Bohemia	23.57	22.22	12.50	61.72	61.54	44.44	61.72	61.54	44.44	0.00	0.00	0.00	28.87	25.00	14.29	18.26	18.18	10.00	-	0.00	0.00	28.87	25.00	14.29

Lower Devonian	Armorica			N. America			S. America			Baltic			Rhenish			Turkey			Bohemia		
	O	D	J	O	D	J	O	D	J	O	D	J	O	D	J	O	D	J	O	D	J
Siberia	0.00	0.00	0.00	51.64	50.00	33.33	40.82	40.00	25.00	-	0.00	0.00	20.41	18.18	10.00	28.87	28.57	16.67	23.57	22.22	12.50
Australia	26.73	22.22	12.50	50.71	50.00	33.33	26.73	22.22	12.50	-	0.00	0.00	26.73	26.67	15.38	18.90	18.18	10.00	61.72	61.54	44.44
N. Africa	53.45	44.44	28.57	33.81	33.33	20.00	0.00	0.00	0.00	-	0.00	0.00	66.82	66.67	50.00	56.69	54.55	37.50	61.72	61.54	44.44
Kazakhstan	0.00	0.00	0.00	51.64	50.00	33.33	81.65	80.00	66.67	-	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Shan-Thai	100	100	100	31.62	28.57	16.67	0.00	0.00	0.00	-	0.00	0.00	50.00	40.00	25.00	35.36	33.33	20.00	28.87	25.00	14.29
Zhusileng	0.00	0.00	0.00	20.00	20.00	11.11	31.62	28.57	16.67	-	0.00	0.00	15.81	15.38	8.33	22.36	22.22	12.50	18.26	18.18	10.00
C. China	-	0.00	0.00	-	0.00	0.00	-	0.00	0.00	-	-	-	-	0.00	0.00	-	0.00	0.00	-	0.00	0.00
S. China	100	100	100	21.62	28.57	16.67	0.00	0.00	0.00	-	0.00	0.00	50.00	40.00	25.00	35.36	33.33	20.00	28.87	25.00	14.29
Armorica	-	-	-	31.62	28.57	16.67	0.00	0.00	0.00	-	0.00	0.00	50.00	40.00	25.00	35.36	33.33	20.00	28.87	25.00	14.29
N. America	31.62	28.57	16.67	-	-	-	63.25	57.14	40.00	-	0.00	0.00	31.62	30.77	18.18	44.72	44.44	28.57	54.77	54.55	37.50
S. America	0.00	0.00	0.00	63.25	57.14	40.00	-	-	-	-	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Baltic	-	0.00	0.00	-	0.00	0.00	-	0.00	0.00	-	-	-	-	0.00	0.00	-	0.00	0.00	-	0.00	0.00
Rhenish	50.00	40.00	25.00	31.62	30.77	18.18	0.00	0.00	0.00	-	0.00	0.00	-	-	-	53.03	50.00	33.33	57.74	57.14	40.00
Turkey	35.36	33.33	20.00	44.82	44.44	28.57	0.00	0.00	0.00	-	0.00	0.00	53.03	50.00	33.33	-	-	-	61.24	60.00	42.86
Bohemia	28.87	25.00	14.29	54.77	54.55	37.50	0.00	0.00	0.00	-	0.00	0.00	57.74	57.14	40.00	61.24	60.00	42.86	-	-	-

TABLE *9*—Faunal similarity coefficients for the Middle Devonian phacopid regions. The Otsuka (O), Dice (D), and Jaccard (J) coefficients were calculated to compare their results. The index at 30 and above indicates a significant correlation.

Middle	Siberia			Australia			N. Africa			Kazakhstan			Shan-Thai			Zhusileng			C. China			S. China		
Devonian	O	D	J	O	D	J	O	D	J	O	D	J	O	D	J	O	D	J	O	D	J	O	D	J
Siberia	-	-	-	50.00	40.00	25.00	16.67	15.38	8.33	70.71	66.67	50.00	35.36	33.33	20.00	28.87	28.57	16.67	50.00	40.00	25.00	35.36	33.33	20.00
Australia	50.00	40.00	25.00	-	-	-	33.33	20.00	11.11	0.00	0.00	0.00	0.00	0.00	0.00	57.74	50.00	33.33	0.00	0.00	0.00	70.71	66.67	50.00
N. Africa	16.67	15.38	8.33	33.33	20.00	11.11	-	-	-	0.00	0.00	0.00	23.57	18.18	10.00	38.49	33.33	20.00	0.00	0.00	0.00	23.57	18.18	10.00
Kazakhstan	70.71	66.67	50.00	0.00	0.00	0.00	0.00	0.00	0.00	-	-	-	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Shan-Thai	35.36	33.33	20.00	0.00	0.00	0.00	38.57	18.18	10.00	0.00	0.00	0.00	-	-	-	40.82	40.00	25.00	70.71	66.67	50.00	0.00	0.00	0.00
Zhusileng	28.87	28.57	16.67	57.74	50.00	33.33	38.49	33.33	20.00	0.00	0.00	0.00	40.82	40.00	25.00	-	-	-	0.00	0.00	0.00	40.82	40.00	25.00
C. China	50.00	40.00	25.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	70.71	66.67	50.00	0.00	0.00	0.00	-	-	-	0.00	0.00	0.00
S. China	35.36	33.33	20.00	70.71	66.67	50.00	23.57	18.18	10.00	0.00	0.00	0.00	0.00	0.00	0.00	40.82	40.00	25.00	0.00	0.00	0.00	-	-	-
Armorica	28.87	28.57	16.67	57.74	50.00	33.33	38.49	33.33	20.00	0.00	0.00	0.00	0.00	0.00	0.00	33.33	33.33	20.00	0.00	0.00	0.00	40.82	40.00	25.00
N. America	57.74	57.14	40.00	57.74	50.00	33.33	38.49	33.33	20.00	40.82	40.00	25.00	0.00	0.00	0.00	33.33	33.33	20.00	0.00	0.00	0.00	40.82	40.00	25.00
S. America	50.00	40.00	25.00	0.00	0.00	0.00	0.00	0.00	0.00	70.71	66.67	50.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Baltic	35.36	33.33	20.00	70.71	66.67	50.00	23.57	18.18	10.00	0.00	0.00	0.00	0.00	0.00	0.00	40.82	40.00	25.00	0.00	0.00	0.00	50.00	50.00	33.33
Rhenish	30.15	26.67	15.38	30.15	16.67	9.09	50.25	50.00	33.33	0.00	0.00	0.00	42.64	30.77	18.18	34.82	28.57	16.67	30.15	16.67	9.09	21.23	15.38	8.33
Turkey	35.36	33.33	20.00	70.71	66.67	50.00	23.57	18.18	10.00	0.00	0.00	0.00	0.00	0.00	0.00	40.82	40.00	25.00	0.00	0.00	0.00	50.00	50.00	33.33
Bohemia	22.36	22.22	12.50	44.72	33.33	20.00	44.72	42.86	27.27	0.00	0.00	0.00	0.00	0.00	0.00	25.82	25.00	14.29	0.00	0.00	0.00	37.62	28.57	16.67

Middle	Armorica			N. America			S. America			Baltic			Rhenish			Turkey			Bohemia		
Devonian	O	D	J	O	D	J	O	D	J	O	D	J	O	D	J	O	D	J	O	D	J
Siberia	28.87	28.57	16.67	57.74	57.14	40.00	50.00	40.00	25.00	35.36	33.33	20.00	30.15	26.67	15.38	35.36	33.33	20.00	22.36	22.22	12.50
Australia	57.74	50.00	33.33	57.74	50.00	33.33	0.00	0.00	0.00	70.71	66.67	50.00	30.15	16.67	9.09	70.71	66.67	50.00	44.72	33.33	20.00
N. Africa	38.49	33.33	20.00	38.49	33.33	20.00	0.00	0.00	0.00	23.57	18.18	10.00	50.25	50.00	33.33	23.57	18.18	10.00	44.72	42.86	27.27
Kazakhstan	0.00	0.00	0.00	40.82	40.00	25.00	70.71	66.67	50.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Shan-Thai	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	42.64	30.77	18.18	0.00	0.00	0.00	0.00	0.00	0.00
Zhusileng	33.33	33.33	20.00	33.33	33.33	20.00	0.00	0.00	0.00	40.82	40.00	25.00	34.82	28.57	16.67	40.82	40.00	25.00	25.82	25.00	14.29
C. China	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	30.15	16.67	9.09	0.00	0.00	0.00	0.00	0.00	0.00
S. China	40.82	40.00	25.00	40.82	40.00	25.00	0.00	0.00	0.00	50.00	50.00	33.33	21.23	15.38	8.33	50.00	50.00	33.33	31.62	28.57	16.67
Armorica	-	-	-	33.33	33.33	20.00	0.00	0.00	0.00	81.56	80.00	66.67	52.22	42.86	27.27	40.82	40.00	25.00	77.46	75.00	60.00
N. America	33.33	33.33	20.00	-	-	-	57.74	50.00	33.33	40.82	40.00	25.00	17.41	14.29	7.69	40.82	40.00	25.00	25.82	25.00	14.29
S. America	0.00	0.00	0.00	57.54	50.00	33.33	-	-	-	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Baltic	81.65	80.00	66.67	40.82	40.00	25.00	0.00	0.00	0.00	-	-	-	42.64	30.77	18.18	50.00	50.00	33.33	63.25	57.14	40.00
Rhenish	52.22	42.86	27.27	17.41	14.29	7.69	0.00	0.00	0.00	42.64	30.77	18.18	-	-	-	21.32	15.38	8.33	40.45	37.50	23.08
Turkey	40.82	40.00	25.00	40.82	40.00	25.00	0.00	0.00	0.00	50.00	50.00	33.33	21.32	15.38	8.33	-	-	-	31.62	28.57	16.67
Bohemia	77.46	75.00	60.00	25.82	25.00	14.29	0.00	0.00	0.00	63.25	57.14	40.00	40.45	37.50	23.08	31.62	28.57	16.67	-	-	-

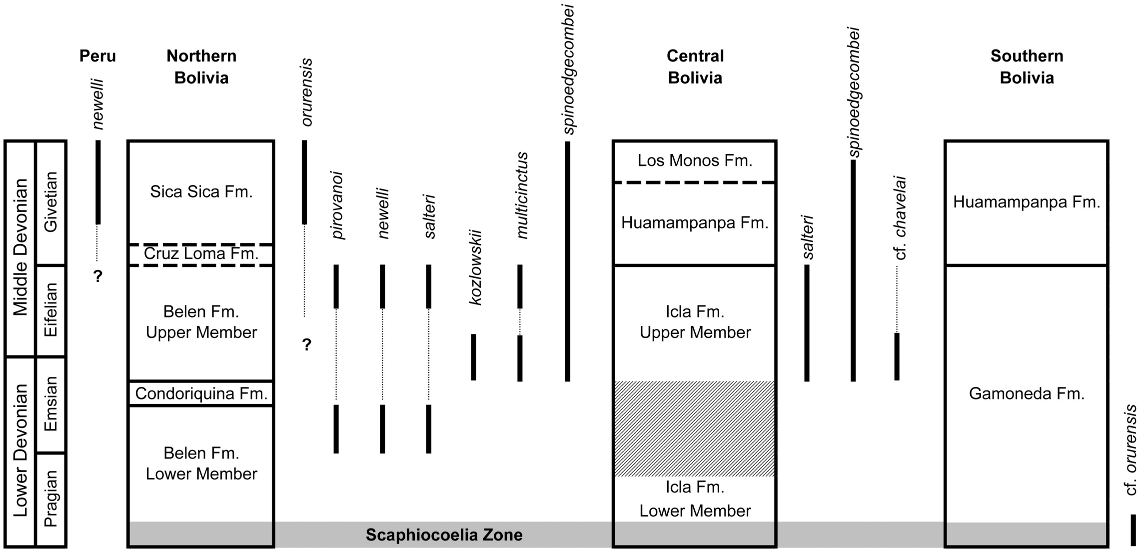
TABLE *10*—Character matrix of *Paciphacops*. Characters of Ramsköld and Werdelin (1991) were used.

species	Characters						
Kainops microps	3 0 3 1 2	0 1 3 1 0	2 2 2 2 2	3 1 1 ? 1	2 ? 1 2 1	1 2 0 1 2	2 2
Kainops veles	3 0 3 1 2	0 1 3 1 0	2 2 2 2 2	3 1 1 ? 2	2 ? 1 2 1	2 2 1 1 2	2 2
Kainops invius	3 0 3 1 2	4 1 3 1 1	1 2 2 2 2	3 1 ? 1 ?	2 ? 1 2 1	1 2 2 2 2	2 2
Kainops raymondi	2 0 2 1 1	3 1 3 1 0	1 2 2 2 2	3 1 1 ? 1	1 0 1 3 1	3 2 2 2 2	2 2
Paciphacops serratus	3 0 2 1 2	5 ? 3 2 ?	2 2 2 2 2	2 ? ? ? ?	2 ? ? 3 1	2 2 2 1 2	3 3
Paciphacops crosslei	3 0 2 1 1	5 1 4 ? 0	1 2 2 2 2	3 ? 1 ? ?	2 2 ? 3 1	2 2 ? ? 2	? 3
Paciphacops latigenalis	? ? 4 1 2	5 1 5 1 0	2 2 2 2 2	3 ? 1 2 ?	2 2 3 3 1	? 2 2 1 2	3 3
Paciphacops eldredgei	3 0 4 1 2	4 1 4 0 0	1 2 1 2 1	3 1 1 ? ?	2 ? 3 3 3	? 3 2 1 2	2 2
Paciphacops hudsonicus	3 0 3 1 2	4 1 4 1 0	1 2 2 2 2	3 0 1 3 1	2 ? 3 3 3	4 2 2 3 2	2 2
Paciphacops logani	2 0 2 1 2	4 1 4 1 0	1 3 0 2 1	1 1 1 ? ?	2 2 2 3 ?	3 ? ? 2 1	2 3
Paciphacops campbelli	3 0 4 1 2	4 1 4 1 0	1 3 2 2 3	3 0 1 3 1	2 2 3 4 3	5 2 2 3 2	2 3
Paciphacops birdsongensis	2 0 3 1 2	5 1 4 1 0	1 3 2 2 3	3 0 1 3 ?	2 ? 3 ? ?	4 2 2 ? ?	2 3
Paciphacops claviger'	1 0 0 1 1	3 1 4 2 0	0 ? 1 2 2	0 1 1 ? ?	1 2 3 4 3	2 3 2 2 2	3 3
Paciphacops waisfeldae	2 0 1 1 2	4 1 3 1 0	1 3 2 2 2	3 0 1 ? 1	2 ? 3 3 3	2 ? ? 3 2	2 ?
Paciphacops crawfordae	? 0 0 1 2	5 ? 3 1 0	2 3 2 2 2	3 2 ? 1 ?	? 1 2 ? 3	2 ? 2 2 0	0 ?
Paciphacops argentinus	? 0 2 1 2	5 ? 4 1 0	2 3 2 2 2	3 2 ? 3 ?	? 1 2 ? 3	2 ? 2 2 0	0 ?
Angulophacops saryarkensis	2 0 0 1 2	5 ? 4 0 0	0 ? ? 2 2	0 2 1 ? ?	2 ? 3 ? ?	3 1 2 ? 1	2 ?
Paciphacops logani balchashensis	3 1 0 1 2	0 ? 4 ? 0	1 ? ? 2 2	3 ? 1 ? ?	2 2 ? ? ?	3 1 0 0 1	2 ?
Phacops natlensis	1 0 4 1 2	4 1 4 0 0	2 3 1 2 3	0 ? 1 ? ?	1 ? 3 4 ?	3 2 ? ? 2	3 3

FIGURE *1*—Map of Bolivia showing localities where *Viaphacops* were found. Modified from Eldredge & Braniša (1980). All localities are within the Cordillera Oriental. Ayo Ayo, Colchani, Chacoma, Patacamaya, Chiarumani, Pujravi, Lahuachaca, Sica Sica, Belén, Huaychani, Pisakaviña (La Paz Department; Belén and Sica Sica Formations) are collectively referred to as northern Bolivia in the text. Localities in central Bolivia are Oruro (Oruro Department; Upper Icla Formation), Totora, Aiquile, Rumicorral, Tolamayu, Kochis (Cochabamba Department; Icla and Huamampampa Formations) and Icla (Chuquisaca Department; Icla and Huamampampa Formations). Southern Bolivia has only one locality, Cerro Picacho (Tarija Department; Gamoneda Formation). Jarajache (Cabanillas Formation) is located in the northwest of Lake Titicaca in Peru.


Jarajache
Ayo Ayo
Colchani
Chacoma
Patacamaya
Sica Sica
Pujravi
Belen
Lahuachaca
Oruro
Totora
Rumicorral
Aiquile
Tolamayu
Kochis
Icla
Cerro Picacho

FIGURE *2*—Stratigraphic distribution of *Viaphacops* in Bolivia. Stratigraphic correlation and age assignment of the formations adapted from Rachebœuf et al. (1993), Blieck et al. (1996), and Adrain and Edgecombe (1996). Possible range of the *Scaphiocoelia* Zone is highlighted. Information for the Cabanillas Formation, Peru, is taken from Newell (1949) and Laubacher et al. (1982). The range for the Lochkovian is omitted here as no *Viaphacops* is reported below the *Scaphiocoelia* Zone.


Peru
Northern Bolivia
Central Bolivia
Southern Bolivia
Middle Devonian
Lower Devonian
Givetian
Eifelian
Emsian
Pragian
newelli
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Sica Sica Fm.
Cruz Loma Fm.
Belen Fm. Upper Member
Condoriquina Fm.
Belen Fm. Lower Member
orurensis
?
pirovanoi
newelli
salteri
kozlowskii
multicinctus
spinoedgecombei
Los Monos Fm.
Huamampanpa Fm.
Icla Fm. Upper Member
Icla Fm. Lower Member
salteri
spinoedgecombei
cf. chavelai
Huamampanpa Fm.
Gamoneda Fm.
cf. orurensis
Scaphiocoelia Zone

FIGURE *3*—*Viaphacops spinoedgecombei* n. sp. 1-5, MHNC 0565, holotype. Plastic cast of an internal mold of a cephalon from Kochis, Cochabamba Department. 1, dorsal view. 2, frontal view. 3, left lateral view. 4, left frontal oblique view. 5, ventral view. 6-9, MHNC 7482B, paratype. Latex peel of an external mold of a cephalon from Kochis, Cochabamba Department. 6, left lateral view. 7, left lateral oblique view. 8, dorsal view. 9, frontal view. 10-12, AMNH 45515, paratype. Internal mold of an incompletely enrolled specimen from Cahuanota, La Paz Department. 10, ventral view of a cephalon and dorsal view of a pygidium. 11, right lateral view. 12, right lateral oblique view. Scale bar equals to 1 cm.

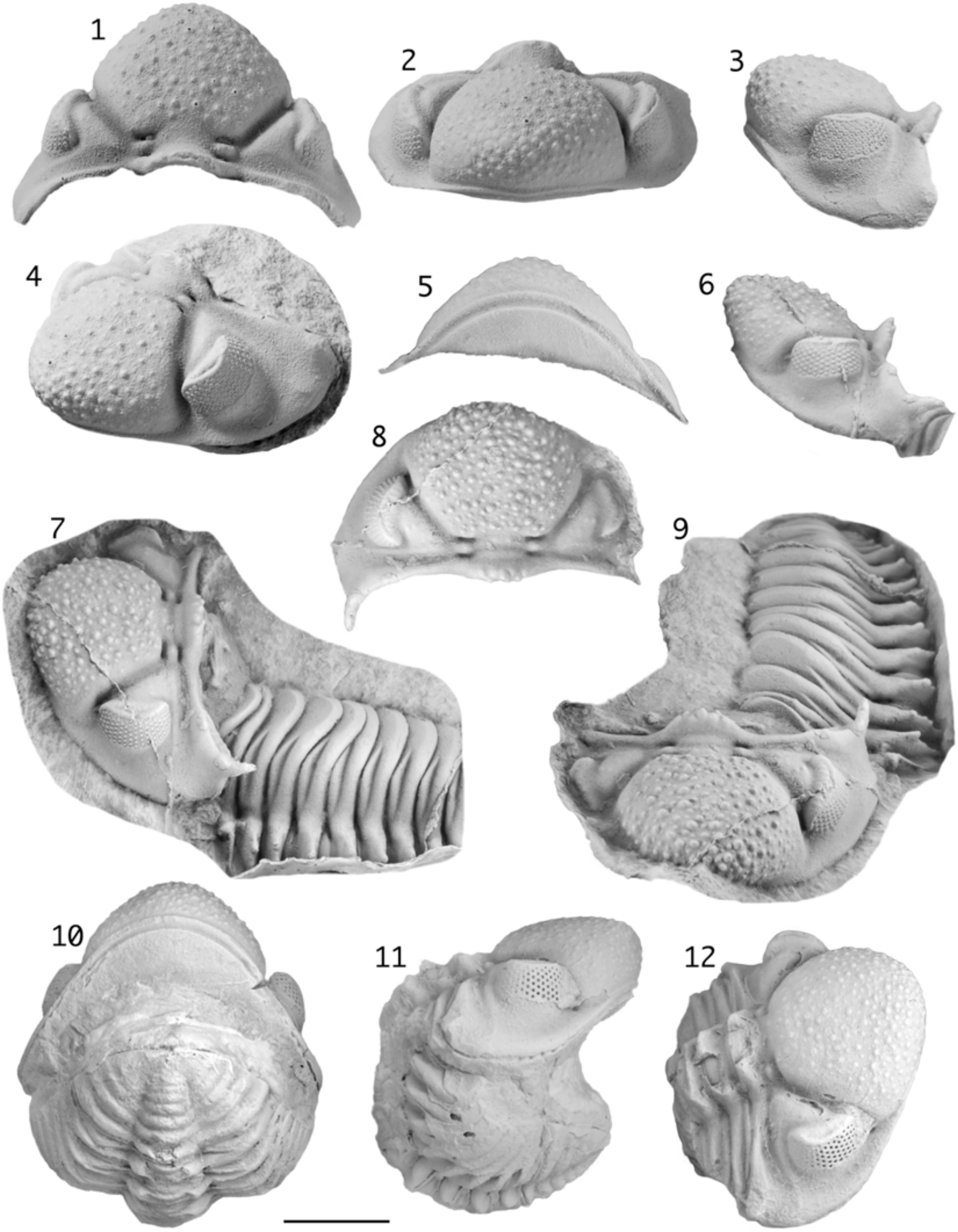
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FIGURE 4—*Viaphacops spinoedgecombei* n. sp. 1-3, AMF 99356, paratype. Latex peel of an external mold of a thoracopygidium. From Totora-Aiquile, Cochabamba Department. 1, dorsal view. 2, left lateral oblique view. 3, left lateral view. 4-6, AMNH 45511, paratype. Latex peel of a pygidium with a partial thorax. From Totora-Aiquile, Cochabamba Department. 4, dorsal view. 5, left lateral oblique view. 6, posterior view. 7, AMNH 63465, paratype. Cephalon with an external mold from Chacoma, La Paz Department. Ventral view, taken by photomicrographic system. Uncoated. Scale bar equals to 1 cm.

FIGURE 5—*Viaphacops newelli* n. sp. 1-4, AMNH 45572, holotype. Internal mold of a cephalon from Chacoma, La Paz Department. 1, dorsal view. 2, frontal view. 3, left lateral view. 4, left lateral oblique view. 5-8, AMNH 45475, paratype. Internal mold of a cephalon from Pujravi, La Paz Department. 5, dorsal view. 6, right lateral oblique view. 7, right lateral view. 8, ventral view. Scale bar equals to 1 cm.

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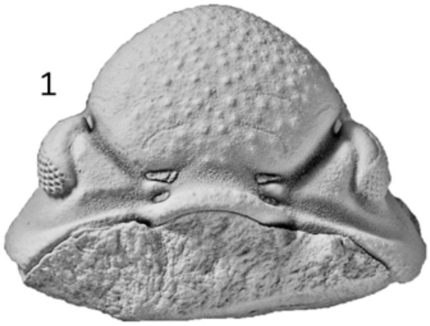

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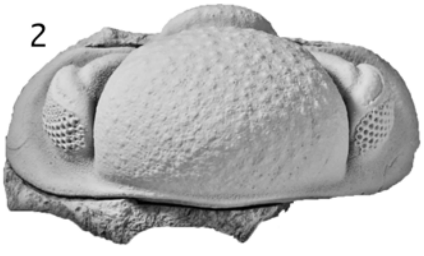

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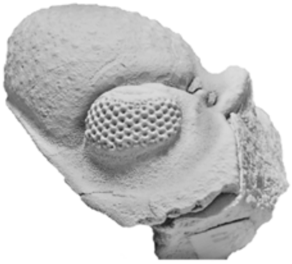

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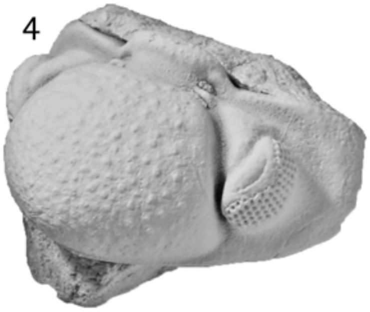

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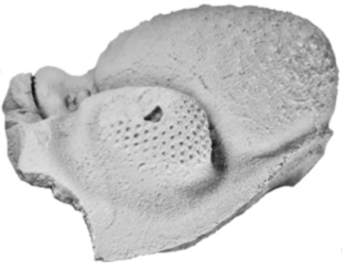

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FIGURE 6—*Viaphacops newelli*, n. sp. 1-3, AMNN 45478, paratype. Internal mold of a pygidium with a partial thorax. From Pujravi, La Paz Department. 1, dorsal view. 2, right lateral oblique view. 3, right lateral view. 4-6, AMNH 63464, paratype. Latex peel of an external mold of a pygidium. From Chacoma, La Paz Department. 4, dorsal view. 5, left lateral oblique view. 6, left lateral view. Scale bar equals to 1 cm.

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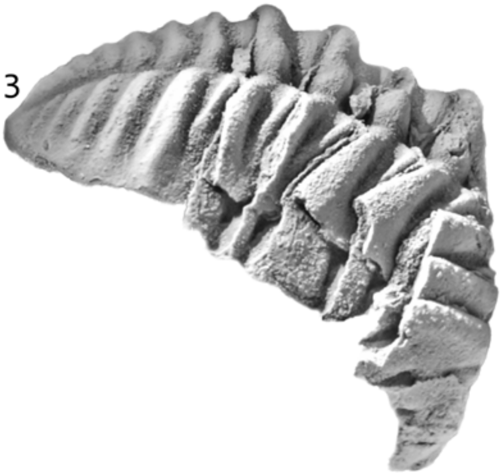

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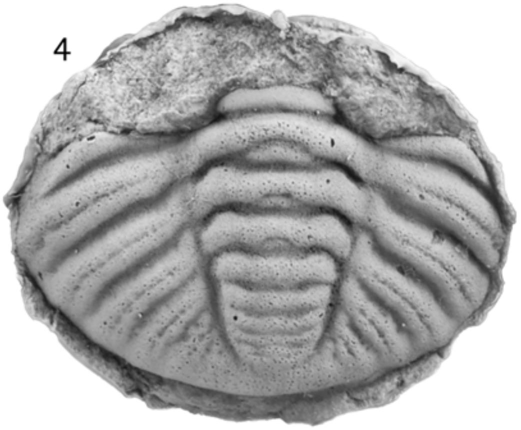

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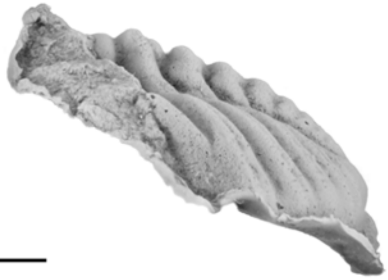

FIGURE 7—*Viaphacops pirovanoi* n. sp. 1-4, AMNH 53024, paratype. Internal mold of a cephalon, from Rumicorral, Cochabamba Department. 1, dorsal view. 2, frontal view. 3, right lateral view. 4, right lateral oblique view. 5-9, AMNH 45486, holotype. Internal mold of a cephalon, from Belén, La Paz Department. 5, dorsal view. 6, frontal view. 7, right lateral oblique view. 8, right lateral view. 9, ventral view. 10-14, AMNH 45488, paratype. Internal mold of a cephalon, from Belén, La Paz Department. 10, dorsal view. 11, frontal view. 12, right lateral oblique view. 13, right lateral view. 14, ventral view. Scale bar equals to 1 cm.

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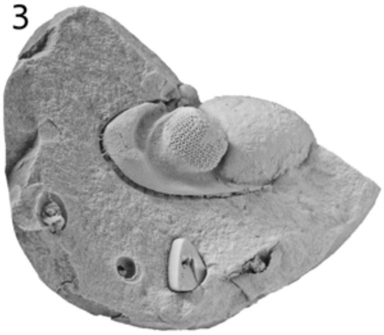

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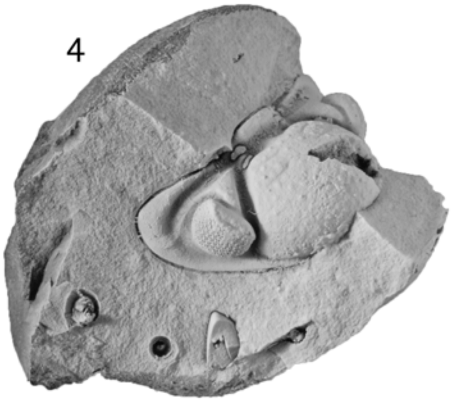

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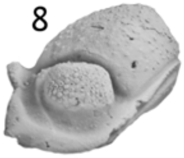

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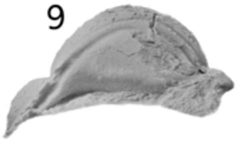

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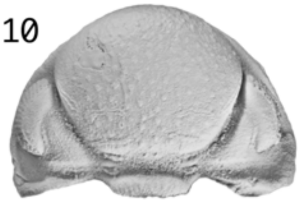

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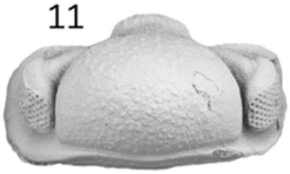

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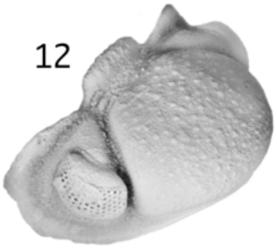

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FIGURE *8*—*Viaphacops pirovanoi* n. sp. 1-5, AMNH 45485, paratype. Internal mold of an enrolled specimen. Thorax missing. From Pisakaviña, La Paz Department. 1, dorsal view. 2, frontal view. 3, left lateral oblique view. 4, right lateral view. 5, dorsal view of a pygidium. 6-8, AMNH 57802, paratype. Counterpart of an incomplete pygidium and its latex peel. 6, counterpart, showing the trace of perforated tubercles as infilling. 7, 8, latex peel, right lateral oblique views from different angles. 9-11, AMNH 45487, paratype. Internal mold of an almost complete specimen. From Belén, La Paz Department. 9, dorsal view. 10, frontal view. 11, SEM photo of thoracic pleural ribs, showing a row of tubercles on each rib. 12-14, AMNH 45484, paratype. Latex peel of an external mold of thoracopygidium. From Belén, La Paz Department. 12, dorsal view. 13, slightly oblique view from left side. 14, left lateral oblique view. Scale bar equals to 1 cm, except for fig. 11 (scale bar = 1 mm).

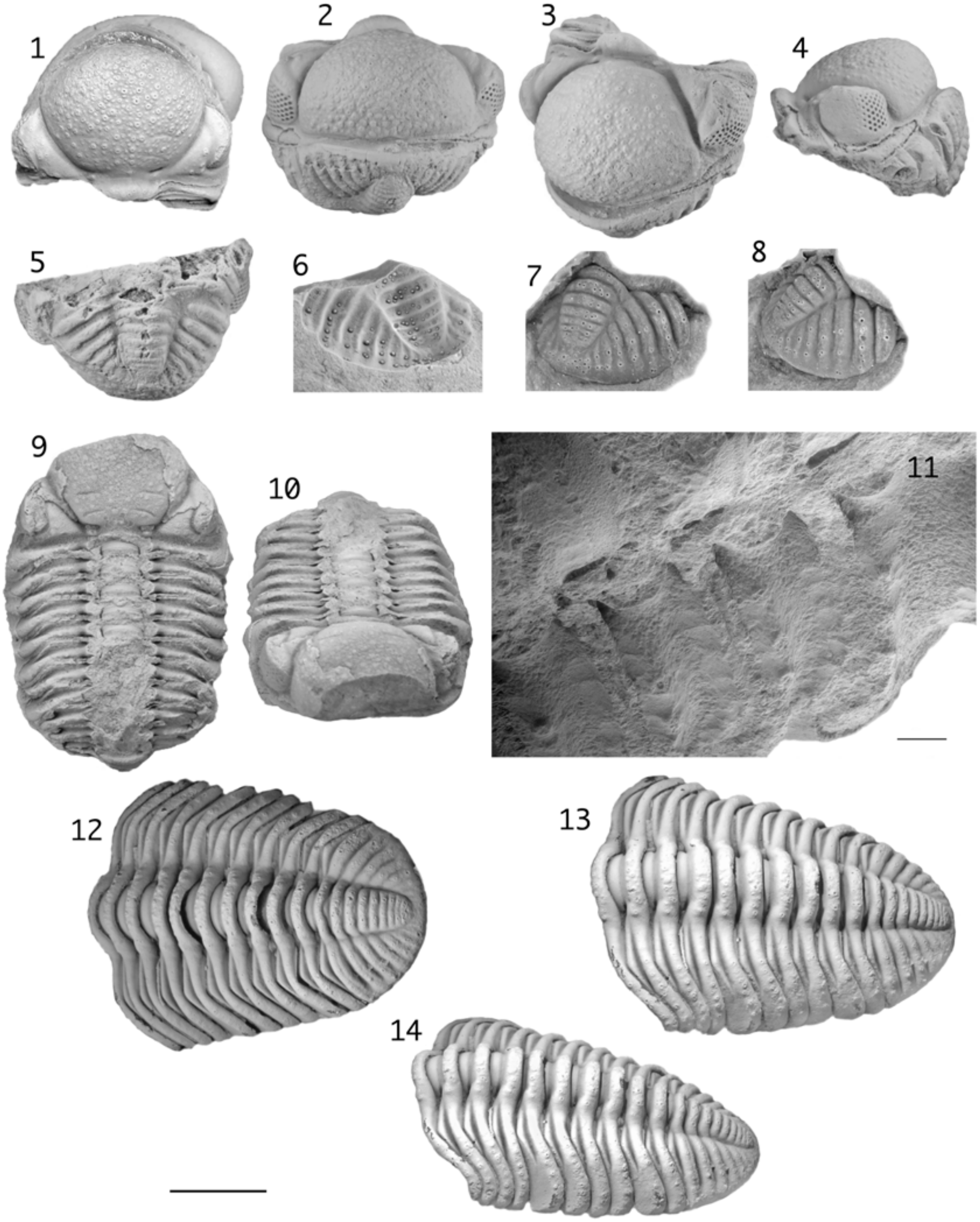
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Figure 9—*Viaphacops orurensis* (Bonarelli, 1921). 1-4, 12, AMNH 63455. Internal mold of a cephalon, with occipital ring bearing a node. From Pisakaviña, La Paz Department. 1, dorsal view. 2, frontal view. 3, left lateral oblique view. 4, left lateral view. 12, ventral view. 5-7, AMNH 45498. Internal mold of a cephalon. From Chacoma, La Paz Department. 8-11, AMNH 57801. Latex peel of an external mold, showing left genal spine. Tuberculated occipital ring triangular with a hint of node. 8, dorsal view. 9, frontal view. 10, left lateral oblique view. 11, left lateral view. 13, AMNH 63466. Internal mold of a cephalon. From Chacoma, La Paz Department. Ventral view. 14, AMNH 63456. Internal mold of a cephalon with a partial external mold, from Chacoma, La Paz Department. Ventral view, taken by photomicroscopic system. Uncoated. Scale bar equals to 1 cm.

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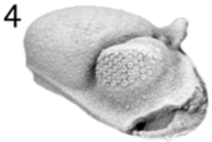

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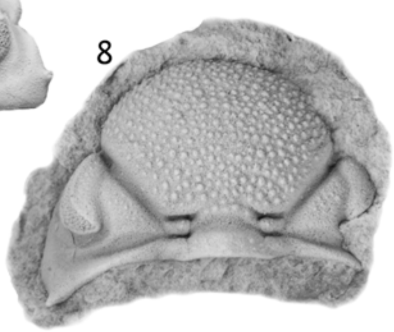

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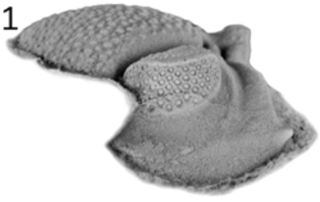

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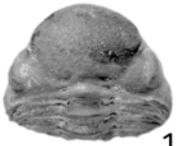
Figure *10—Viaphacops orurensis* (Bonarelli, 1921). 1-6, AMNH 45497. Slightly enrolled specimen with cephalon and a partial thorax, showing a triangular occipital ring and thoracic rings. From Chacoma, La Paz Department. 1-5 taken by photomicrographic system, 6 by SEM. 1, dorsal view. 2, frontal view. 3, left lateral oblique view. 4, right lateral oblique view. 5, right lateral view. 6, SEM photo showing a close up of the rings. Scale bar equals to 1 mm. 7-10, AMNH 45492. Latex peel of an almost complete specimen, bearing a low occipital ring and thoracic rings. 7, dorsal view. 8, frontal view. 9, left lateral oblique view. 10, left lateral view. 11-14, AMNH 57800. Latex peels of two incomplete cephala, one each incomplete thorax and pygidium from a single concretion from Chacoma, La Paz Department. 11, dorsal view of a cephalon and a partial pygidium. 12, frontal view of a cephalon. 13, left lateral oblique view. 14, frontal view of another cephalon with a partial thorax. Scale bar equals to 1 cm, except for fig. 6.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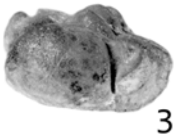
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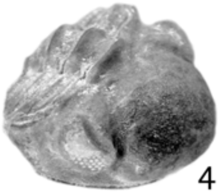
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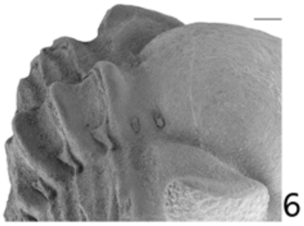
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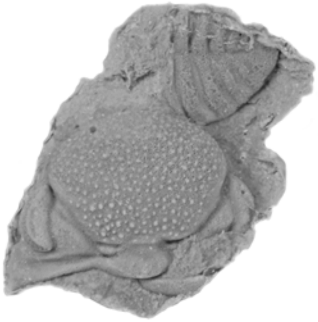
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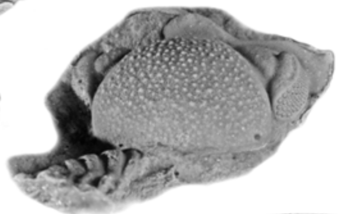
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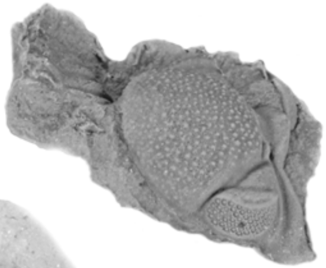
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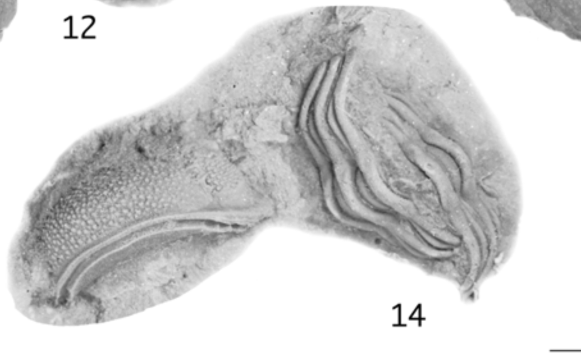
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Figure *11—Viaphacops orurensis* (Bonarelli, 1921). 1, 2, AMNH 57796. Latex peel of a thoracopygidium. From Lahuachaca, La Paz Department. 1, dorsal view. 2, dorsal view, slightly frontal, showing the configuration of thoracic rings. 3, 4, AMNH 57797. Latex peel of a thoracopygidium. From Chacoma, La Paz Department. 3, dorsal view. 4, frontal view. 5-9, AMNH 45490. Latex peel of a partial thorax, showing nodes on thoracic rings. Internal mold of a cephalon attached (not photographed). From Chacoma, La Paz Department. 5, dorsal view. 6, frontal view. 7, 8, left lateral oblique views from different angles. 9, left lateral view. 10-13, AMNH 63463. Latex peel of an incomplete thoracopygidium, showing low and round thoracic rings. From Pisakaviña, La Paz Department. 10, dorsal view. 11, 12, right lateral oblique views from different angles. 13, right lateral view, slightly oblique. Scale bar equals to 1 cm.

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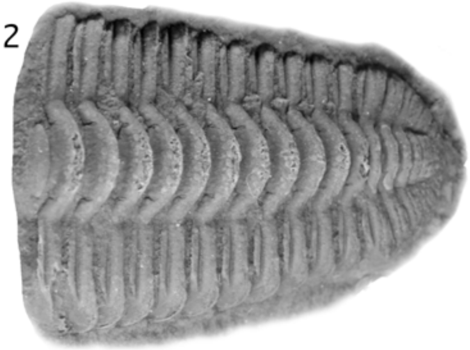

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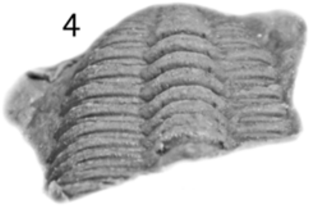

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Figure *12—Viaphacops* cf. *orurensis* (Bonarelli 1921). 1-6, AMNH 45512. Internal mold of an almost complete specimen from Cerro Picacho, Tarija Department, Bolivia. Partially enrolled. 1, dorsal view. 2, frontal view. 3, left lateral view. 4, left oblique view. 5, latex peel, dorsal view, showing tuberculation on the thoracic rings. 6, latex peel, oblique frontal view, showing tuberculated thoracic rings, occipital ring, and palpebral area. Scale bar equals to 1cm.

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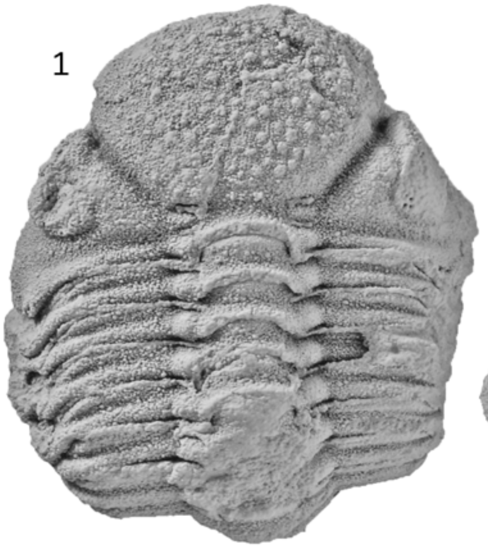

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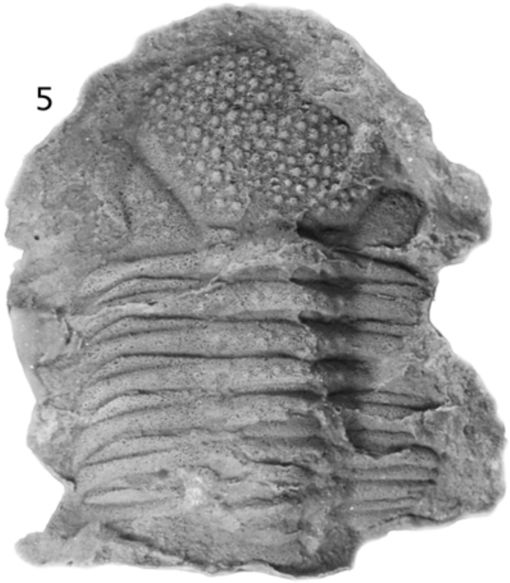

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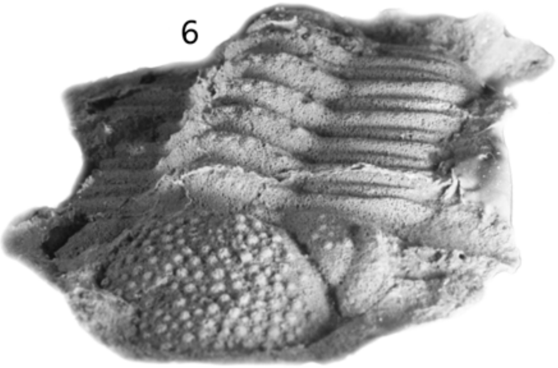

Figure *13—Viaphacops multicinctus* Pek and Vanek, 1991. 1-5, AMNH 46252. Internal mold of a cephalon from Chiarumani, La Paz Department. 1, dorsal view. 2, frontal view. 3, right lateral oblique view. 4, right lateral view. 5, ventral view. 6-11, AMNH 46253. Internal mold of a cephalon with occipital ring bearing tubercles on its frontal wall. 6, dorsal view. 7, 8, frontal views, from slightly different angles. 9, left lateral view. 10, left lateral oblique view. 11, ventral view. 12-15, AMNH 53025. Internal mold of an enrolled specimen. Incomplete. From Chacoma, La Paz Department. 12, dorsal view. 13, frontal view. 14, left frontal oblique view. 15, left lateral view. Scale bar equals to 1 cm.

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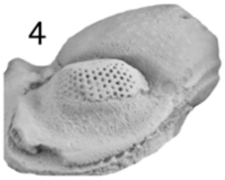

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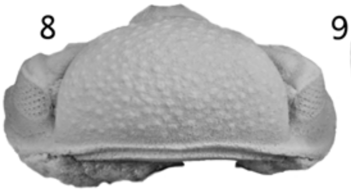

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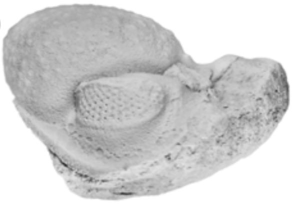

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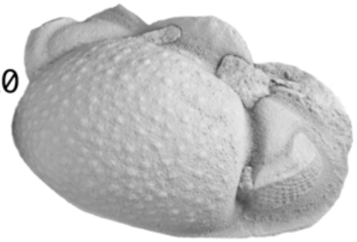

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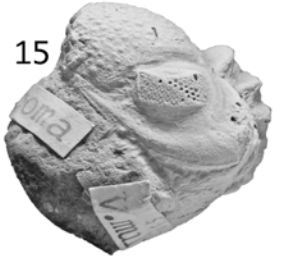
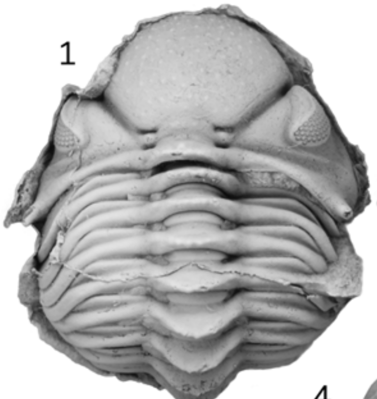


Figure *14—Viaphacops multicinctus* Pek and Vanek, 1991. 1-7, USNM 540771. Latex peel of an external mold of an enrolled specimen, showing well-developed genal spines and tuberculated occipital and thoracic rings. ?Belén, La Paz Department. 1, 2, 5, dorsal views from slightly different angles. 3, frontal oblique view. 4, frontal view. 6, 7, right lateral oblique views. 8, 9, AMNH 45462. Internal mold of an incomplete specimen. Photos taken on the pygidium. From Chacoma, La Paz Department. 8, dorsal view. 9, left lateral oblique view. 10-12, AMNH 57799. Latex peel of a partial thorax, showing tuberculation on thoracic rings. From Pujravi, La Paz Department. 10, left lateral oblique view. 11, dorsal view. 12, frontal view. Scale bar equals to 1 cm.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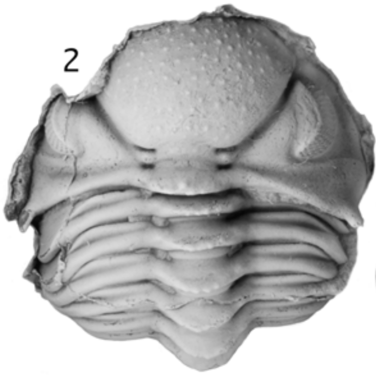
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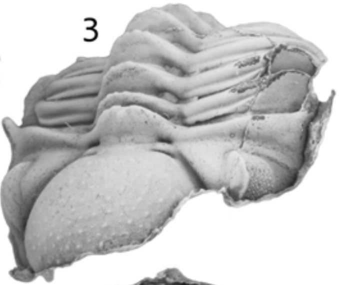
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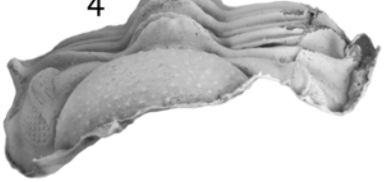
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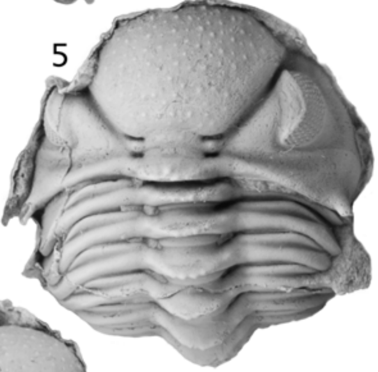
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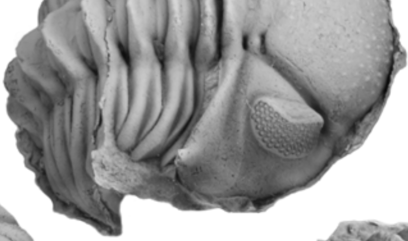
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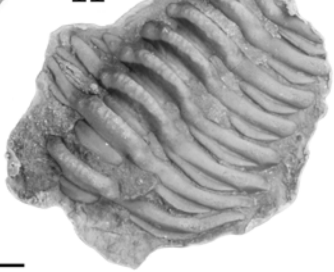
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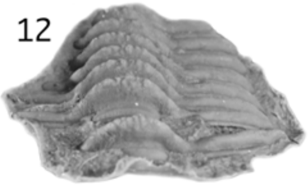
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Figure *15*—*Viaphacops salteri* (Kozlowski, 1923). 1-4, AMNH 46603. Internal mold of a cephalon from Chacoma, La Paz Department. 1, dorsal view. 2, left lateral oblique view. 3, left lateral view. 4, frontal view. 5-7, 13, AMNH 45470. Internal mold of a cephalon from Colchani, La Paz Department. 5, dorsal view. 6, frontal view. 7, left lateral oblique view. 13, ventral view. 8, 9, AMNH 57798. Latex peel of an incomplete cephalon from ?Chacoma, La Paz Department. 8, dorsal view. 9, right lateral view. 10, 11, 14, AMNH 63462. Internal mold of a cephalon from Chacoma, La Paz Department. 10, left lateral view. 11, left lateral oblique view. 14, ventral view. 12, AMNH 63461. Internal mold of a cephalon from Chacoma, La Paz Department. Ventral view. 15, AMNH 63460. Internal mold of a cephalon from Chacoma, La Paz Department. Ventral view, taken by photomicrographic system. Scale bar equals to 1 cm.

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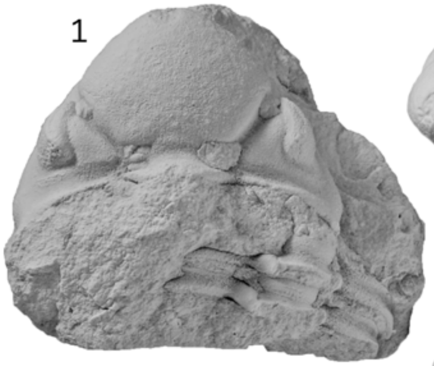

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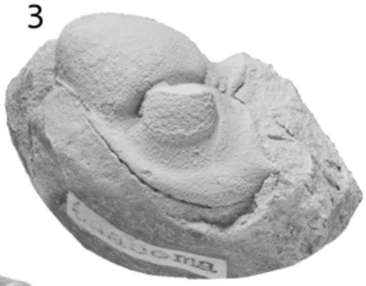

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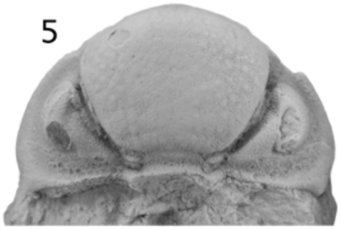

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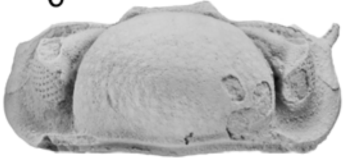

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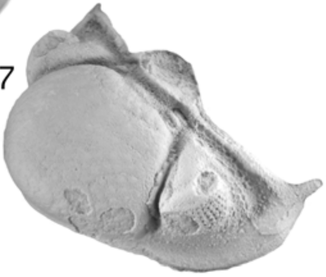

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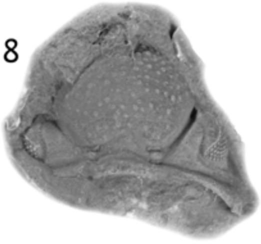

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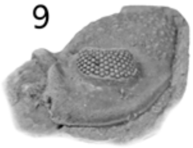

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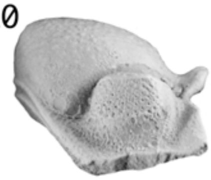

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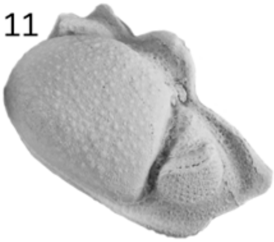

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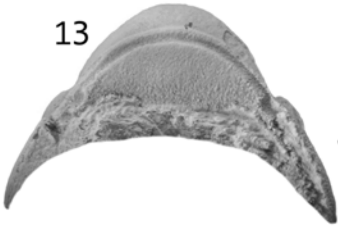

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Figure *16—Viaphacops salteri* (Kozlowski, 1923). 1-3, AMNH 46610. Latex peel of an external mold of a thorax from Chacoma, La Paz Department. 1, dorsal view. 2, left lateral oblique view. 3, right lateral view. 4, 5, AMNH 63457. Internal mold of a pygidium from Belén, La Paz Department. 4, dorsal view. 5, left lateral oblique view. Scale bar equals to 1 cm.

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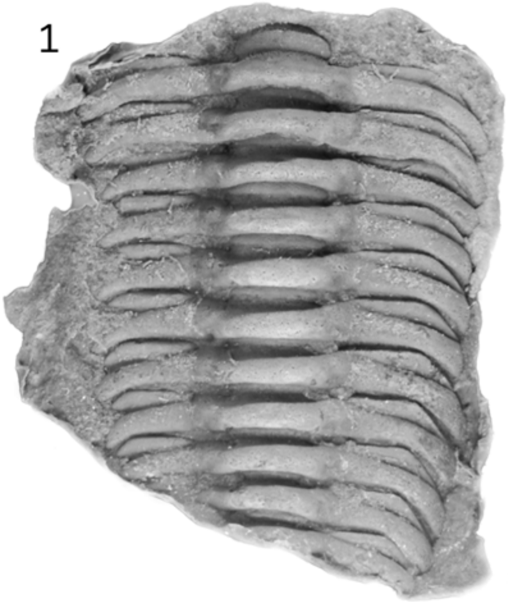

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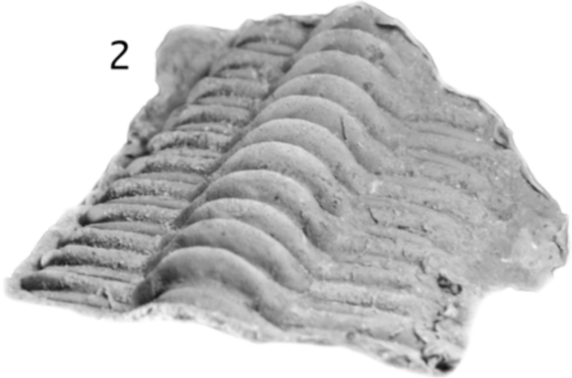

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Figure *17—Viaphacops* cf. *chavelai* (Baldis and Longobucco, 1977) . 1-6, AMNH 45483. Internal mold of an almost complete, dorsally flexed specimen from Icla, Chuquisaca Department. Lower Icla Fm. 1, dorsal view of cephalon. 2, dorsal view, focusing on the thoracic axis. 3, frontal view. 4, left lateral oblique view. 5, ventral view of cephalon. 6, left lateral view. Scale bar equals to 1 cm.

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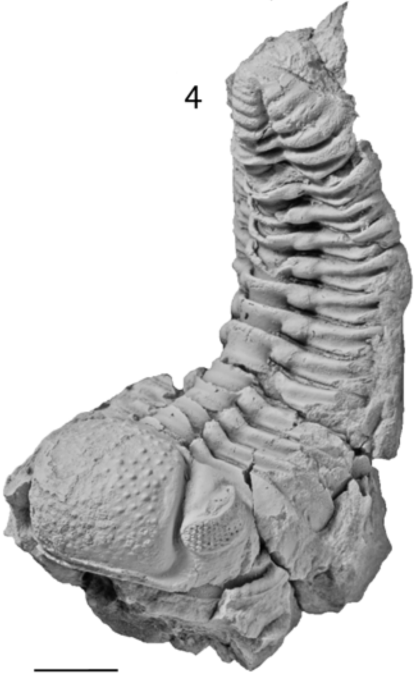

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Figure *18—Viaphacops kozlowskii* Pek and Vanek, 1991. 1-4, AMNH 45578. Internal mold of a cephalon and a partial thorax. From Chacoma, La Paz Department. 1, dorsal view. 2, frontal view. 3, left lateral oblique view. 4, left lateral view. 5-8, AMNH 45506. Internal mold of a cephalon and a partial thorax. From Chacoma, La Paz Department. 5, left lateral view. 6, frontal view. 7, dorsal view. 8, left lateral oblique view. 9-12, AMNH 46254. Incompletely enrolled specimen. From Pujravi, La Paz Department. 9, ventral view. 10, right lateral oblique view. 11, right lateral view. 12, frontal view. Scale bar equals to 1 cm.

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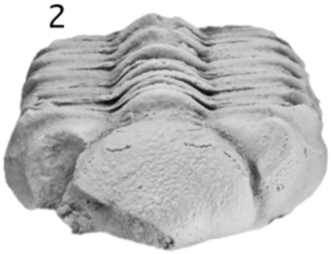
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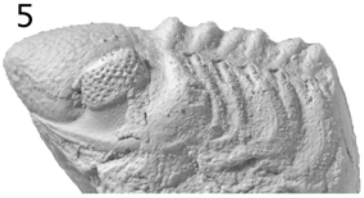
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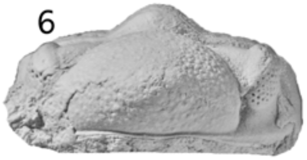
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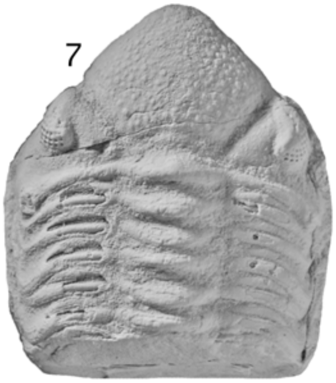
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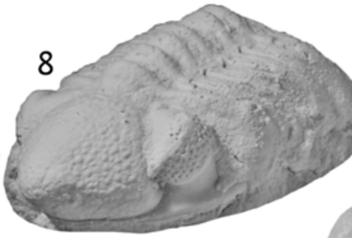
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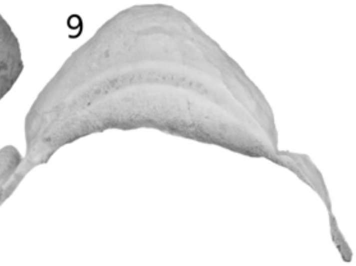
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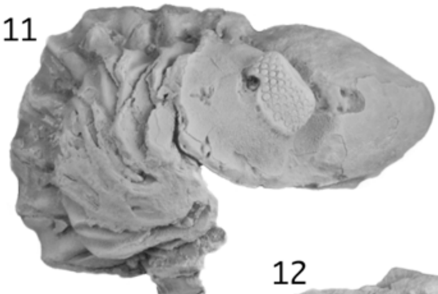
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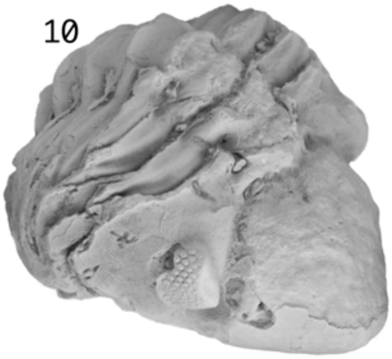
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Figure *19—Viaphacops kozlowskii* Pek and Vanek, 1991. 1-3, AMNH 53028. Left part of a cephalon and a partial thorax, slightly enrolled. Internal mold with some external mold. From Chacoma, La Paz Department. 1, overview of the ventral side of the specimen, taken by photomicrographic system. Uncoated. 2, SEM photo of a doublure. 3, SEM photo of thoracic pleural tips, showing granulation. 4-6, AMNH 53027. Internal mold of a cephalon and a partial thorax. From Chacoma, La Paz Department. 4, overview of the ventral side, taken by photomicrographic system. Uncoated. 5, SEM photo of the medial portion of doublure and vincular furrow. 6, SEM photo showing vincular notches and laterally connected graunules on doublure. Scale bars for figs. 1 and 4 equal to 1 cm; 1 mm for the rest.

equals to 1 cm.

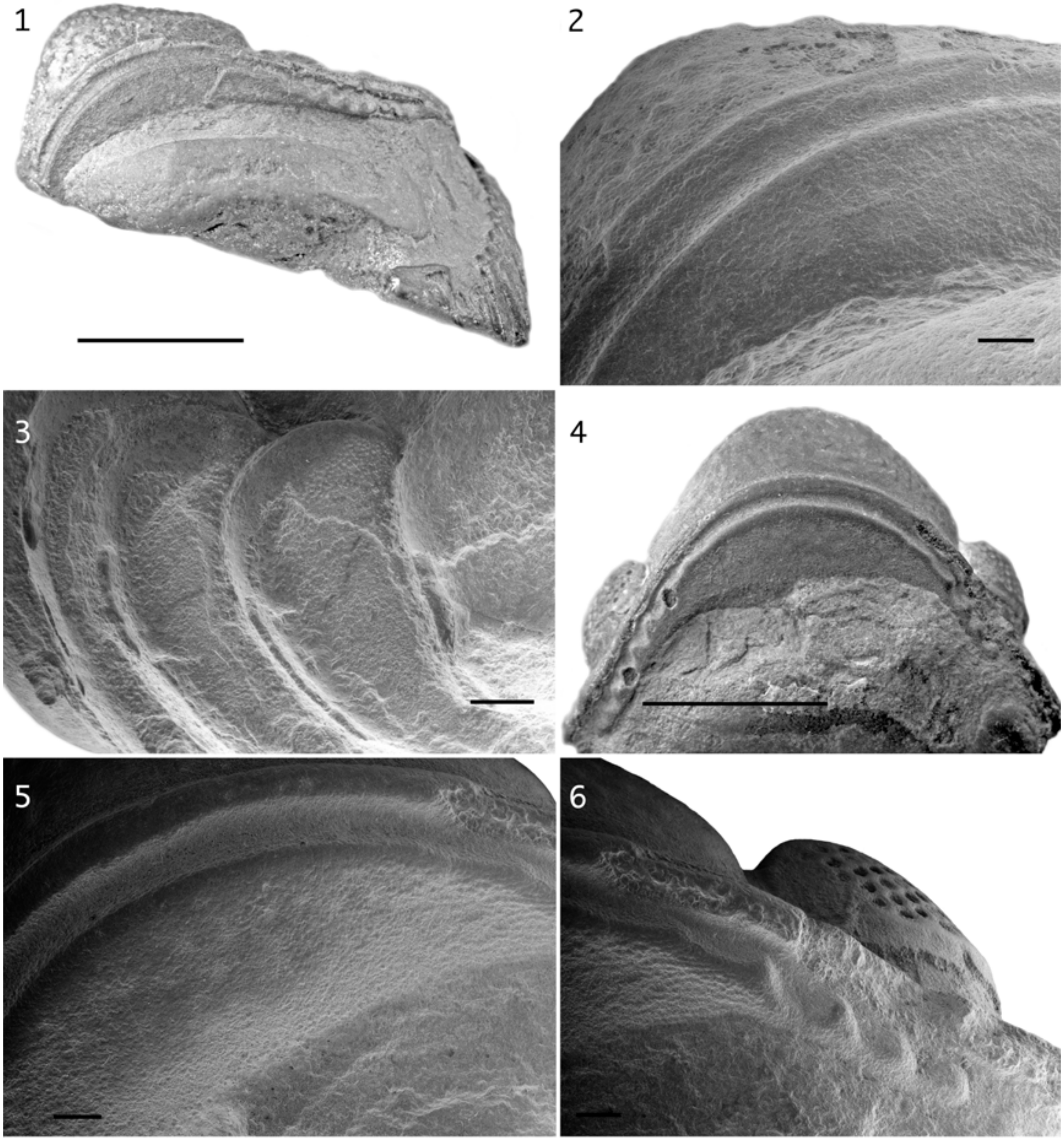
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Figure *20*—SEM photos showing ornamentation on the right palpebral area. 1, 2, *Viaphacops orurensis* (Bonarelli, 1921). 3, *Viaphacops pirovanoi* n. sp. 1, AMNH 45501. Almost complete cephalon with an external mold. From Chacoma, La Paz Department. 2, AMNH 63456. Internal mold of a cephalon with a partial external mold, from Chacoma, La Paz Department. 3, AMNH 45485, paratype. Internal mold of an enrolled specimen. From Pisakaviña, La Paz Department. Note the centrally perforated tubercles. Scale bars equal to 1 mm.

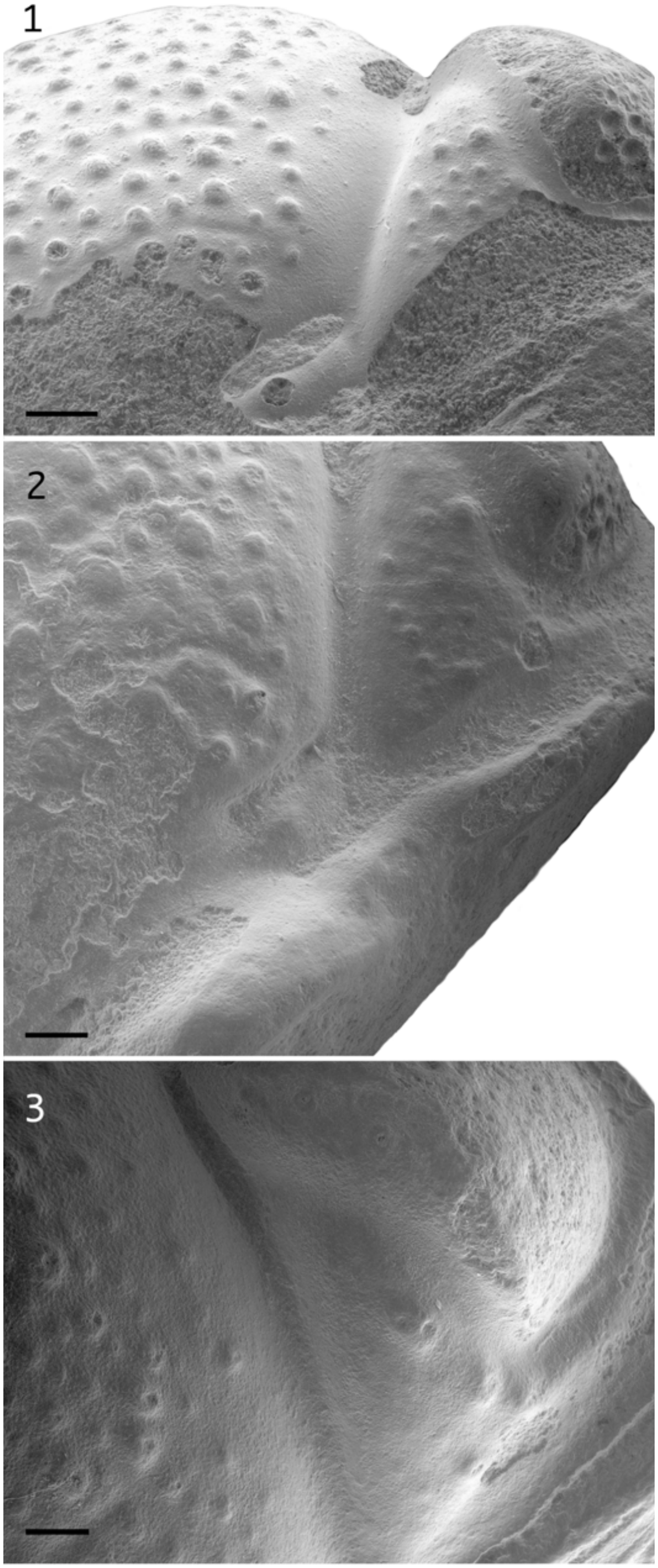
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Figure *21*—SEM photos showing the texture of ventral side. 1-3, *Viaphacops spinoedgecombei* n. sp. 4, *Viaphacops multicinctus* Pek and Vanek, 1991. 5, *Viaphacops kozlowskii* Pek and Vanek, 1991. 6, *Viaphacops newelli* n. sp. 1, 2, AMNH 63465, paratype. Cephalon with an external mold from Chacoma, La Paz Department. 1, showing granulation on the medial doublure. 2, showing granulation on the left lateral doublure. Notice no significant difference in granulation size and density on the entire doublure. 3, AMNH 45513, paratype. Cephalon with an external mold from Chacoma, La Paz Department. Partial ventral view, showing large granules covering the vincular furrow and frontal glabellar wall, on and between glabellar tubercles. 4, AMNH 45493. Cephalon with an external mold. From Chiarumani, La Paz Department. Ventral view, showing granulation at the margin of doublure and vincular furrow. 5, AMNH 45505. Glabella with an external mold. From Chacoma, La Paz Department. Ventral view, showing large granules on the vincular furrow and frontal wall of glabella. 6, AMNH 45480, paratype. Internal mold of a glabella with external mold showing granulation on and between tubercles. From Pujravi, La Paz Department. Scale bars for 1 and 2 equal to 1 mm; 500 μm for the rest.

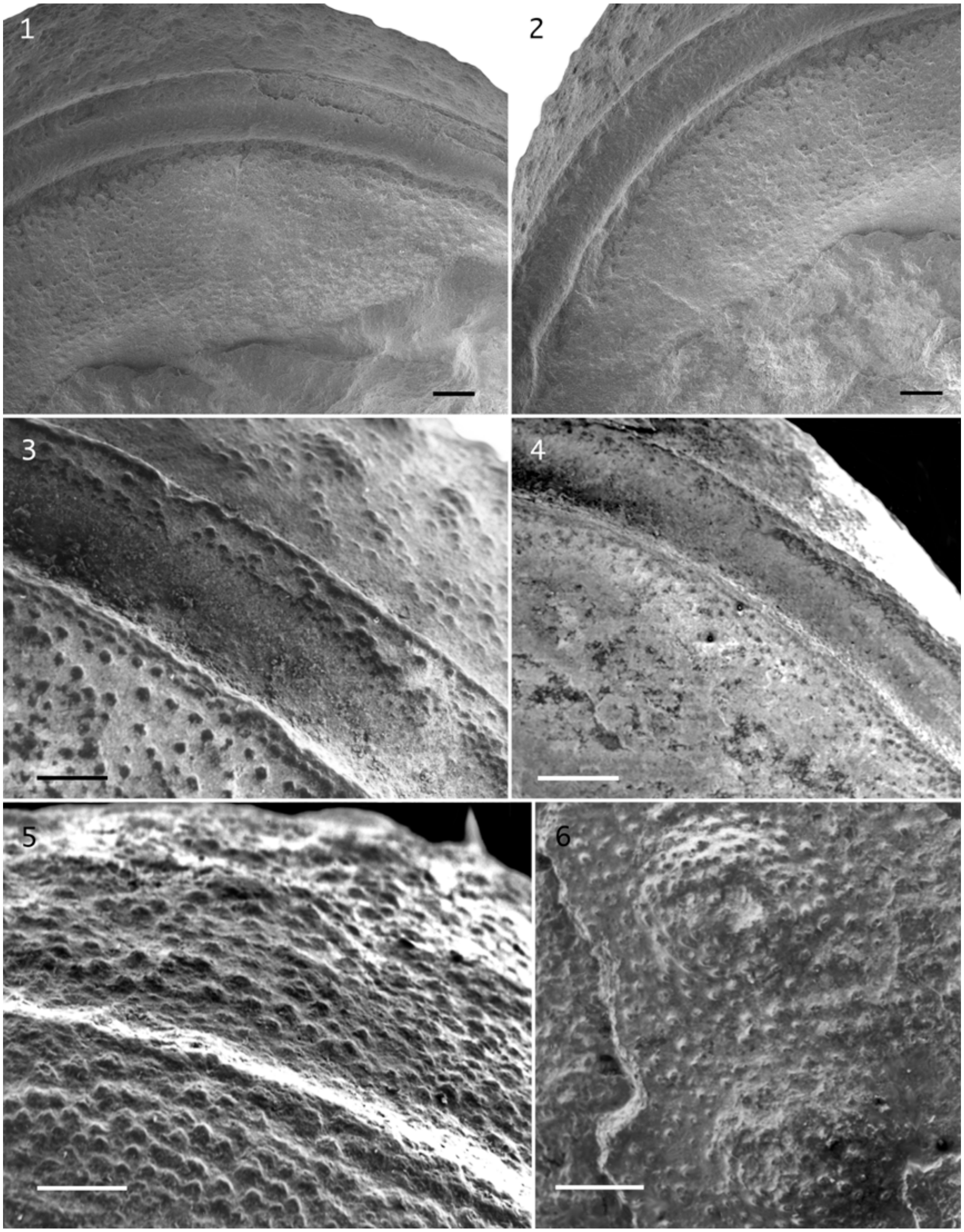
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FIGURE *22*—A resolved cladogram of *Viaphacops* for the 9 Bolivian taxa and 8 North American taxa using *Paciphacops waisfeldae* as an outgroup. Ratchet (Island Hopper) was used for the analysis calculated in NONA. *P. logani* is placed within an ingroup clade. Tree length of 191, consistency index (CI) of 39, retention index (RI) of 46. Closed circles indicate no homoplasy; closed circles homoplasy. Characters and character states are above and below the circles, respectively. The Bolivian taxa are shown in italics; North American taxa in bold letters.

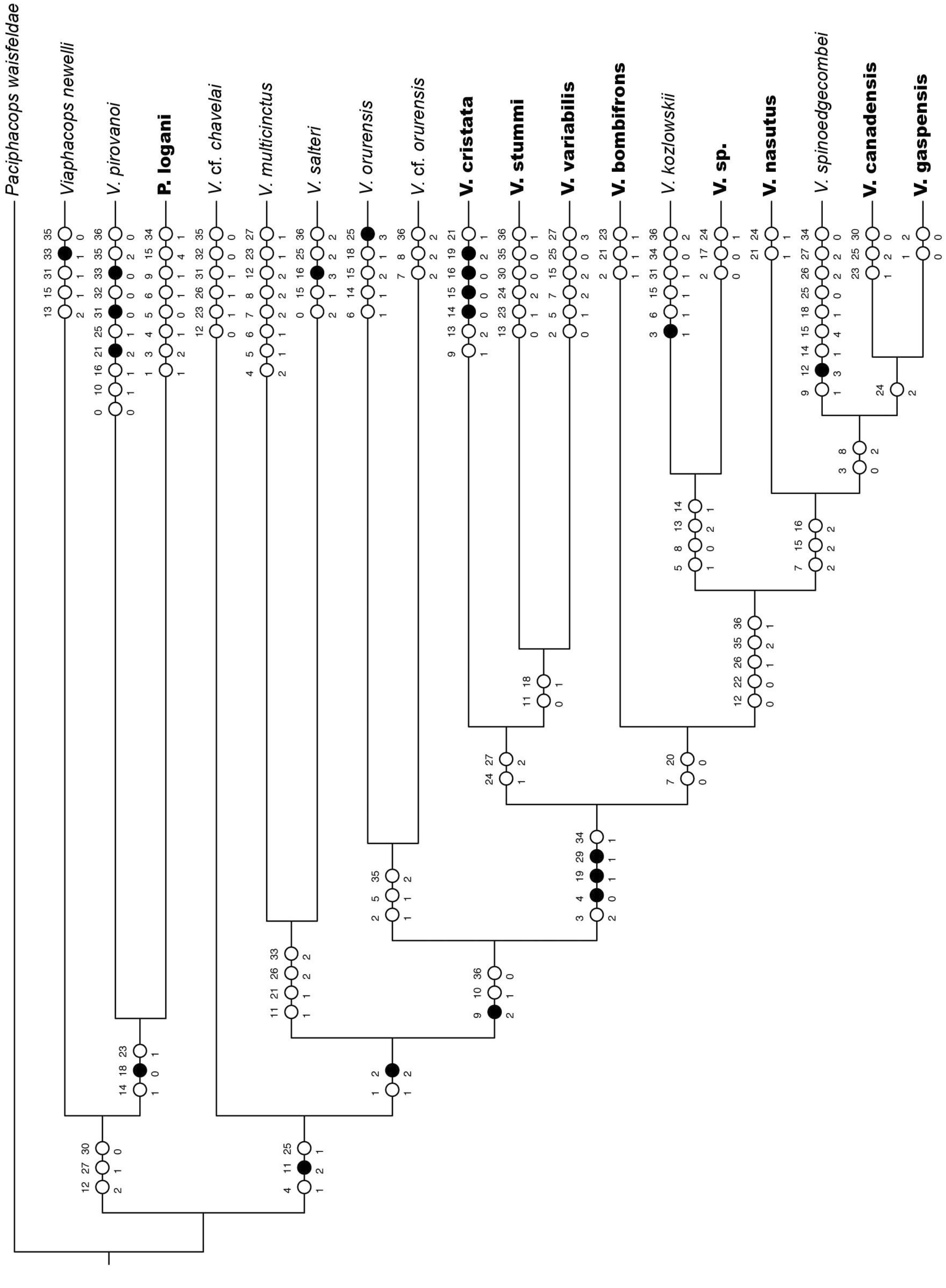
Paciphacops waisfeldae
Viaphacops newelli
V. pirovanoi
P. logani
V. cf. *chavelai*
V. multicinctus
V. salteri
V. orurensis
V. cf. *orurensis*
V. cristata
V. stummi
V. variabilis
V. bombifrons
V. kozlowskii
V. sp.
V. nasutus
V. spinoedgecombei
V. canadensis
V. gaspensis

FIGURE *23*—A resolved cladogram of *Viaphacops* for the 9 Bolivian taxa and 8 North American taxa using *Paciphacops logani* as an outgroup. Ratchet (Island Hopper) was used for the analysis calculated in NONA. *P. waisfeldae* is placed within an ingroup clade. Tree length of 191, consistency index (CI) of 39, retention index (RI) of 46. Closed circles indicate no homoplasy; closed circles homoplasy. Characters and character states are above and below the circles, respectively. The Bolivian taxa are shown in italics; North American taxa in bold letters.

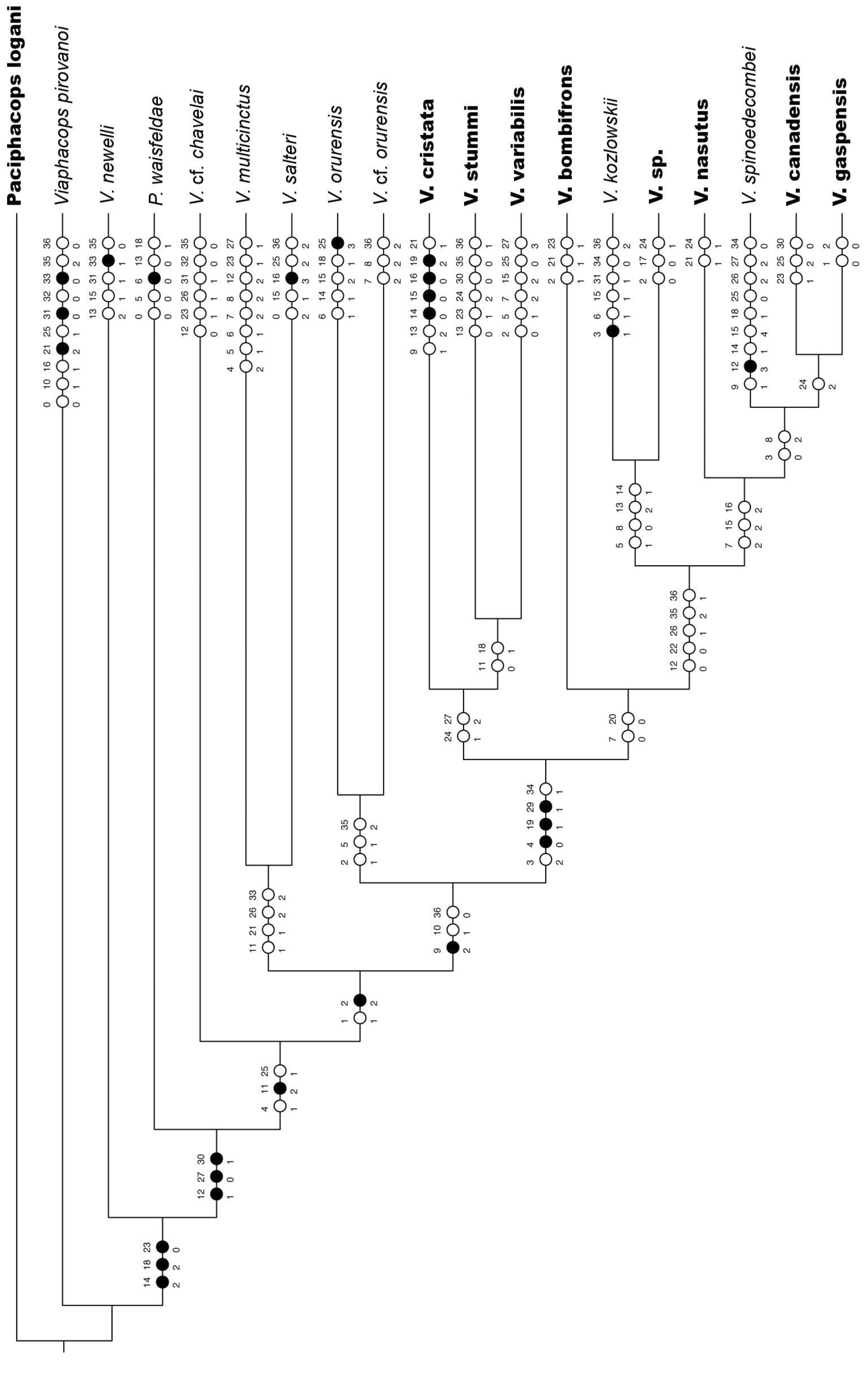
Paciphacops logani
Viaphacops pirovanoi
V. newelli
P. waisfeldae
V. cf. chavelai
V. multicinctus
V. salteri
V. orurensis
V. cf. orurensis
V. cristata
V. stummi
V. variabilis
V. bombifrons
V. kozlowskii
V. sp.
V. nasutus
V. spinoedecombei
V. canadensis
V. gaspensis

FIGURE *24*—Twenty-five Devonian rugose coral regions of Pedder and Oliver (1990) labeled from A to Y. Refer to text for detailed locality information.

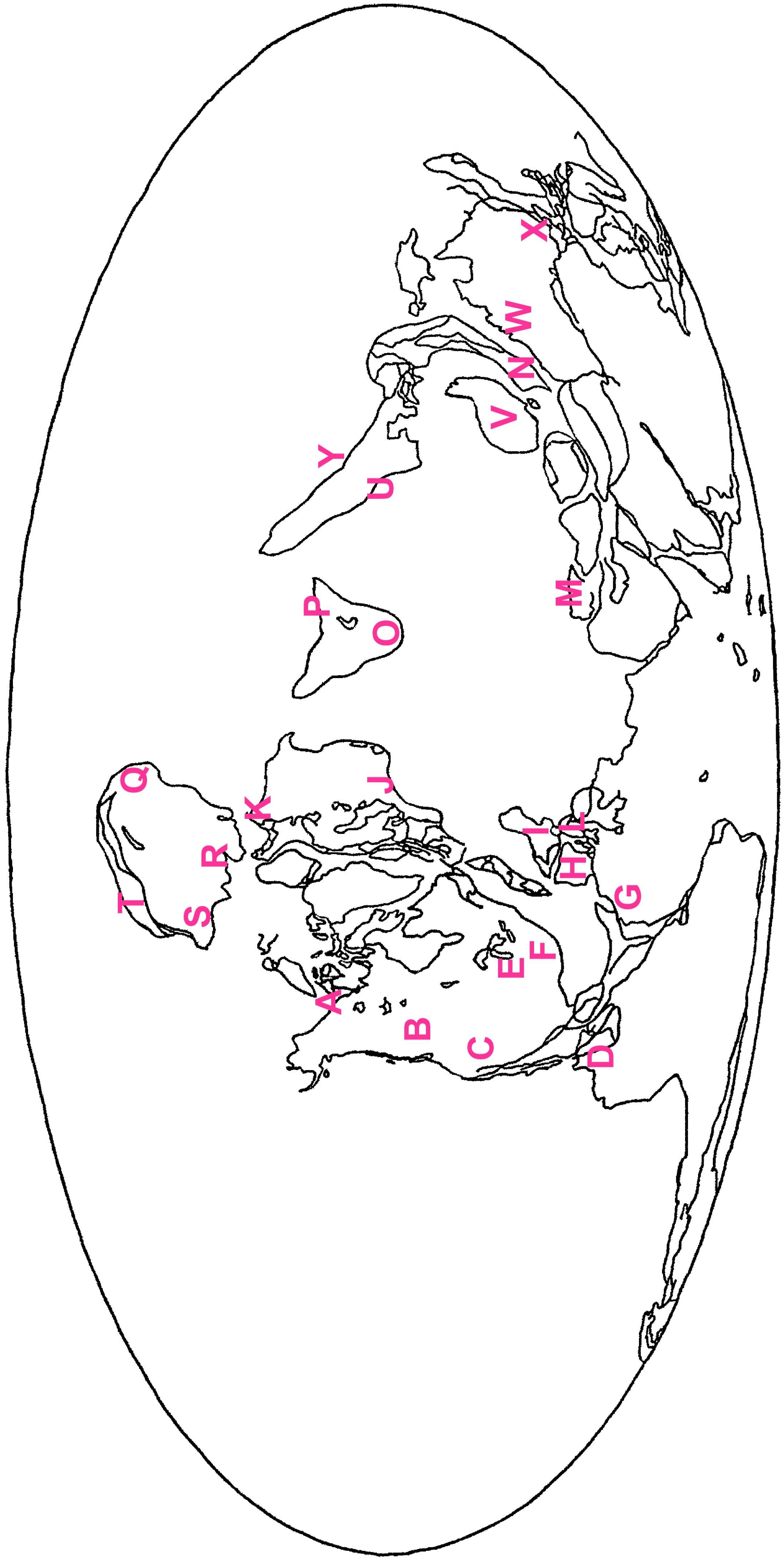
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FIGURE *25*—Lower Devonian rugose coral distributions of Pedder and Oliver (1990). Blue shades over the letters indicate the regions they studied. Based on the Otsuka Coefficients in their analysis, possible paleocurrents are suggested here. See text for details.

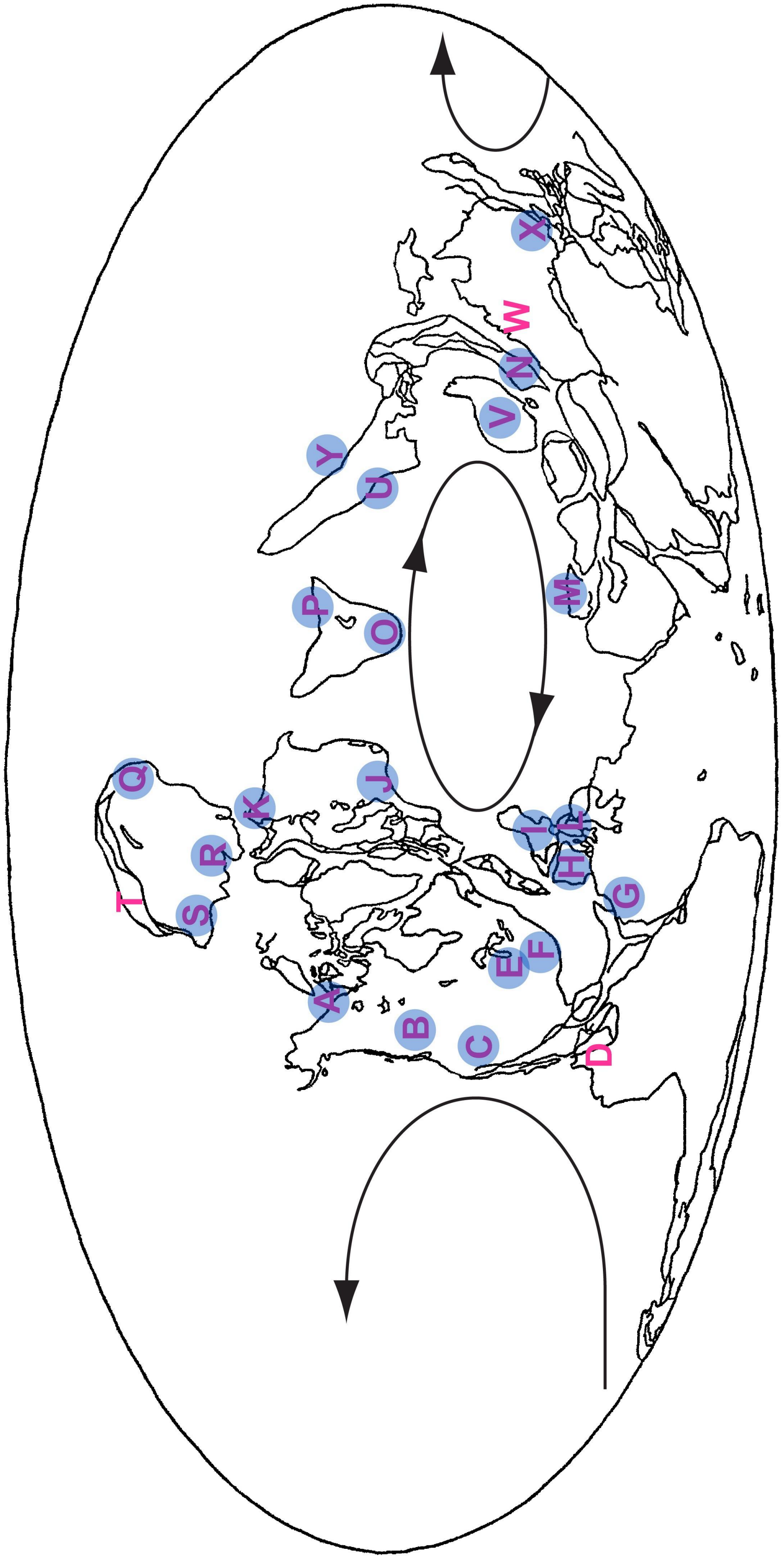
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FIGURE *26*—Lower Devonian phacopid distribution and possible paleocurrents reconstructed from the faunal similarity coefficients. The Tethyan region is in red shade. The regions shaded in blue have fewer interactions with the Tethyan regions. See text for details.

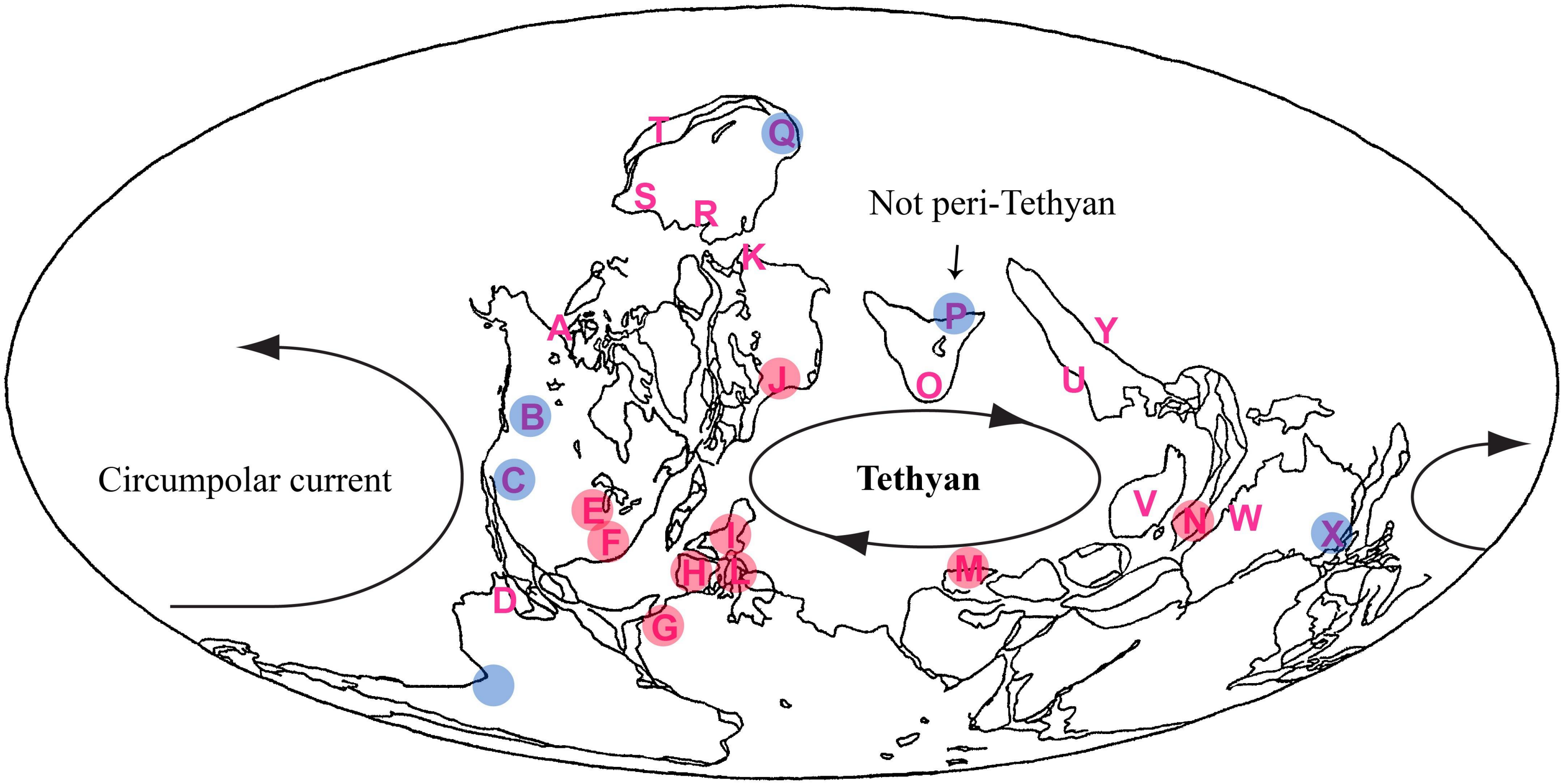
T
Q
S
R
K
Not peri-Tethyan
A
P
Y
J
O
U
B
Circumpolar current
C
Tethyan
E
V
N
W
F
I
X
H
L
M
D
G

FIGURE *27*—Middle Devonian phacopid distribution and possible paleocurrents reconstructed from the faunal similarity coefficients. The Tethyan region is in red shade. The regions shaded in blue have less interaction with the Tethyan regions. Three strong connections between the regions were found: Arctic route connecting eastern Panthalassa to Siberia, possibly into Kazakhstan; southern Tethyan route from Bohemia into Australia; and Eastern North America and North Africa. See text for details.

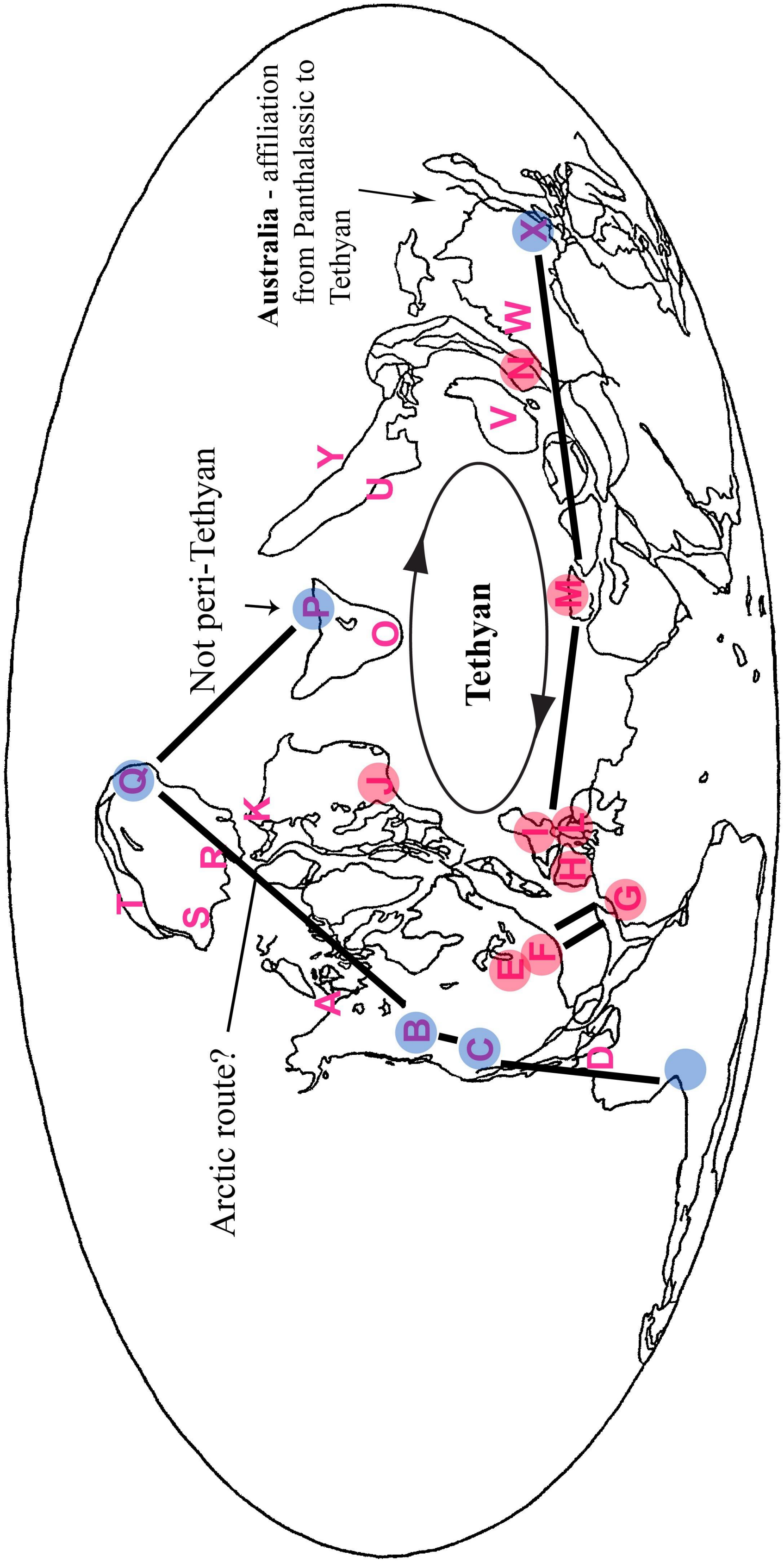
Australia - affiliation from Panthalassic to Tethyan
Not peri-Tethyan
Tethyan
Arctic route?
A
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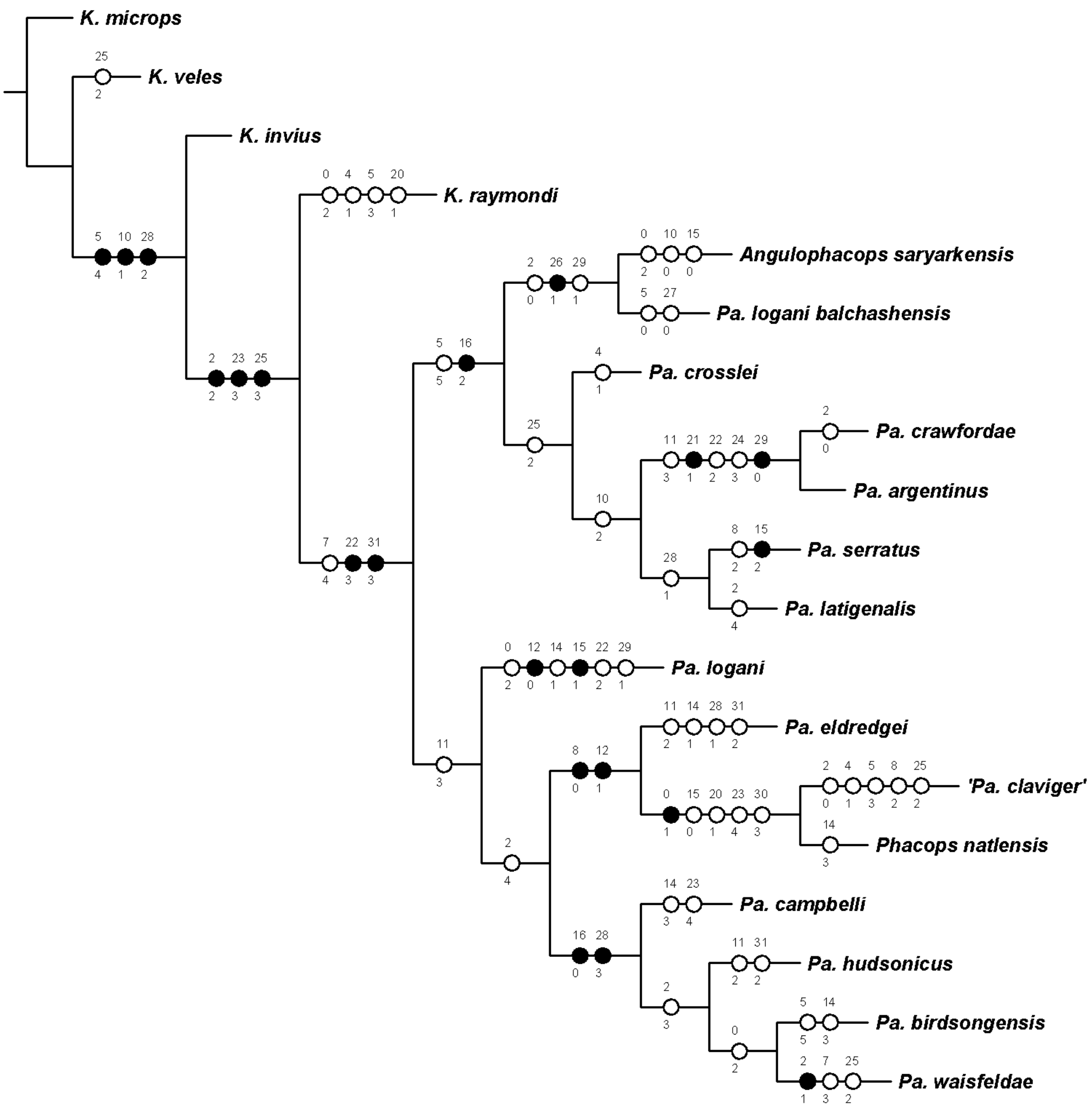
FIGURE *28*—A resolved tree of *Paciphacops* generated by heuristic analysis in NONA after eliminating uninformative characters. The tree length of 95, consistency index of 54, retention index of 59. Closed circles indicate no homoplasy; closed circles homoplasy. Characters and character states are above and below the circles, respectively.


K. microps
25
2
K. veles
5 10 28
4 1 2
K. invius
2 23 25
2 3 3
0 4 5 20
2 1 3 1
K. raymondi
7 22 31
4 3 3
5 16
5 2
2 26 29
0 1 1
0 10 15
2 0 0
Angulophacops saryarkensis
5 27
0 0
Pa. logani balchashensis
25
2
4
1
Pa. crosslei
10
2
11 21 22 24 29
3 1 2 3 0
2
0
Pa. crawfordae
Pa. argentinus
28
1
8 15
2 2
Pa. serratus
2
4
Pa. latigenalis
11
3
0 12 14 15 22 29
2 0 1 1 2 1
Pa. logani
2
4
8 12
0 1
11 14 28 31
2 1 1 2
Pa. eldredgei
0 15 20 23 30
1 0 1 4 3
2 4 5 8 25
0 1 3 2 2
'Pa. claviger'
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3
Phacops natlensis
16 28
0 3
14 23
3 4
Pa. campbelli
2
3
11 31
2 2
Pa. hudsonicus
0
2
5 14
5 3
Pa. birdsongensis
2 7 25
1 3 2
Pa. waisfeldae

FIGURE *29*—The area cladogram of *Paciphacops* based on Figure 28. The taxon names were replaced by their locality. Within North America, those belong to the Appalachian region is indicated by NA (E), NA (C) for central North America (Oklahoma, specifically), and NA (W) to include Nevada and southwestern Canada.

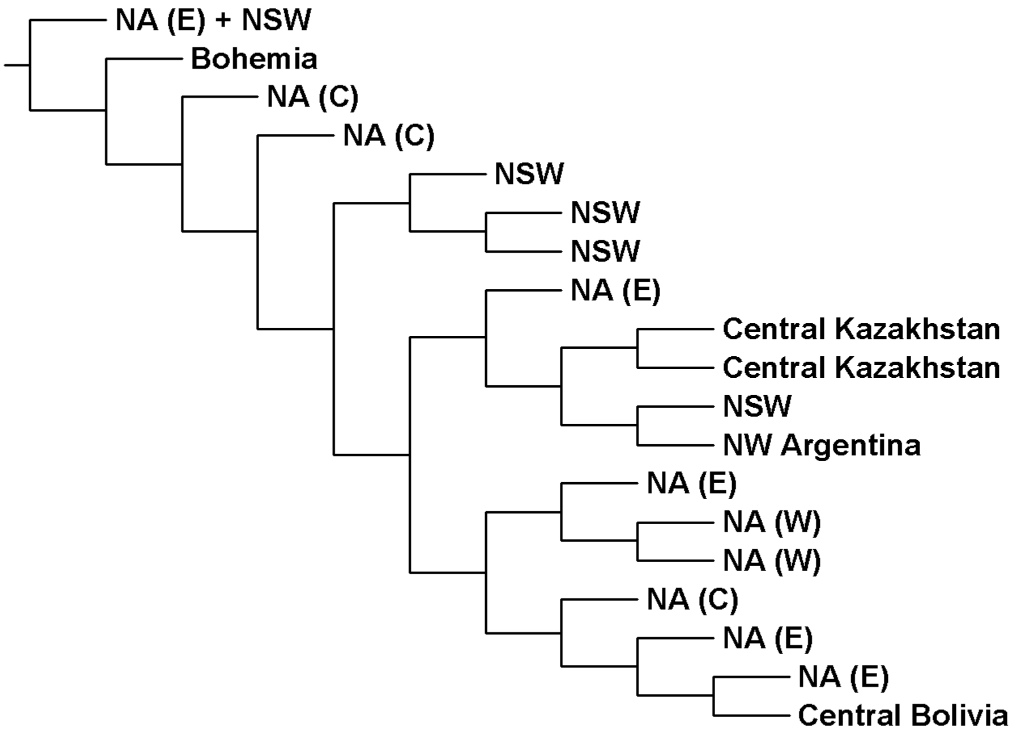
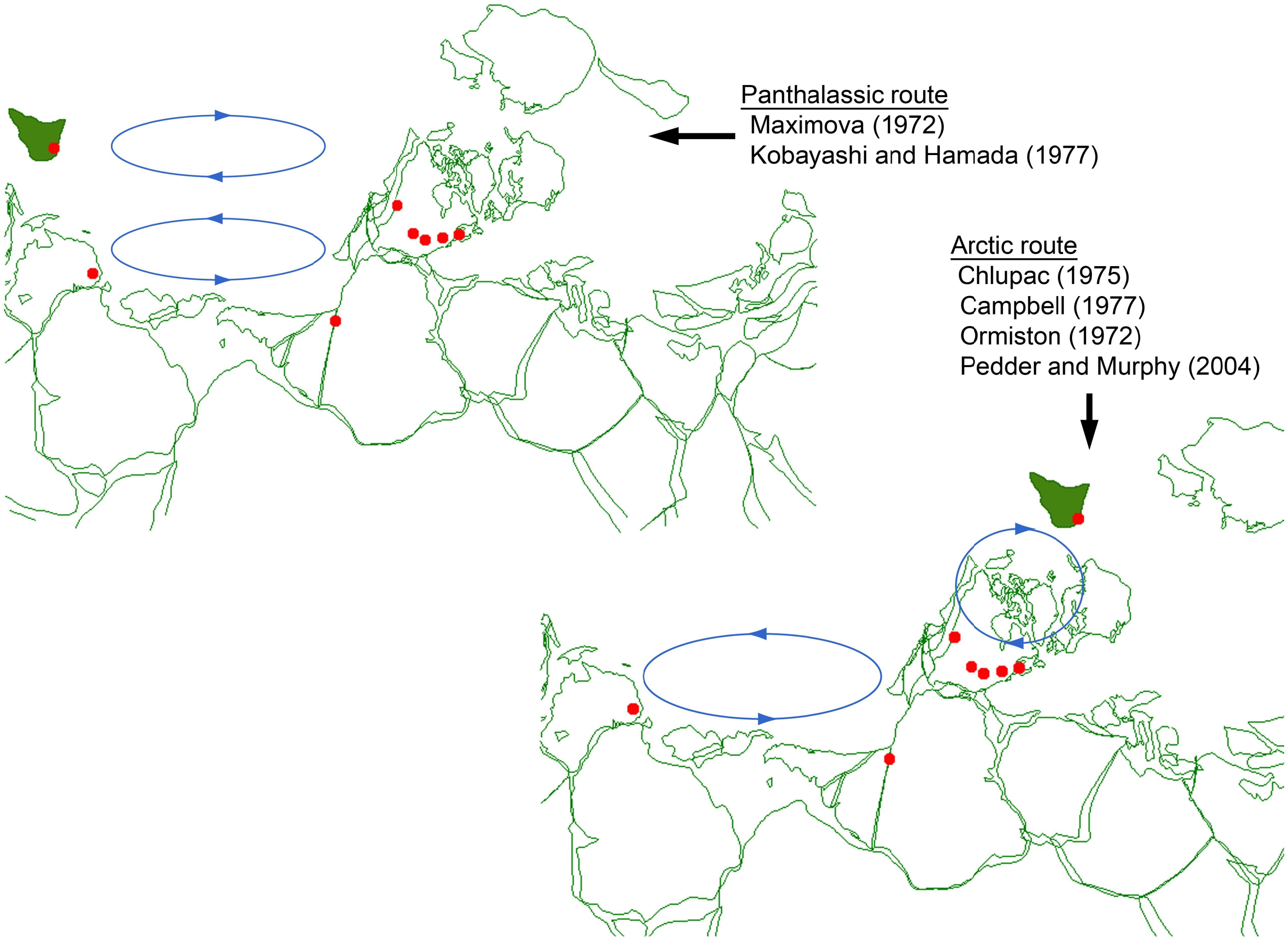

NA (E) + NSW
Bohemia
NA (C)
NA (C)
NSW
NSW
NSW
NA (E)
Central Kazakhstan
Central Kazakhstan
NSW
NW Argentina
NA (E)
NA (W)
NA (W)
NA (C)
NA (E)
NA (E)
Central Bolivia

FIGURE *30*—Based on the distribution pattern and area cladogram of *Paciphacops*, two hypothetical paleomaps concerning the position of Kazakhstan are proposed. Plate Tracker (Eldridge, Walsh, and Scotese, 2000) was used to reconstruct the map. The age is set to 400 Ma. The position of Kazakstan (in solid green) is modified. The map on the top shows a hypothesis of Kazakhstan being on the periphery of the Panthalassa, which is in agreement with the study of Maximova (1972) and Kobayashi and Hamada (1977). Two ocean currents north and south of the approximate paleoequator are indicated in yellow circle. The occurrence of *Paciphacops* is shown in red dots. The map on the bottom places Kazakhstan as a northern extension of Laurentia. Many European species from the western Tethys are found in North America, and some are said to have been migrated via the Arctic route. In this hypothesis, the relationship of Kazakhstan with North America would be established, but not so well with Eastern Australia.

Key words: Migration from Kazakhstan to Nevada into Oklahoma



Panthalassic route
Maximova (1972)
Kobayashi and Hamada (1977)

Arctic route
Chlupac (1975)
Campbell (1977)
Ormiston (1972)
Pedder and Murphy (2004)

APPENDIX

APPENDIX *1*—Bolivian *Viaphacops* characters used for cladistic analysis in Winclada.

A. Cephalon. -- Variability of anterior outline of glabella, configuration and appearance of glabellar furrows, and development of "intercalating ring" have been recognized by various authors (see Chlupáč, 1977: pp. 130-131).

0. Shape of anterior glabella, dorsally: 0) round; 1) round to triangular; 2) triangular.

   Chlupáč (1977) notes that anterior outline of glabella can vary from round to angular, particularly among the species with an overhanging glabellar frontal wall.

1. Shape of genal angle: 0) round; 1) withdrawn posteriorly.

   Eldredge (1977) used this character as one of the keys to distinguish North American Devonian *Paciphacops* and *Viaphacops* species.

2. Genal spine: 0) none; 1) small; 2) large.

   This character is common among young phacopid individuals, but often disappears at the adult stage (Chlupáč, 1977). Having a spine is a derived character (Eldredge, 1973).

3. Postocular platform: 0) well developed; 1) weakly developed; 2) pinched out.

   Absence of this character in North American *Viaphacops* was noted by Eldredge (1973).

4. Height of palpebral lobe, relative to palpebral area: 0) palpebral lobe higher, inflated; 1) about same level; 2) palpebral area higher.

   This is character 13 of Ramsköld and Werdelin (1991).

5. Degree of inflation/depression of medial L1: 0) inflated, forming an intercalating ring; 1) slightly inflated, punctuated by occipital furrow; 2) flat, depressed, continuous from occipital furrow.

   Oftentimes this character is called intercalating ring or preoccipital ring. However, not all phacopid species form a ring as evidenced by *Viaphacops* here, and because it corresponds to the glabellar lobe L1 in other species, it is treated as such here. Consequently, lateral preoccipital lobes are called lateral L1 lobes. The reduction of this character (state 1) was treated as diagnostic of *Viaphacops* by Maximova (1972), which was questioned by subsequent authors as intraspecifically variable (Eldredge, 1973) or as appearing differently on the internal and external molds (Chlupáč, 1977). However, Campbell (1977) accepted it.

6. Appearance of S1 furrows: 0) distinct; 1) weak medially, but continuous transversely; 2) distally only, merged medially with preoccipital lobe.

   This character is of particular importance in determining generic level taxonomy, according to Chlupáč (1977).

7. Appearance of S2: 0) clear, deep; 1) visible, distinct; 2) weak.

   The expression of glabellar furrows S2 as well as S3 (character 8 below) are characters that Chlupáč (1977) noted to be controlled by ontogeny (younger specimens have deeper S2 and S3).

8. Appearance of S3: 0) clear, deep; 1) visible, distinct; 2) weak.

9. Facial suture on librigena: 0) clearly visible; 1) faint; 2) not visible or none.

   This character was functional when molting at the younger stage (Chlupáč, 1977).

10. Width of glabella relative to cephalic width: 0) equal to or less than 60% (average of all specimens measured); 1) 61% or more.

    Measurements were taken for all the specimens available for examination and the average was calculated to be 61% for the glabellar width relative to cephalic width. Species level calculation was done and each average was computed.

11. Shape of occipital ring: 0) low, sagittally wide; 1) tall, sagittally narrow; 2) low, dorsally narrowing.

    The narrowness of occipital ring is one of characteristics of *Viaphacops* listed by Maximova (1972), but it is rejected by Campbell (1977: 33) and Chlupáč (1977: 67).

12. Ornament on occipital ring: 0) none; 1) hint of node; 2) tubercles; 3) spinose.

Eldredge (1973) discussed the development of spines on the occipital ring and genal angle. The presence of an occipital node is a diagnostic character of some North American *Phacops logani* group or *Paciphacops*. The occipital node is a common feature among *Acernaspis* juveniles (Ramsköld and Werdelin, 1991: character 9), and they interpret the absence of a node as being a primitive condition (character state 0 here).

13. Apodemes on glabellar lobe L1, or lateral glabellar L1 lobes: 0) larger than occipital apodemes, to equal, strong; 1) distinct, smaller than occipital apodemes; 2) weak, continuous from medial L1.

Character 5 of Ramsköld and Werdelin (1991). Larger lateral L1 lobes are considered to be more derived. Among the Bolivian *Viaphacops*, lateral L1 lobes are somewhat similar in size, but the distinctness of their appearance differs.

14 – 16. Glabellar tuberculation. Character 8 of Ramsköld and Werdelin (1991) is divided into 3 subcategories (14-16).

14. Uniformity of glabellar tubercles: 0) none; 1) 2 sizes or more; 2) more or less uniform.

15. Appearance of glabellar tubercles: 0) none; 1) indistinct; 2) distinct; 3) prominent; 4) coarse.

16. Density of glabellar tuberculation: 0) none; 1) dense; 2) moderate; 3) sparse.

The density of glabellar tuberculation is determined by the space between the tubercles. When the space is less than a diameter of a tubercle, it is considered to be dense; when more or less equal, it is medium; and when more than that, it is sparse.

17. Ornament on cephalic borders: 0) granules on anterior border only; 1) tubercles only; 2) no ornament; 3) pitted or perforated.

    Character 20 of Ramsköld and Werdelin (1991). Among Bolivian *Viaphacops*, there is no pitted sculpture on cephalic borders as reported by Ramsköld and Werdelin (1991) for many phacopid taxa. Instead, either tubercles or granules can be observed. In North American *Viaphacops*, the sculpture on cephalic border is often pitted.

18. Ornament on palpebral areas: 0) granules and tubercles; 1) tubercles only; 2) smooth.

    Character 19 of Ramsköld and Werdelin (1991). Maximova (1972) notes that *Viaphacops* (*Phacops cristata* group in North America and Kazakhstan) commonly have a tuberculated palpebral area. Again, no pitted or perforated sculpture is observed in Bolivian *Viaphacops*.

19. Ornament on doublure: 0) granules; 1) granules, laterally weakly interconnected; 2) scaly, laterally interconnected; 3) tubercles; 4) smooth.

The presence of wavy ridges on North American phacopid species was recognized by Eldredge (1972). Ornamentation on the doublure is regarded as a morphocline and phylogenetically an important character (Eldredge, 1973). Granulation develops from covering the entire doublure (i.e. *Paciphacops*) to anteromedially only with connected granules posterolaterally (*Viaphacops*) to terrace lines (*Phacops*).

20. Hypostomal suture: 0) straight to arched posteriorly; 1) arched anteriorly to straight; 2) straight.

The course of the hypostomal suture is a phylogenetically significant character recognized by Campbell (1967; see Campbell, 1967, Fig. 2), changing from anteriorly convex to concave. Eldredge (1973) also recognized this character as a possible morphocline, from slightly convex (i.e. *Paciphacops*) to straight (i.e. *Viaphacops*) to concave (i.e. *Phacops*).

21. Vincular furrow: 0) deep, narrow; 1) shallow, wide; 2) medially shallower.

Maximova (1972) distinguished *Paciphacops* (and *Viaphacops*) from the older phacopid genus *Ananaspis* by the development of continuous vincular furrow. Eldredge (1973) noted that the vincular furrow of some *Paciphacops* is medially shallow and that of *Viaphacops* is uniformly continuous. Chlupáč (1977) recognized a deeper vincular furrow on younger specimens, however, he noted that depth and sharpness of this character can vary in internal molds of adults. Campbell (1977) rejected this character as a diagnostic feature of

Viaphacops, and interpreted the varying degree of appearance of this character as dimorphic (p. 36-37). Lespérance (1991) examined vincular furrows of some phacopid species and urged that more attention be paid to this feature in systematics. This is character 24 of Ramsköld and Werdelin (1991).

22. Ornament on vincular furrow: 0) granulated or tuberculated;1) smooth.

The vincular furrow can be variably smooth or ornamented with granules only anteromedially (Eldredge, 1973).

23. Large eye index (eye length/glabellar length): 0) equal to or less than 49% (average of all the specimens measured): 1) 50% or more.

Measurement for the large eye index follows Wolfart (1968). Available specimens were measured at the species level, then each average was calculated. The average of all the species is 49%.

24. Dorsoventral convexity of visual surface: 0) straight; 1) slightly convex; 2) spherical.

This character is distinct when *Viaphacops* species of Bolivia are compared against North American and Kazakhstan species that have character state 1 or 2. All the Bolivian species have character state 0.

25. Palpebral furrow: 0) distinct to strong; 1) distinct, weakening at midpoint; 2) weak.

Character 15 of Ramsköld and Werdelin (1991).

B. Thorax. --

26. Shape of thoracic axial rings: 0) low and wide; 1) low, dorsally narrow; 2) tall, narrow.

This character corresponds to character 11.

27. Ornament on thoracic axial rings: 0) none; 1) tuberculated; 2) spinose; 3) hint of a median node.

A presence of axial nodes on thoracic rings is considered important by Chlupáč (1977), even at generic level. However, Campbell (1977) reports dimorphism of this character as well as on occipital node.

28. Tubercles on thoracic pleurae: 0) present on entire pleurae; 1) present on distal parts only; 2) none.

Character state 0 is an autapomorphy of *Viaphacops pirovanoi* and state 1 is for *V. newelli* only. Other species have character state 2, including the outgroup taxon *Paciphacops waisfeldae*. Eldredge (1973) reports the presence of tubercles on the distal portion of the posterior band of the pleurae in *Phacops cristata stummi*.

29. Apodemes on thoracic axial rings: 0) large, distinct (larger than occipital apodemes); 1) small.

This character is related to the occipital apodemes (character 13), although their appearance and distinctness may differ.

C. Pygidium. --

30. Tubercles on pygidial surface: 0) present; 1) absent.

Chlupáč (1977) considered that this, together with ornamentation on the glabella, is one of the phylogenetically important characters for the phacopids at generic level (p. 133).

31. Number of pygidial axial rings: 0) equal to or more than 9; 1) 8; 2) 7 or less.

Campbell (1977) rejects the notion of weakly segmented pygidium as one of the characters to differentiate *Viaphacops* from *Paciphacops* as reported by Maximova (1972), but Chlupáč (1977) accepted its validity.

32. Terminal piece: 0) absent; 1) present.

Character 28 of Ramsköld and Werdelin (1991). The terminal piece is the medially fused posterior segments on the pygidial axis.

33. Number of visible pleurae: 0) equal to 8 or more; 1) 7; 2) 6; 3) 5.

As in character 33, *Viaphacops* has less segmentation of the pygidium than is the case for *Paciphacops*.

34. Termination of pygidial axis into posterior pleural field or postaxial region: 0) terminates clearly; 1) effaced into posterior pleural field or postaxial region.

Eldredge (1977) reports one of the characters which differentiates *Paciphacops* and *Viaphacops* is the relationship of terminal piece of pygidium and posterior pleural field. In *Paciphacops* it is bluntly rounded posteriorly and in *Viaphacops* it is gradually merged into the posterior pleural field.

35. Pleural furrows: 0) deep, strong, somewhat narrow; 1) distinct, not so deep; 2) wide and shallow.

Character 32 of Ramsköld and Werdelin (1991).

36. Interpleural furrows: 0) deep, strong, somewhat narrow; 1) distinct, not so deep; 2) wide and shallow.

Character 31 of Ramsköld and Werdelin (1991). This is one of the characters Campbell (1977: 36) recognized as dimorphic. However, Chlupáč (1977) took this as a phylogenetic signal.

APPENDIX *2*—List of all the Lower and Middle Devonian phacopid species used in the Otsuka, Dice, and Jaccard Coefficient analyses. Areas analyzed do not follow the scheme of Pedder and Oliver (1990), but are collectively categorized into 15 major areas (Armorica, Australia, Baltica, Bohemia, Central China, Kazakhstan, North Africa, North America, Rhenish, Shan-Thai, South America, South China, Siberia, Turkey, and Zhusilengharhan). For correlation of these areas with Pedder and Oliver's, see text. Literature sources are given next to the area. Age and more specific area at country level are given for each species.

From Armorica (Alberti, 1970; Chlupáč, 1972; Struve, 1972).

Phacops saberensis Morzadec, 1969. Lower Devonian. Spain.

Phacops sabolensis Pillet, 1972. Lower Devonian. France.

Phacops potieri Bayle, 1878. Lower Devonian. France.

Plagiolaria cf. *kockeli* (Alberti, 1968). Lower Devonian. Southeast Sardinia.

Chotecops? *supradevonicus* (Frech, 1887). Middle Devonian. France.

Pedinopariops? *oehlerti* (Morzadec, 1969). Middle Devonian. France.

Phacops occitanicus Barrios, 1886. Middle Devonian. France.

From Shan-Thai (Chlupáč, 1972; Kobayashi and Hamada, 1977; Maximova, 1965; Crônier and Fortey, 2006).

Phacops giganteus Tint and Wai, 1970. Lower Devonian. Burma.

Phacops minutus Tint and Wai, 1970. Lower Devonian. Burma.

Phacops ponensis Reed, 1915. Lower Devonian. Burma.

Phacops shanensis Reed, 1915. Lower Devonian. Burma.

Phacops taungtalonensis Tint and Wai, 1970. Lower Devonian. Burma.

Phacops thahlai Tint and Wai, 1970. Lower Devonian. Burma.

Plagiolaria poothaii Kobayashi and Hamada, 1968. Lower Devonian. Thailand and Malaysia.

Plagiolaria orientalis Maximova, 1965. Middle Devonian. Vietnam.

Reedops vietnamicus Maximova, 1965. Middle Devonian. Vietnam.

From Zhusilengharhan region, western Inner Mongolia (Zhou and Campbell, 1990; Lin, 2008; Yuan and Li, 2008; Zhou and Zhen, 2008).

Boeckops orbiculatus (Nan, 1980). Lower Devonian. Northeast Heilongjiang.

Boeckops xilingolensis (Nan, 1980). Lower Devonian. Northeast Heilongjiang.

Echinophacops mirabilis Zhou, 1983. Lower Devonian. Inner Mongolia.

Rhinophacops schizoloma (Zhou, 1983). Lower Devonian. Inner Mongolia.

Toxophacops (*Toxophacops*) *costata* Zhou and Campbell, 1983. Lower Devonian. Inner Mongolia.

Toxophacops (*Zhusilengops*) *ejinensis* Zhou and Campbell, 1983. Lower Devonian. Inner Mongolia.

Viaphacops delunhudungeensis (Nan, 1976). Lower Devonian. Northeast Inner Mongolia.

Viaphacops genliheensis (Nan, 1980). Lower Devonian. Northeast Heilongjiang.

Viaphacops xiaowoniushanensis (Nan, 1980). Lower Devonian. Northeast Heilongjiang.

Viaphacops cornatus (Nan, 1980). Lower Devonian. Northeast Heilongjiang.

Phacops guranensis Maximova, 1969. Middle Devonian. Far East.

Phacops cf. *okanoi* Sugiyama, 1944. Middle Devonian. Far East.

Phacops manchuricus Kobayashi and Hamada, 1977. Middle Devonian. Far East.

Phacops okanoi Sugiyama, 1944. Middle Devonian. Far East.

Phacops sp. Middle Devonian. Inner Mongolia.

Phacops sp. Middle Devonian. Northeast Heilongjiang.

Reedops nonakai (Okubo, 1956). Middle Devonian. Far East.

Toxophacops (*Atophacops*) *apiculata* Zhou and Campbell, 1990. Middle Devonian. Inner Mongolia.

Toxophacops (*Atophacops*) *cornigera* Zhou and Campbell, 1990. Middle Devonian. Inner Mongolia.

Toxophacops (*Atophacops*) *lepida* Zhou and Campbell, 1990. Middle Devonian. Inner Mongolia.

From Central China (Lin, 2008; Yuan and Li, 2008; Zhou and Zhen, 2008).

Plagiolaria sp. Middle Devonian. Southern Sichuan.

Plagiolaria sp. Middle Devonian. Southwestern Sichuan.

From South China (Lin, 2008; Yuan and Li, 2008; Zhou and Zhen, 2008).

Phacops sp. Lower Devonian. Northern Guangxi.

Plagiolaria sp. Lower Devonian. Northern Guangxi.

Ductina (*Illaenula*) *laevigatus* (Chang and Yin in Yin and Lee, 1978). Middle Devonian. Northern Guangxi.

Ductina (*Illaenula*) sp. Middle Devonian. Southern Yunnan.

Phacops sp. Middle Devonian. Northern Guangxi.

From Australia (Chlupáč, 1972; Feist and Talent, 2000; Kobayashi and Hamada, 1977; Ramsköld and Werdelin, 1991; Sherwin, 1971; Sandford, 2002, 2003; Wright and Haas, 1990).

Echidnops hollowayi Sandford, 2002. Lower Devonian. Victoria, Australia.

Echidnops serratus (Foerste, 1888). Lower Devonian. New South Wales, Australia.

Echidnops sherwini Sandford, 2002. Lower Devonian. Victoria, Australia.

Echidnops sp. A Sandford, 2002. Lower Devonian. Victoria, Australia.

Echidnops wrighti Sandford, 2002. Lower Devonian. Victoria, Australia.

Kainops ekyphymus (Jones et al., 1986). Lower Devonian. New South Wales, Australia.

Kainops microps (Chatterton, Johnson and Campbell, 1979). Lower Devonian. New South Wales, Australia.

Lochkovella rutherfordi (Sherwin, 1968). Lower Devonian. New South Wales, Australia.

Lochkovella longisulcata (Shergold, 1968). Lower Devonian. Victoria, Australia.

Nephranomma debrae Sandford, 2003. Lower Devonian. Victoria, Australia.

Nephranomma janinae Sandford, 2003. Lower Devonian. Victoria, Australia.

Nephranomma lynnae Sandford, 2003. Lower Devonian. Victoria, Australia.

Nephranomma sweeti (Etheridge and Mitchell, 1895). Lower Devonian. Victoria, Australia.

Paciphacops latigenalis (Etheridge and Mitchell, 1895). Lower Devonian. New South Wales, Australia.

Paciphacops crosslei (Etheridge and Mitchell, 1895). Lower Devonian. New South Wales, Australia.

Paciphacops crawfordae Wright and Haas, 1990. Lower Devonian. New South Wales, Australia.

Paciphacops edgecombei Sandford, 2001. Lower Devonian. Victoria, Australia.

Paciphacops mansfieldensis (Etheridge and Mitchell, 1895). Lower Devonian. New South Wales, Australia.

Paciphacops sp. Ebach, 1999. Lower Devonian. New South Wales, Australia.

Phacops? *spedeni* Chatterton, 1971. Lower Devonian. New South Wales, Australia.

Prokops moorei Sandford, 2004. Lower Devonian. Victoria, Australia.

Phacops brocki Feist and Talent, 2000. Middle Devonian. Queensland, Australia.

From Baltica (Chlupáč, 1972; Struve, 1972).

Pedinopariops soblewi (Kielan, 1954). Middle Devonian. Holy Cross Mts., Poland.

Phacops grzegorzowicensis Kielan, 1954. Middle Devonian. Holy Cross Mts., Poland.

Phacops skalensis Kielan, 1954. Middle Devonian. Holy Cross Mts., Poland.

Phacops sobolevi Kielan, 1954. Middle Devonian. Holy Cross Mts., Poland.

From Bohemia (Budil and Kolář, 2007; Chlupáč, 1972; Ramsköld and Werdelin, 1991; Struve, 1972)

Boeckops delphinoides Chlupáč, 1972. Lower Devonian. Barrandian, Bohemia.

Boeckops zenonis Chlupáč, 1972. Lower Devonian. Barrandian, Bohemia.

Boeckops boecki (Hawle and Corda, 1847). Lower Devonian. Barrandian, Bohemia.

Kainops chlupaci Budil and Kolář, 2007. Lower Devonian. Prague Basin, Bohemia.

Kainops veles (Chlupáč, 1972). Lower Devonian. Barrandian, Bohemia.

Lochkovella misera (Barrande, 1852). Lower Devonian. Europe.

Phacops degener Barrande, 1852. Lower Devonian. Barrandian, Bohemia.

Phacops? *hanusi* Chlupáč, 1972. Lower Devonian. Barrandian, Bohemia.

Prokops hoeninghausi Barrande, 1846. Lower Devonian. Barrandian, Bohemia.

Prokops prokopi Chlupáč, 1971. Lower Devonian. Barrandian, Bohemia.

Reedops decorus Hawle and Corda, 1847. Lower Devonian. Barrandian, Bohemia.

Reedops modestus Barrande, 1872. Lower Devonian. Barrandian, Bohemia.

Reedops bronni (Barrande, 1846). Lower Devonian. Barrandian, Bohemia.

Reedops cephalotes Hawle and Corda, 1847. Lower Devonian. Barrandian, Bohemia.

Reedops intermedius Barrande, 1852. Lower Devonian. Barrandian, Bohemia.

Reedops prospicens Chlupáč, 1972. Lower Devonian. Barrandian, Bohemia.

Reedops sternbergi Hawle and Corda, 1847. Lower Devonian. Barrandian, Bohemia.

Chotecops auspex (Chlupáč, 1971). Middle Devonian. Barrandian, Bohemia.

Chotecops hoseri (Hawle and Corda, 1947). Middle Devonian. Barrandian, Bohemia.

Chotecops glabrens Chlupáč, 1972. Middle Devonian. Barrandian, Bohemia.

Chotecops? *breviceps* (Barrande, 1846). Middle Devonian. Barrandian, Bohemia.

Pedinopariops regius (Chlupáč, 1971). Middle Devonian. Barrandian, Bohemia.

Phacops insequens Chlupáč, 1972. Middle Devonian. Barrandian, Bohemia.

Phacops major Barrande, 1852. Middle Devonian. Barrandian, Bohemia.

Phacops superior Chlupáč, 1972. Middle Devonian. Barrandian, Bohemia.

Phacops superstes Barrande, 1852. Middle Devonian. Barrandian, Bohemia.

Signatops signatus (Hawle and Corda, 1847). Middle Devonian. Barrandian, Bohemia.

Struveaspis fugitiva (Barrande, 1872). Middle Devonian. Barrandian, Bohemia.

Struveaspis micromma (Roemer, 1852). Middle Devonian. Europe and Morocco.

From Kazakhstan (Kobayashi and Hamada, 1977; Maximova, 1960, 1967, 1968, 1972, 1974, 1978).

Angulophacops saryarkensis (Maximova, 1968). Lower Devonian. Central Kazakhstan.

Angulophacops balchaschensis (Maximova, 1968). Lower Devonian. Central Kazakhstan.

Paciphacops aff. *boecki* (Hawle and Corda, 1847). Lower Devonian. Central Kazakhstan.

Paciphacops fecundus orientalis (Maximova, 1968). Lower Devonian. Central Kazakhstan.

Viaphacops dentatus (Maximova, 1968). Lower Devonian. Central Kazakhstan.

Viaphacops praepipa (Maximova, 1968). Lower Devonian. Central Kazakhstan.

Viaphacops pustulatus (Maximova, 1968). Lower Devonian. Central Kazakhstan.

Angulophacops angulatus (Maximova, 1968). Middle Devonian. Central Kazakhstan.

Angulophacops acutus (Maximova, 1968). Middle Devonian. Central Kazakhstan.

Angulophacops alticus (Tschernyshew, 1893). Middle Devonian. Rudny Altai (Siberia) and central Kazakhstan.

Viaphacops aff. *pustulatus* (Maximova, 1968). Middle Devonian. Central Kazakhstan.

Viaphacops mongolicus Maximova, 1974. Middle Devonian. Mongolian Altai.

Viaphacops subcristatus (Khalfin, 1955). Middle Devonian. Central Kazakhstan.

From North Africa (Alberti, 1970, 1980, 1981, 1983; Chatterton et al., 2006; Chlupáč, 1972; Fortey and Morris, 1977; Haas, 1968; McKellar and Chatterton, 2009; Richter and Richter, 1943; Struve, 1982, 1995; Termier and Termier, 1950).

Austerops smoothops (Chatterton et al., 2006). Lower Devonian, Morocco.

Barrandeops granulops (Chatterton et al., 2006). Lower Devonian. Morocco

Boeckops algericus Alberti, 1983. Lower Devonian. Algeria.

Boeckops maidericus Alberti, 1983. Lower Devonian. Morocco.

Phacops akouchensis Termier and Termier, 1960. Lower Devonian. Morocco.

Phacops? *hollardinus* Alberti, 1983. Lower Devonian. Morocco.

Plagiolaria? *senex* Alberti, 1983. Lower Devonian. Algeria.

Prokops benziregensis Alberti, 1983. Lower Devonian. Algeria.

Prokops chlupaci Alberti, 1983. Lower Devonian. Algeria.

Prokops ezzhiligensis Alberti, 1983. Lower Devonian. Morocco.

Prokops slimanensis Alberti, 1981. Lower Devonian. Morocco.

Prokops bonnoides (Richter and Richter, 1943). Lower Devonian. Morocco.

Reedops modestus sp. A (Barrande, 1872). Lower Devonian. Morocco.

Reedops algericanus Alberti, 1983. Lower Devonian. Morocco.

Reedops hamlagdadianus Alberti, 1983. Lower Devonian. Morocco.

Reedops sp. A aff. *akouchensis* Termier and Termier, 1950. Lower Devonian. Morocco.

Reedops maurulus (Alberti, 1970). Lower Devonian. Morocco.

Reedops platilegnotor Alberti, 1970. Lower Devonian. Morocco.

Reedops aff. *sternbergi* (Hawle and Corda, 1847). Lower Devonian. Morocco and Thuringia, Germany.

Reedops cf. *sternbergi* (Hawle and Corda, 1847). Lower Devonian. Morocco.

Reedops paenecaecus Alberti, 1970. Lower Devonian. Germany.

Reedops sp. aff. *maurulus* Alberti, 1970. Lower Devonian. Morocco.

Reedops cf. *bronni* (Barrande, 1846). Lower Devonian. Morocco.

Reedops struveianus Alberti, 1983. Lower Devonian. Algeria.

Barrandeops lebesus (Chatterton et al., 2006). Middle Devonian. Morocco

Chotecops zizensis Alberti, 1983. Middle Devonian. Morocco.

Chotecops gr. *hoseri* (Hawle and Corda, 1847). Middle Devonian. Morocco.

Chotecops occidomaurus Alberti, 1981. Middle Devonian. Morocco.

Chotecops despujolsi (Richter and Richter, 1943). Middle Devonian. Morocco.

Drotops megalomanicus Struve, 1990. Middle Devonian. Morocco.

Drotops subornatus Struve, 1995. Middle Devonian. Morocco.

Drotops armatus forma *accurata* Struve, 1995. Middle Devonian. Morocco.

Drotops armatus forma *armata* Struve, 1995. Middle Devonian. Morocco.

Drotops armatus forma *hoplites* Struve, 1995. Middle Devonian. Morocco.

Drotops armatus forma *perspinosa* Struve, 1995. Middle Devonian. Morocco.

Eldredgeops africanus (Bruton and Eldredge, 1974). Middle Devonian. Morocco.

Eldredgeops tindoufensis (Bruton and Eldredge, 1974). Middle Devonian. Morocco.

Eocryphops termieri Richter and Richter, 1943. Middle Devonian. Morocco.

Hypsipariops lyncops Struve, 1982. Middle Devonian. Morocco.

Hypsipariops vagabundus Struve, 1990. Middle Devonian. Morocco.

Phacops papulatus Richter and Richter, 1943. Middle Devonian. Morocco.

Phacops batracheus Whidbourne, 1889. Middle Devonian. Morocco.

Phacops campbelli Alberti, 1983. Middle Devonian. Morocco.

Phacops tafilaltanus Alberti, 1983. Middle Devonian. Morocco.

Phacops turco aff. *praecedens* Haas, 1968. Middle Devonian. Morocco.

Phacops? *menchikoffi* La Maître, 1952. Middle Devonian. Algeria.

Phacops? *speculator* Alberti, 1970. Middle Devonian. Morocco.

Reedops? *bronnoides* Richter and Richter, 1943. Middle Devonian. Morocco.

Struveaspis maroccanica Alberti, 1970. Middle Devonian. Morocco.

Struveaspis micromma (Roemer, 1852). Middle Devonian. Europe and Morocco.

Struveaspis ougartensis Alberti, 1981. Middle Devonian. Morocco.

From North America (Campbell, 1977; Chlupáč, 1972; Eldredge, 1973; Lespérance, 1991; Merriam, 1973; Ramsköld and Werdelin, 1991; Stewart, 1922; Tansey, 1922).

Kainops invius (Campbell, 1977). Lower Devonian. Oklahoma.

Kainops raymondi (Delo, 1935). Lower Devonian. Eastern North America.

Paciphacops birdsongensis (Delo, 1940). Lower Devonian. Eastern North America.

Paciphacops cf. *birdsongensis* (Delo, 1940). Lower Devonian. Eastern North America.

Paciphacops campbelli Ramsköld and Werdelin, 1991. Lower Devonian. Eastern North America.

Paciphacops clarkei (Eldredge, 1973). Lower Devonian. Eastern North America.

Paciphacops eldredgei Ramsköld and Werdelin, 1991. Lower Devonian. Eastern North America.

Paciphacops hudsonicus (Hall, 1861). Lower Devonian. Eastern North America.

Paciphacops logani (Hall, 1861). Lower Devonian. Eastern North America.

Paciphacops sp. A (Eldredge, 1973). Lower Devonian. Eastern North America.

Paciphacops n. sp. Campbell, 1977. Lower Devonian. Nevada.

Paciphacops sp. B (Merriam, 1973). Lower Devonian. Nevada.

Paciphacops claviger (Haas, 1968). Lower Devonian. Nevada.

Paciphacops natlensis (Perry and Chatterton, 1976). Lower Devonian. NW Territory, Canada.

Phacops? *deckeri* (Delo, 1935). Lower Devonian. Oklahoma.

Reedops amsdeni Ormiston, 1968. Lower Devonian. Oklahoma.

Reedops? n. sp. Haas, 1968. Lower Devonian. Nevada.

Viaphacops cf. *bombifrons* (Hall, 1861). Lower Devonian. Eastern North America.

Viaphacops cristata (Hall, 1861). Lower Devonian. Eastern North America.

Viaphacops gaspensis (Clarke, 1908). Lower Devonian. Eastern North America.

Viaphacops. sp. Campbell, 1977. Lower Devonian. Oklahoma.

Viaphacops variabilis (Eldredge, 1973). Lower Devonian. Eastern North America.

Eldredgeops milleri (Steward, 1927). Middle Devonian. Eastern North America.

Phacops alpenensis Stumm, 1953. Middle Devonian. Eastern North America.

Phacops crassituberculata Stumm, 1953. Middle Devonian. Eastern North America.

Phacops paucituberculata Eldredge, 1972. Middle Devonian. Eastern North America.

Phacops iowensis Delo, 1935. Middle Devonian. Eastern North America.

Phacops southworthi Stumm, 1953. Middle Devonian. Eastern North America.

Phacops norwoodensis Stumm, 1953. Middle Devonian. Eastern North America.

Phacops rana (Green, 1832). Middle Devonian. Eastern North America.

Viaphacops bombifrons (Hall, 1861). Middle Devonian. Eastern North America.

Viaphacops canadensis (Stumm, 1954). Middle Devonian. Eastern North America.

Viaphacops nasutus (Stumm, 1954). Middle Devonian. Eastern North America.

Viaphacops stummi (Eldredge, 1973). Middle Devonian. Eastern North America.

Viaphacops vitrea Lespérance, 1991. Middle Devonian. Eastern North America.

From Rhenish (Alberti, 1970; Basse, 1998, 2006; Chlupáč, 1972; Struve, 1972, 1982, 1992; van Viersen, 2007).

Arduennops michelsi Struve, 1970. Lower Devonian. Eifel Mts., Germany.

Boeckops "*zinkeni*" (Roemer, 1849). Lower Devonian. Harz Mts., Germany.

Boeckops planilimbatus (Wedekind, 1914). Lower Devonian. Kellerwald Mts., Germany.

Cultrops werneri Struve, 1970. Lower Devonian. Eifel Mts., Germany.

Liolophops hefteri Struve, 1970. Lower Devonian. Rheinland, Germany.

Phacops obtusiceps Struve, 1970. Lower Devonian. Eifel Mts., Germany.

Phacops delivifrons Struve, 1970. Lower Devonian. Eifel Mts., Germany.

Phacops? *zorgensis* Kayser, 1878. Lower Devonian. Harz Mts., Germany.

Plagiolaria kockeli (Alberti, 1968). Lower Devonian. Kellerwald Mts., Germany.

Prokops? *denckmanni* (Wedekind, 1914). Lower Devonian. Kellerwald Mts., Germany.

Prokops? *rubidus* (Wedekind, 1914). Lower Devonian. Kellerwald Mts., Germany.

Reedops schmidti Eichenberg, 1930. Lower Devonian. Rheinland, Germany.

Reedops bodei Alberti, 1968. Lower Devonian. Harz Mts., Germany.

Reedops? *schuebelbergensis* Alberti, 1970. Lower Devonian. Frankenwald area, Germany.

Reedops steinhornensis (Wedekind, 1914). Lower Devonian. Kellerwald Mts., Germany.

Reedops? *walcotti* (Wedekind, 1914). Lower Devonian. Kellerwald Mts., Germany.

Chotecops hassiacus (Hermann, 1911). Middle Devonian. Rheinland, Germany.

Chotecops latissimus (Holzapfel, 1895). Middle Devonian. Rheinland, Germany.

Chotecops spectabilis (Meischner, 1965). Middle Devonian. Kellerwald Mts., Germany.

Chotecops? *hyla* (Holzapfel, 1895). Middle Devonian. Rheinland, Germany.

Eocryphops cyclophthalmus (Walther, 1907). Middle Devonian. Thuringia, Germany.

Eocryphops kayseri (Herrmann, 1911). Middle Devonian. Rheinland, Germany.

Geesops schlotheimi (Bronn, 1852). Middle Devonian. Eifel Mts., Germany.

Geesops cf. *schlotheimi* (Bronn, 1852). Middle Devonian. Ardennes, Belgium.

Geesops sparsinodosus (Struve, 1970). Middle Devonian. Eifel Mts., Germany.

Geesops battidohmi Struve, 1992. Middle Devonian. Eifel Mts., Germany.

Geesops brunopauli Struve, 1982. Middle Devonian. Rhenish Mts., Germany.

Geesops gallicus Struve, 1982. Middle Devonian. Ardennes, Belgium.

Geesops synapticus Struve, 1982. Middle Devonian. Eifel Mts., Germany.

Geesops grevensteinensis Basse, 1998. Middle Devonian. W. Sauerland, Germany.

Geesops miles Basse, 1998. Middle Devonian. W. Sauerland, Germany.

Geesops sp. n. aff. *brunopauli* Struve, 1982. Middle Devonian. Herscheider Mts., Germany.

Geesops sp. E Basse, 1998. Middle Devonian. Endorf, Germany.

Geesops sp. L Basse, 1998. Middle Devonian. Attendorn, Germany.

Hypsipariops kowalskii Struve, 1992. Middle Devonian. Eifel Mts., Germany.

Liolophops sublevatus Struve, 1970. Middle Devonian. Eifel Mts., Germany.

Nyterops nyter Struve, 1970. Middle Devonian. Eifel Mts., Germany.

Nyterops yetieifelensis Basse, 2006. Middle Devonian. Eifel Mts., Germany.

Nyterops hollandi van Viersen, 2007. Middle Devonian. Ardennes, Belgium.

Pedinopariops lentigifer Struve, 1970. Middle Devonian. Eifel Mts., Germany.

Pedinopariops proniceps Struve, 1970. Middle Devonian. Eifel Mts., Germany.

Pedinopariops richterianus Struve, 1970. Middle Devonian. Eifel Mts., Germany.

Pedinopariops erebeus Struve, 1992. Middle Devonian. Germany and Belgium.

Pedinopariops brongniarti (Steininger, 1831). Middle Devonian. Eifel Mts., Germany.

Pedinopariops eurycaulus (Struve, 1970). Middle Devonian. Gummersbach, Germany.

Pedinopariops simulator Basse, 1998. Middle Devonian. W. Sauerland, Germany.

Pedinopariops sp. A Basse, 1998. Middle Devonian. Endorf, Germany.

Pedinopariops sp. aff. *lentigifer* Struve, 1970. Middle Devonian. Gummersbach, Germany.

Pedinopariops sp. B Basse, 1998. Middle Devonian. Gummersbach, Germany.

Pedinopariops sp. C Basse, 1998. Middle Devonian. Gummersbach, Germany.

Pedinopariops sp. H Basse, 1998. Middle Devonian. Dillenburg, Germany.

Pedinopariops? sp. 168 Basse, 1998. Middle Devonian. Hangenden, Germany.

Pedinopariops? sp. 417 Basse, 1998. Middle Devonian. Hangenden, Germany.

Pedinopariops? *syringes* (Struve, 1992). Middle Devonian. Wildungen, Germany.

Phacops dolosus Struve, 1970. Middle Devonian. Eifel Mts., Germany.

Phacops fragosus Struve, 1970. Middle Devonian. Eifel Mts., Germany.

Phacops imitator Struve, 1970. Middle Devonian. Eifel Mts., Germany.

Phacops latifrons (Bronn, 1825). Middle Devonian. Eifel Mts., Germany.

Phacops soetenicus Struve, 1970. Middle Devonian. Eifel Mts., Germany.

Phacops s.l. cf. *spectabilis* (Meischner, 1965). Middle Devonian. Goddelsheim, Germany.

Phacops s.l. gr. *koeneni* Holzapfel, 1895. Middle Devonian. Rothaargebirge, Germany.

Phacops s.l. *rhenanus* Novak, 1890. Middle Devonian. Kellerwald Mts., Germany.

Phacops s.l. sp. A Basse, 1998. Middle Devonian. Wildungen, Germany.

Phacops s.l. sp. aff. *major* Barrande, 1852. Middle Devonian. Wildungen, Germany.

Phacops s.l. sp. B Basse, 1998. Middle Devonian. Ense-Grenzweg, Germany.

Phacops s.l. sp. C Basse, 1998. Middle Devonian. Ense-Grenzweg, Germany.

Phacops s.l. sp. M Basse, 1998. Middle Devonian. Hohenlimberg, Germany.

Phacops s.l. sp. P Basse, 1998. Middle Devonian. Hohenlimberg, Germany.

Phacops s.l. sp. R Basse, 1998. Middle Devonian. Lahn Mts., Germany.

Phacops s.l. spp. Basse, 1998. Middle Devonian. Dillenburg, Germany.

Phacops s.l.? sp. D Basse, 1998. Middle Devonian. Langenaubach, Germany.

Phacops s.l.? sp. E Basse, 1998. Middle Devonian. Hangenden, Germany.

Plagiolaria plagiophthalma (R. Richter, 1931). Middle Devonian. Thuringia, Germany.

Reedops? *hercyniae* Alberti, 1968. Middle Devonian. Harz Mts., Germany.

Reedops? *thuringicus* Kegel, 1931. Middle Devonian. Thuringia, Germany.

Teichertops bardenheueri Struve, 1992. Middle Devonian. Europe.

Teichertops soetenicus Struve, 1970. Middle Devonian. Cürten/Rodert, Germany.

From South America (Ahlfeld and Braniša, 1960; Baldis and Longobucco, 1977; Braniša, 1965; Carvalho and Moody, 2000; Edgecombe and Ramsköld, 1994;

Eldredge and Ormiston, 1979; Kozlowski, 1923; Newell, 1949; Pek and Vaněk, 1991; Wolfart, 1968).

Paciphacops argentinus (Thomas, 1905). Lower Devonian. NW Argentina.

Paciphacops spatiosus (Pek and Vaněk, 1991). Lower Devonian. Bolivia.

Paciphacops waisfeldae Edgecombe and Ramsköld, 1994. Lower Devonian. Central Bolivia.

Viaphacops cf. *orurensis* (Bonarelli, 1921). Lower Devonian. Bolivia.

Viaphacops pirovanoi n. sp. Lower Devonian. Bolivia.

Viaphacops newelli n. sp. Lower Devonian. Bolivia and southern Peru.

Viaphacops salteri (Kozlowski, 1923). Lower Devonian. Bolivia.

Viaphacops cf. *chavelai* (Baldis and Longobucco, 1977). Middle Devonian. Bolivia.

Viaphacops cf. *salteri* (Kozlowski, 1923). Middle Devonian. Colombia.

Viaphacops chavelai (Baldis and Longobucco, 1977). Middle Devonian. NW Argentina.

Viaphacops kozlowskii Pek and Vaněk, 1991. Middle Devonian. Bolivia.

Viaphacops multicinctus Pek and Vaněk, 1991. Middle Devonian. Bolivia.

Viaphacops orurensis (Bonarelli, 1921). Middle Devonian. Bolivia.

Viaphacops spinoedgecombei n. sp. Middle Devonian. Bolivia.

Viaphacops venezuelensis Carvalho and Moody, 2000. Middle Devonian. Venezuela.

From Siberia (Chlupáč, 1972; Kobayashi and Hamada, 1977; Maximova, 1960, 1972, 1978; Zhou and Zhen, 2008).

Paciphacops solidus (Hsiang and Zhang, 1983). Lower Devonian. Northern Xinjiang.

Paciphacops mangkeluensis (Hsiang and Zhang, 1983). Lower Devonian. Northern Xinjiang.

Reedops sp. Lower Devonian. Northeastern Xinjiang.

Struveaspis xingjiangensis (Hsiang and Zhang, 1983). Lower Devonian. Northeastern

Angulophacops sublatifrons (Tchernysheva, 1951). Middle Devonian. Kuznetsk Basin, southern Siberia.

Phacops ulbensis Maximova, 1960. Middle Devonian. Rudny Altai, southern Siberia.

Plagiolaria sp. Middle Devonian. Northern Xinjiang.

Viaphacops cf. *cristata* var. *pipa* (Hall and Clarke, 1888). Middle Devonian. Rudny Altai, southern Siberia.

Viaphacops ex gr. *cristata* (Hall and Clarke, 1888). Middle Devonian. Rudny Altai, southern Siberia.

Viaphacops oculeus (Maximova, 1960). Middle Devonian. Rudny Altai, southern Siberia.

Angulophacops alticus (Tschernyshew, 1893). Middle Devonian. Rudny Altai, southern Siberia and central Kazakhstan.

Viaphacops cf. *altaicus* (Tschernyshew, 1893). Middle Devonian. Rudny Altai, southern Siberia.

From Turkey (Chlupáč, 1972; Haas, 1968)

Boeckops proponticus (Haas, 1968). Lower Devonian. Turkey (Pontides).

Chotecops successor (Haas, 1968). Lower Devonian. Turkey (Pontides).

Phacops corallinus Richter and Richter, 1939. Lower Devonian. Turkey (Pontides).

Phacops pantichionensis Haas, 1968. Lower Devonian. Turkey (Pontides).

Reedops seleniomma Haas, 1968. Lower Devonian. Turkey (Pontides).

Boeckops confluens (Richter and Richter, 1939). Middle Devonian. Turkey (Pontides).

Phacops praecendens Haas, 1968. Middle Devonian. Turkey (Pontides).

Phacops turco Richter and Richter, 1939. Middle Devonian. Turkey (Pontides).

APPENDIX *3*—Genera studied, their type species and distribution.

Angulophacops Maximova, 1978. *Phacops angulatus* Maximova, 1968. Lower and Middle Devonian (pre-Givetian). Central Kazakhstan and southern Siberia.

Arduennops Struve, 1972. *Phacops michelsi* Hawle and Corda, 1847. Emsian (Lower Devonian). Luxemburg. Monotypic.

Austerops McKellar and Chatterton, 2009. *Phacops smoothops* Chatterton et al., 2006. Upper Emsian (Lower Devonian). Morocco.

Barrandeops McKellar and Chatterton, 2009. *Phacops granulops* Chatterton et al., 2006. Upper Emsian (Lower Devonian). Morocco.

Boeckops Chlupáč, 1972. *Phacops boecki* Hawle and Corda, 1847. Pragian (Lower Devonian) to Eifelian (Middle Devonian). Bohemia, Germany (Thuringia), North Africa (Morocco, Algeria), and Turkey (Pontides).

Chotecops Chlupáč, 1971. *Chotecops auspex* Chlupáč, 1971. Eifelian (Lower Devonian). Bohemia, Germany (Thuringia), Siberia (Urals, Rudny Altai), North Africa (Morocco), Turkey and France (?).

Cultrops Struve, 1995. *Phacops werneri* Struve, 1970. Emsian (Lower Devonian). Eifel Mts., Germany. Monotypic.

Drotops Struve, 1990. *Drotops megalomanicus* Struve, 1995. Midde Devonian. North Africa (Morocco).

Ductina (*Illaenula*) Chlupáč, 1977. *Ductina* (*Illaenula*) *illaenoides* Chlupáč, 1977. Middle Devonian. Europe, Asia (Ural Mts., Southeast Asia).

Echidnops Sandford, 2002. *Echidnops wrighti* Sandford, 2002. Lower Devonian. Australia (New South Wales and Victoria).

Echinophacops Zhou, 1983. *Echinophacops mirabilis* Zhou, 1983. Emsian (Lower Devonian). Inner Mongolia.

Eldredgeops Struve, 1990. *Phacops milleri* Stewart, 1927. Eifelian-Givetian (Middle Devonian). Eastern North America and North Africa (Morocco).

Eocryphops Richter and Richter, 1931. *Phacops kayseri* Herrmann, 1909. Middle Devonian. Germany (Thuringia) and North Africa (Morocco).

Geesops Struve, 1972. *Calymene schlotheimi* Bronn, 1825. Eifelian-Givetian (Middle Devonian). Germany (Thuringia).

Hypsipariops Struve, 1982. *Pedinopariops* (*Hypsipariops*) *lyncops* Struve, 1982. Eifelian-Givetian (Middle Devonian). Germany (Thuringia) and North Africa (Morocco).

Kainops Ramsköld and Werdelin, 1991. *Paciphacops microps* Chatterton, Johnson, and Campbell, 1979. Lower Devonian. Bohemia and Australia (New South Wales).

Liolophops Struve, 1972. *Phacops sublevatus* Struve, 1970. Upper Emsian (Lower Devonian) to Eifelian (Middle Devonian). Germany (Thuringia).

Lochkovella Chlupáč, 1972. *Phacops misera* Barrande, 1852. Lower Devonian. Bohemia and Australia (New South Wales, Victoria).

Nephranomma Erben, 1952. *Phacopidella* (*Nephranomma*) *drepanomma* Erben, 1952. Lower Devonian. Australia (Victoria).

Nyterops Struve, 1972. *Phacops nyter* Struve, 1970. Givetian (Middle Devonian). Germany. Monotypic.

Paciphacops Maximova, 1972. *Phacops logani* Hall, 1961. Lower Devonian. Kazakhstan, central Bolivia, northern Argentina, Eastern North America, Oklahoma, Nevada, Alaska, and Australia (New South Wales, Victoria).

Pedinopariops Struve, 1972. *Phacops lentigifer* Struve, 1970. Emsian (Lower Devonian) to Givetian (Middle Devonian). Armorica (France), Baltica (Poland), Bohemia, Belgium and Germany (Thuringia).

Phacops Emmrich, 1839. *Calymene latifrons* Brongniart, 1825. Pragian (Lower Devonian) to Upper Devonian. Armorica (Spain, France), Asia (Far East, Burma), Australia (Queensland, New South Wales), Baltica (Poland), Bohemia, North Africa (Morocco, Algeria), Eastern North America, Germany (Thuringia), Siberia (Rudny Altai), and Turkey (Pontides).

Plagiolaria Kegel, 1925. *Phacops plagiophthlamus* Richter, 1865. Pragian (Lower Devonian) to Middle Devonian. Armorica (Sardinia), Germany (Thuringia), Asia (Vietnam, Thailand, Malaysia), North Africa (Algeria).

Prokops Chlupáč, 1971. *Prokops prokopi* Chlupáč, 1971. Pragian (Lower Devonian) into Middle Devonian. North Africa (Morocco, Algeria), Australia (Victoria), Germany (Thuringia), Bohemia.

Reedops Richter and Richter, 1925. *Phacops bronni* Barrande, 1846. Lochkovian (Lower Devonian) to Middle Devonian. Asia (Far East, Vietnam), Bohemia, North Africa (Morocco, Algeria), North America (Oklahoma, Nevada), Germany (Thuringia), Turkey (Pontides).

Rhinophacops Kaneko, 1990. *Echinophacops schizoloma* Zhou, 1983. Emsian (Lower Devonian). Inner Mongolia.

Signatops Přibyl and Vaněk, 1971. *Phacops signatus* Hawle and Corda, 1847. Middle Devonian. Bohemia.

Struveaspis Alberti, 1966. *Phacops micromma* Roemer, 1854. Eifelian (Middle Devonian). North Africa (Morocco) and Bohemia.

Teichertops Struve, 1992. *Teichertops bardenheueri* Struve, 1992. Middle Devonian. Germany (Thuringia).

Toxophacops Zhou and Campbell, 1990. *Toxophacops* (*Toxophacops*) *costata* Zhou and Campbell, 1990. Emsian (Lower Devonian) to Eifelian (Middle Devonian). Inner Mongolia.

Viaphacops Maximova, 1972. *Phacops cristata* var. *pipa* Hall and Clarke, 1888. Lower to Middle Devonian. Central Kazakhstan, Mongolian Altai, southern Siberia (Rudny Altai), Eastern North America, Oklahoma, Bolivia, Peru, Venezuela and Colombia.

APPENDIX *4*—A total of nineteen phacopid taxa analyzed for area cladistics. Four *Kainops* species are selected for outgroup taxa. For the ingroup taxa, 12 *Paciphacops*, one species assigned to it with uncertainty (i.e. ‘*Paciphacops’ claviger*), one *Angulophacops* and one *Phacops* were selected. They occur semi-globally in the Lower Devonian, except for *Paciphacops latigenalis* which occurs in the Upper Silurian. They are completely absent from Europe.

Kainops microps (Chatterton, Johnson and Campbell 1979). Pragian. Garra Fm., New South Wales, Australia and Birdsong Fm., Tennessee, North America.

Kainops veles (Chlupáč 1972). Pragian. Upper Koneprusy Ls., Barrandian, Bohemia.

Kainops invius (Campbell 1977). Lower Lochkovian (or Gedinnian). Bois d'Arc Fm., Oklahoma, North America.

Kainops raymondi (Delo 1935). Lower Lochkovian (or Gedinnian). Haragan Fm., Oklahoma, North America.

Echidnops serratus (Foerste 1888). Lower Lochkovian (Lower Gedinnian). Elmside Fm., New South Wales, Australia.

(It is treated as *Paciphacops* in this analysis.)

Paciphacops crosslei (Etheridge and Mitchell 1895). Lower Lochkovian (Lower Gedinnian). Elmside Fm., New South Wales, Australia.

Paciphacops latigenalis (Etheridge and Mitchell 1895). Upper Ludlow, Silurian. Rosebank Sh., New South Wales, Australia.

Paciphacops eldredgei Ramsköld and Werdelin 1991. Lower Lochkovian (or Gedinnian). Birdsong Fm., Tennessee, North America.

Paciphacops hudsonicus (Hall 1861). Lower Lochkovian (or Gedinnian). Kalkberg-New Scotland Fms., NY, North America.

Paciphacops logani (Hall 1861). Lower Lochkovian (or Gedinnian). New Scotland Fm., NY, North America.

Paciphacops campbelli Ramsköld and Werdelin 1991. Lower Lochkovian (or Gedinnian). Haragan Fm., Oklahoma, North America.

Paciphacops birdsongensis (Delo 1940). Lower Lochkovian (or Gedinnian). Birdsong Fm., Tennessee, North America.

Paciphacops claviger (Haas 1968). Upper Lochkovian – Lower Pragian (or Siegenian). Wenban Ls., Nevada, North America.

Paciphacops waisfeldae Edgecombe and Ramsköld 1994. Lower Lochkovian. Catavi Fm., Cochabamba Dept., Bolivia, Central Bolivia.

Paciphacops crawfordae Wright and Haas 1990. Upper Pragian. Limekiln Fm., New South Wales, Australia.

Paciphacops argentinus (Thomas 1905). Pridolian or early Lochkovian. Los Espejos Fm., San Juan, NW Argentina.

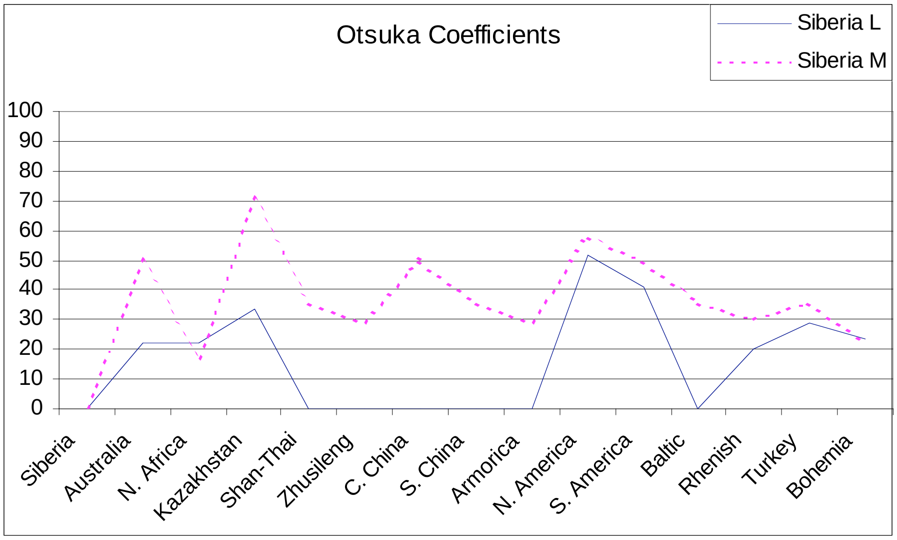
Angulophacops saryarkensis (Maximova 1968). Lower Lochkovian (or Gedinnian). Central Kazakhstan.

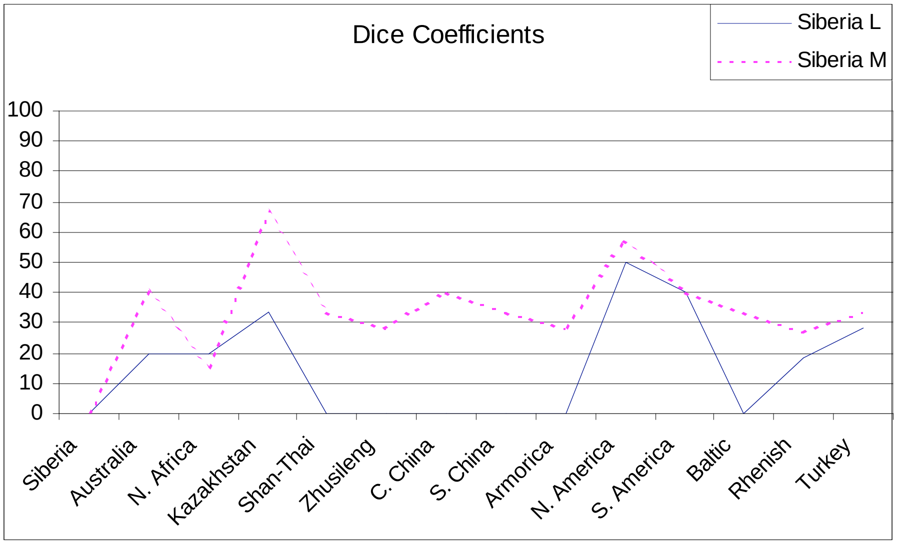
Angulophacops balchaschensis (Maximova 1968). Lower Lochkovian (or Gedinnian). Central Kazakhstan.

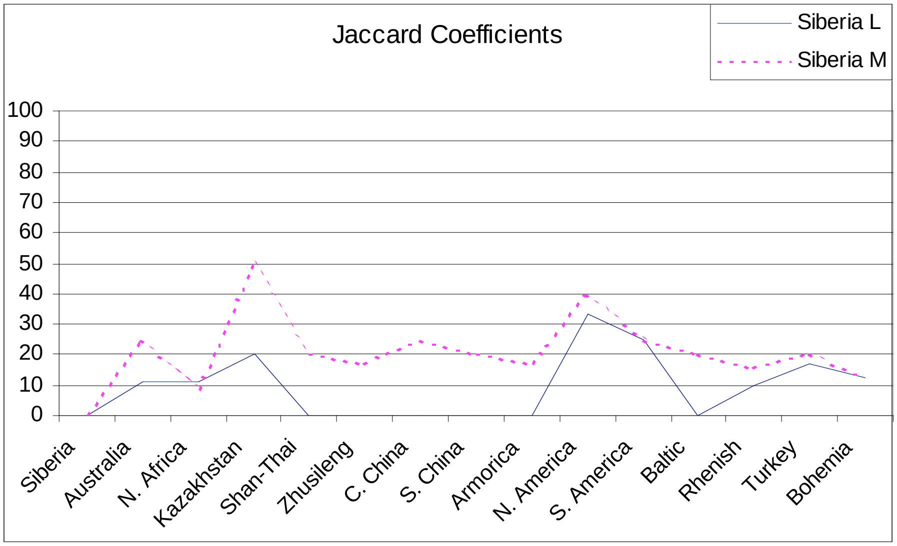
Paciphacops natlensis (Perry and Chatterton) 1976. Pragian. Delorme Fm., NW Territory, Canada. (It is assigned to *Phacops* in the analysis).

APPENDIX *5*—Comparison of faunal similarity indices for the Lower and Middle Devonian among 15 phacopid regions. L next to the region's name indicates Lower Devonian and is expressed in dotted line; M is for Middle Devonian and in solid line. The Coefficient value over 30 is considered to show high similarity between two regions compared.

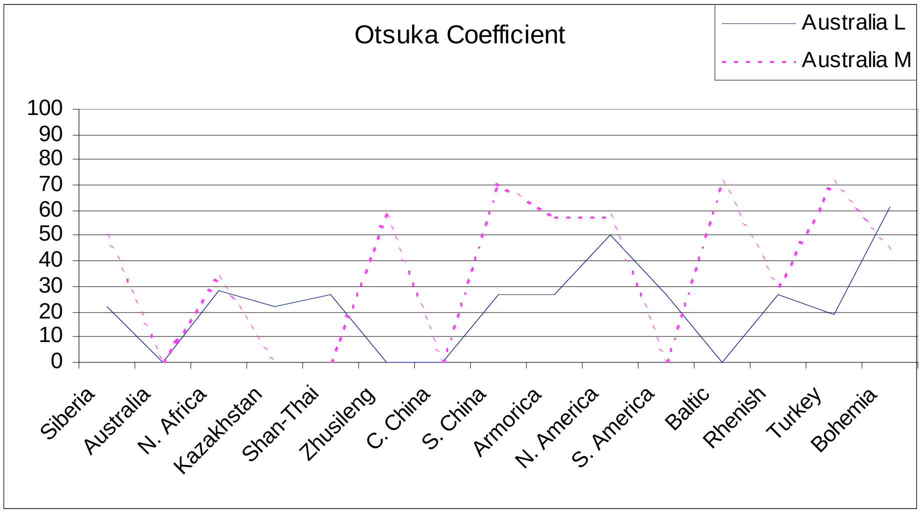
Siberia

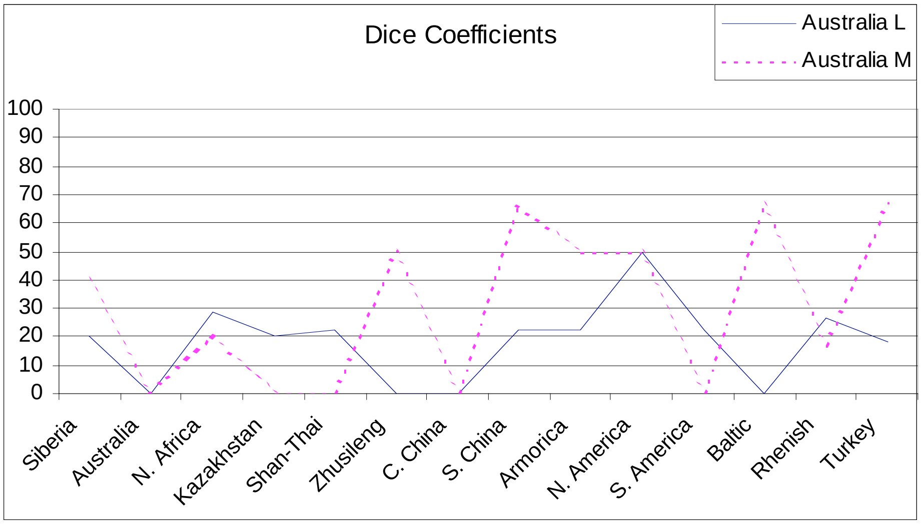

Otsuka Coefficients
Siberia L
Siberia M
100
90
80
70
60
50
40
30
20
10
0
Siberia
Australia
N. Africa
Kazakhstan
Shan-Thai
Zhusileng
C. China
S. China
Armorica
N. America
S. America
Baltic
Rhenish
Turkey
Bohemia


Dice Coefficients
Siberia L
Siberia M
100
90
80
70
60
50
40
30
20
10
0
Siberia
Australia
N. Africa
Kazakhstan
Shan-Thai
Zhusileng
C. China
S. China
Armorica
N. America
S. America
Baltic
Rhenish
Turkey


Jaccard Coefficients
Siberia L
Siberia M
100
90
80
70
60
50
40
30
20
10
0
Siberia
Australia
N. Africa
Kazakhstan
Shan-Thai
Zhusileng
C. China
S. China
Armorica
N. America
S. America
Baltic
Rhenish
Turkey
Bohemia

Australia


Otsuka Coefficient
Australia L
Australia M
100
90
80
70
60
50
40
30
20
10
0
Siberia
Australia
N. Africa
Kazakhstan
Shan-Thai
Zhusileng
C. China
S. China
Armorica
N. America
S. America
Baltic
Rhenish
Turkey
Bohemia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Australia L
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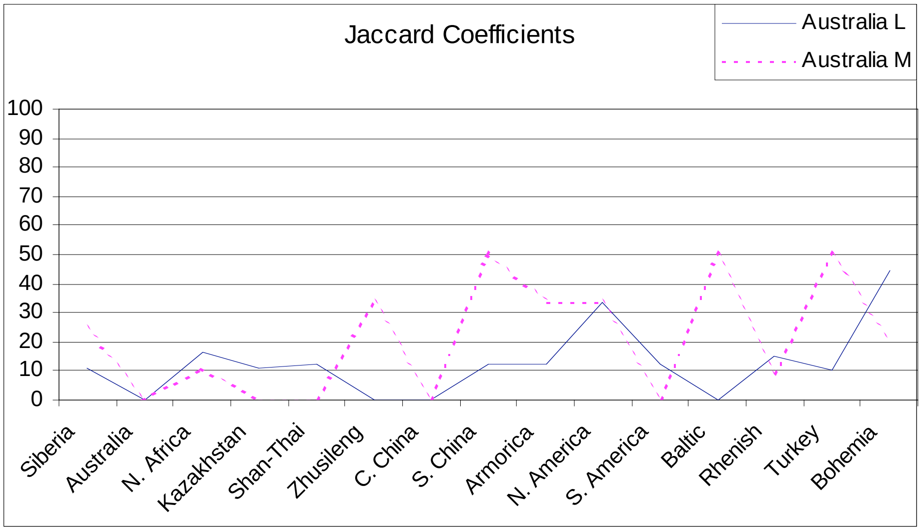
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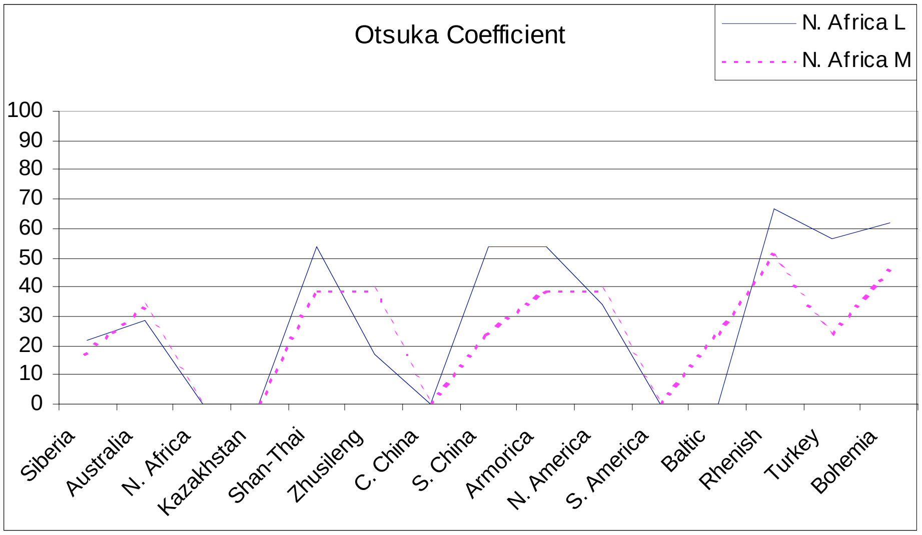
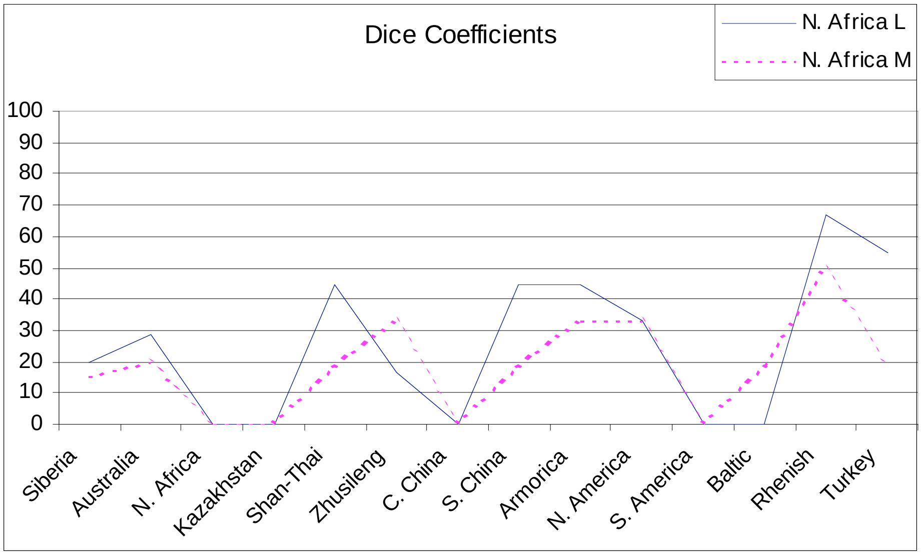
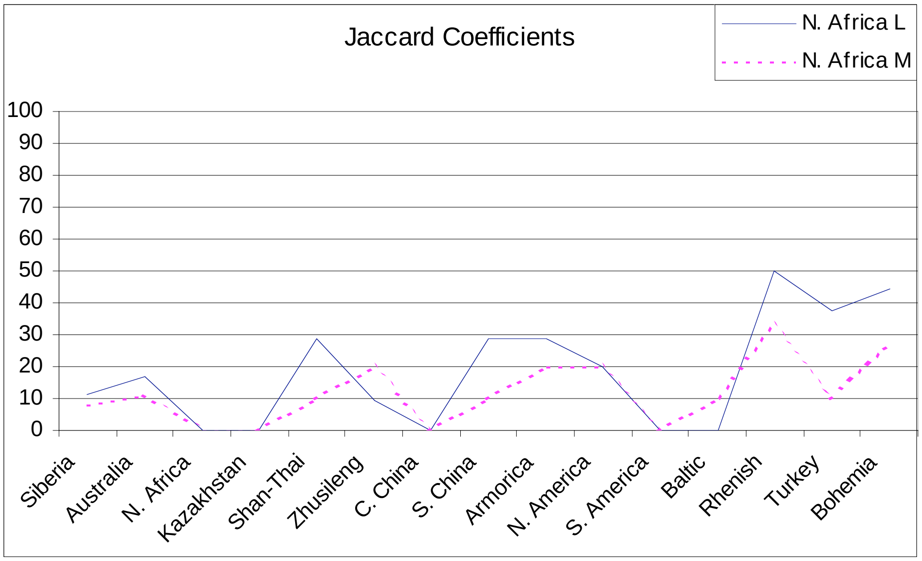
North Africa







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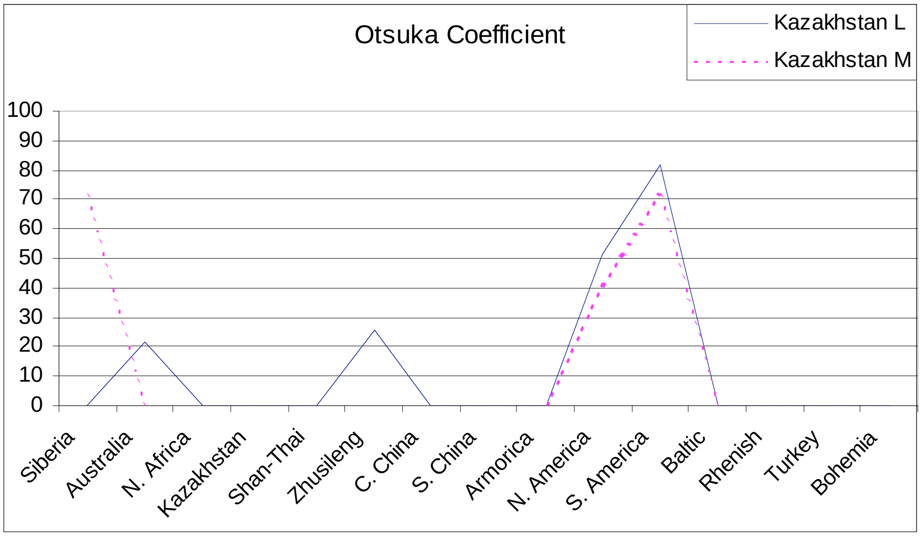
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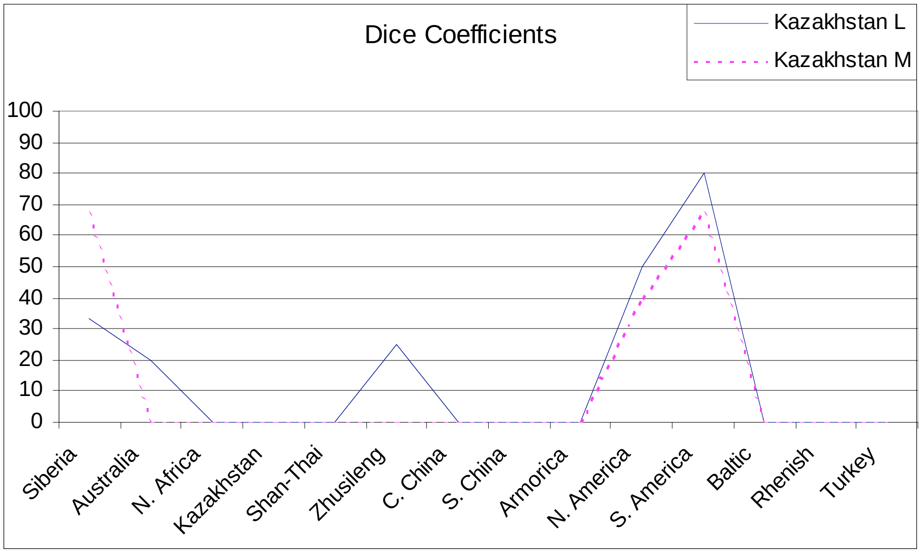
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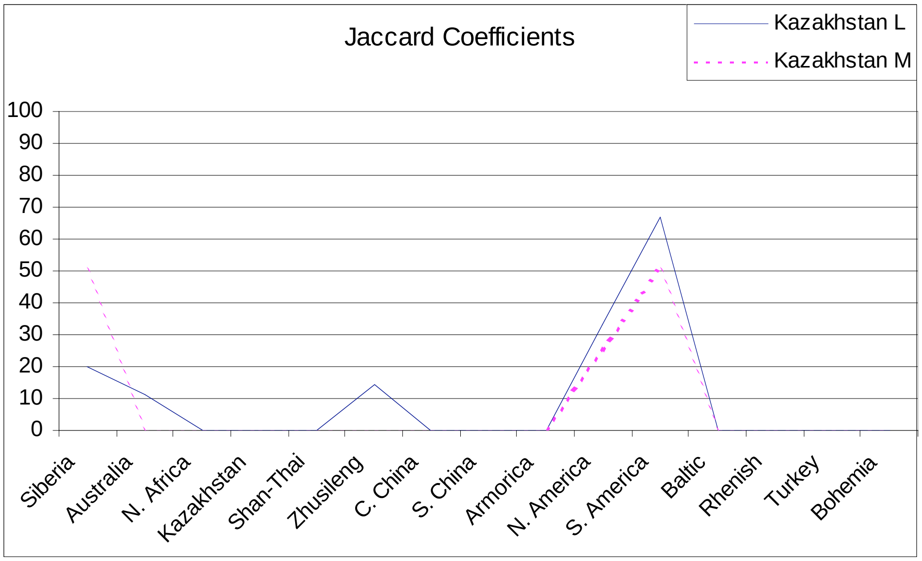
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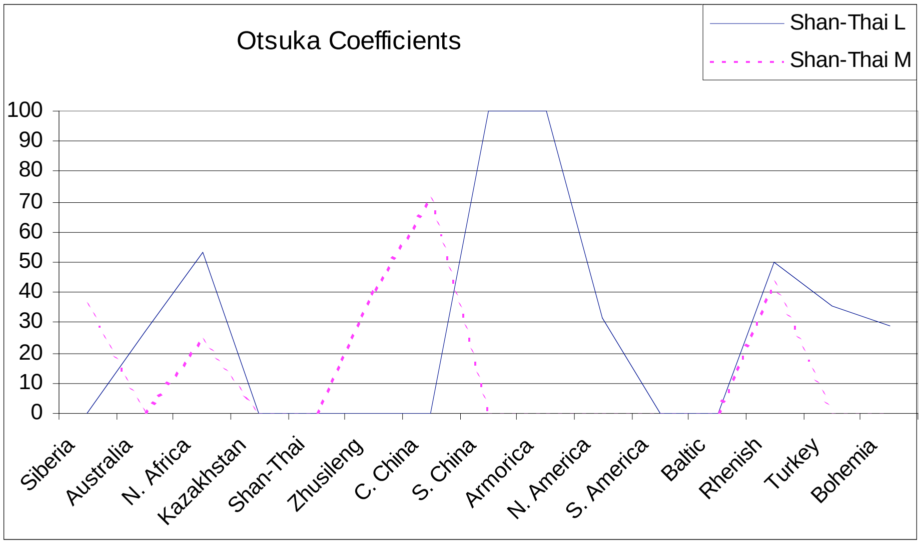
Shan-Thai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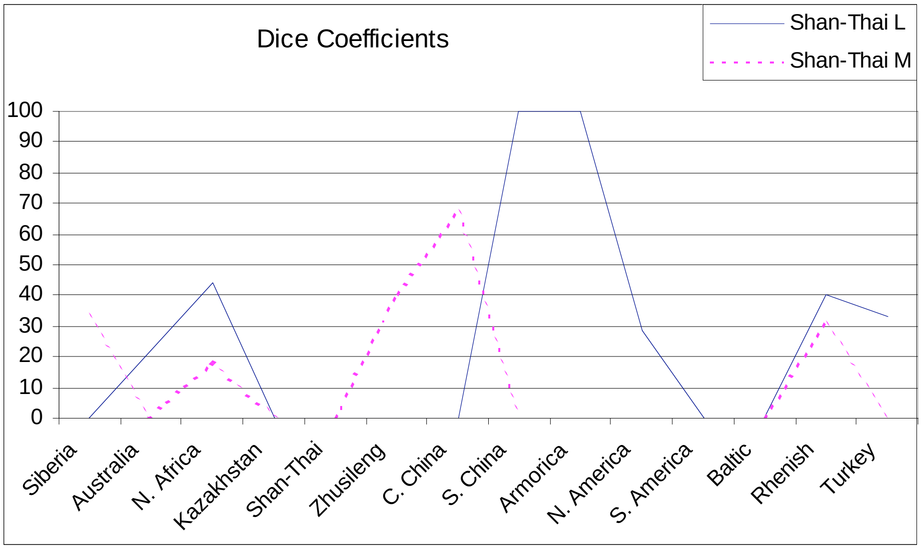
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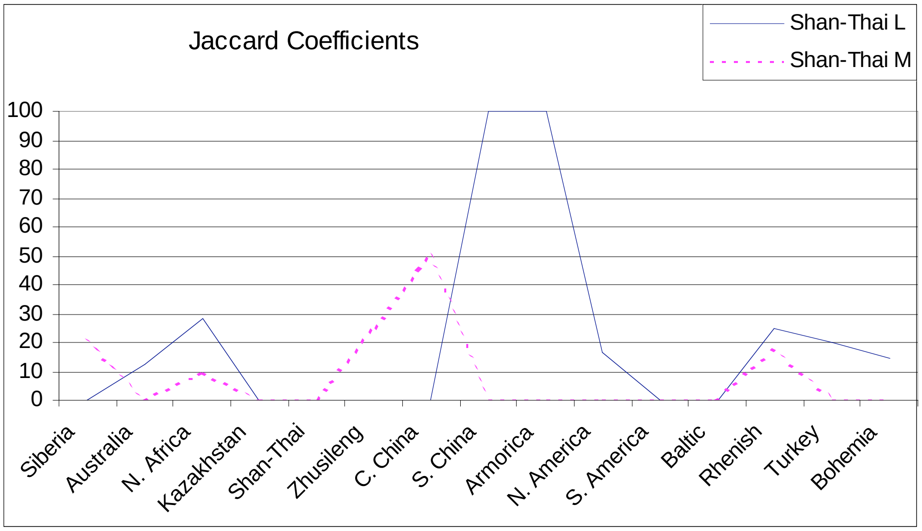
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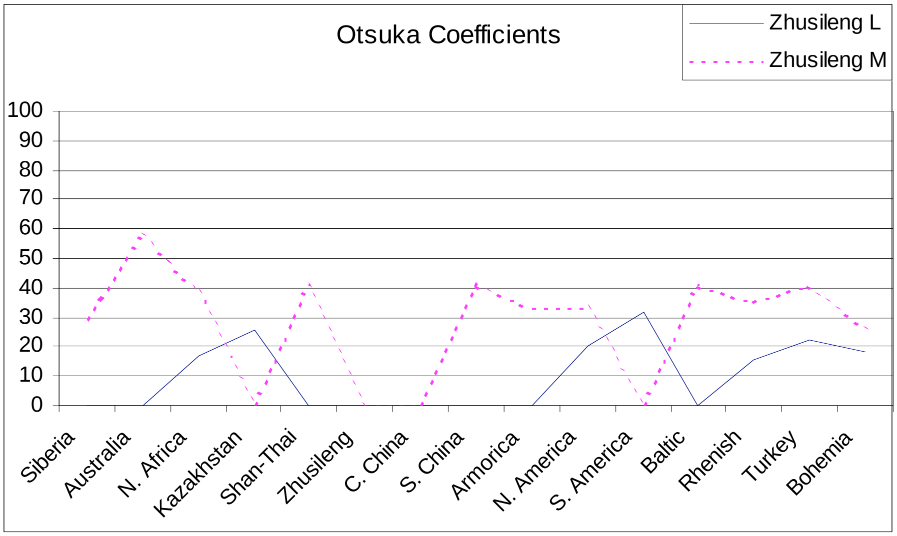
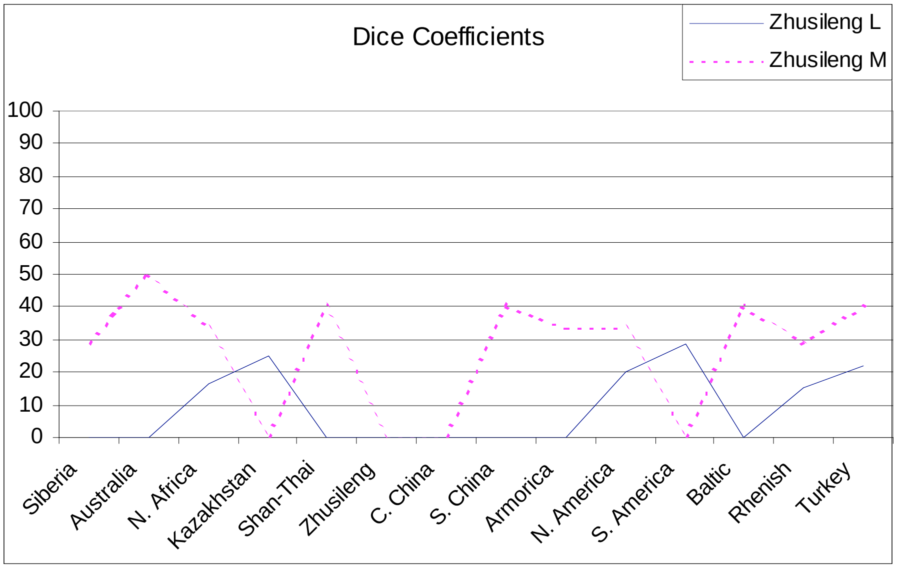
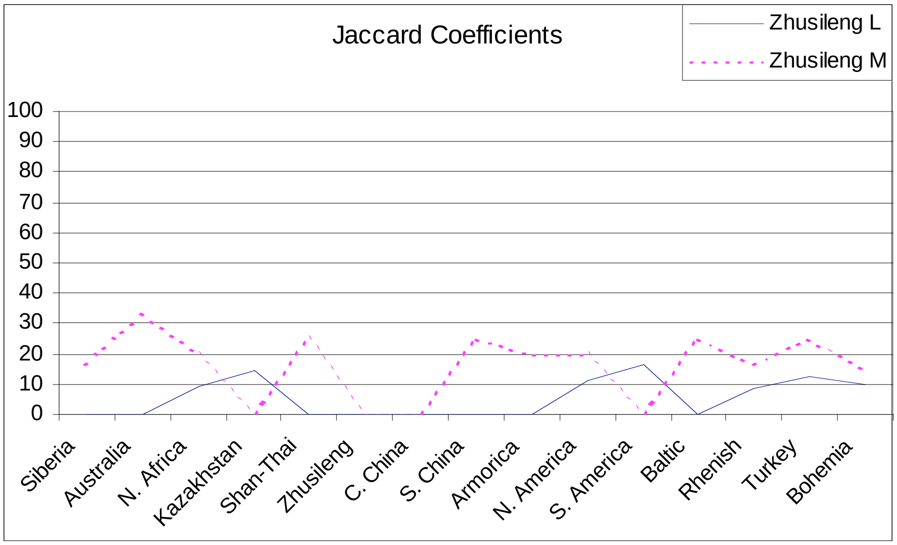
Zhusilengharhan







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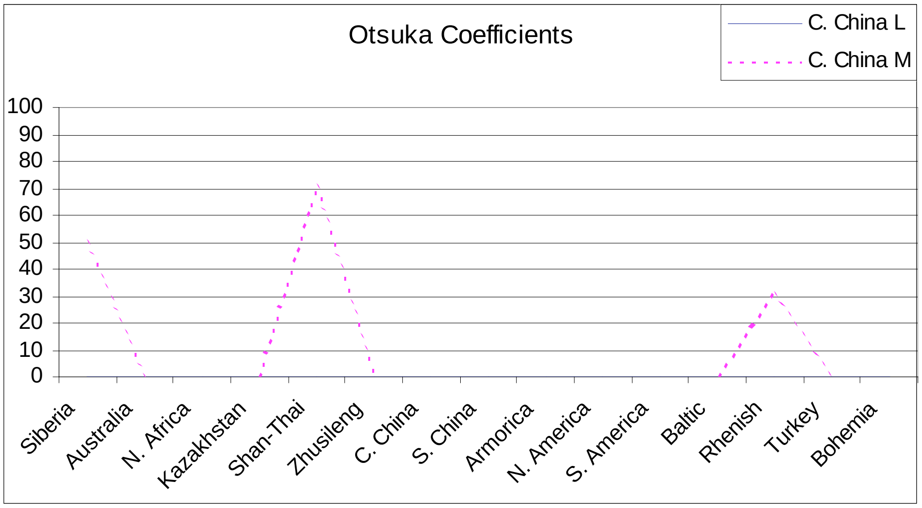

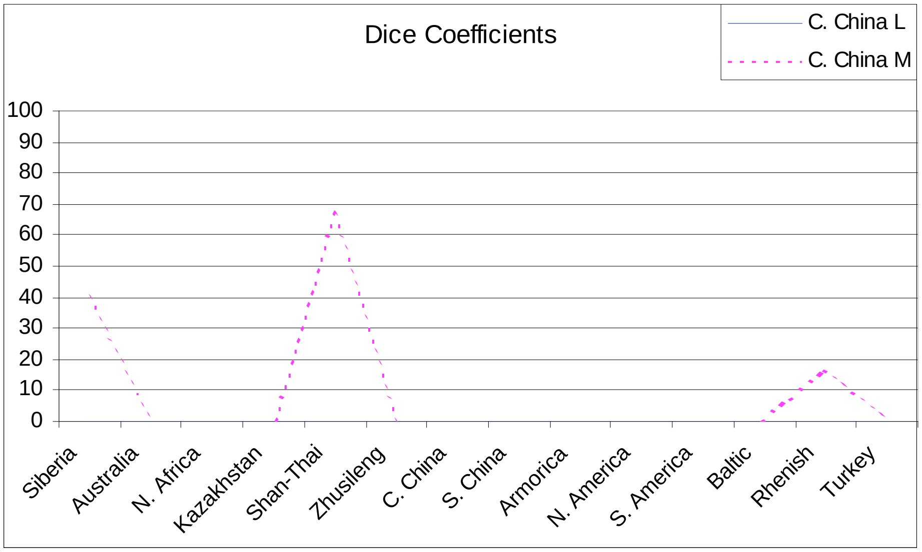

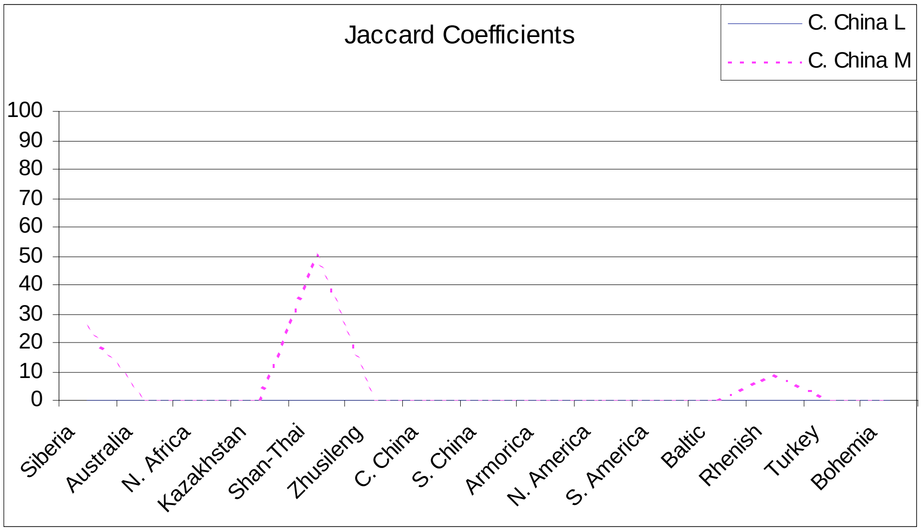

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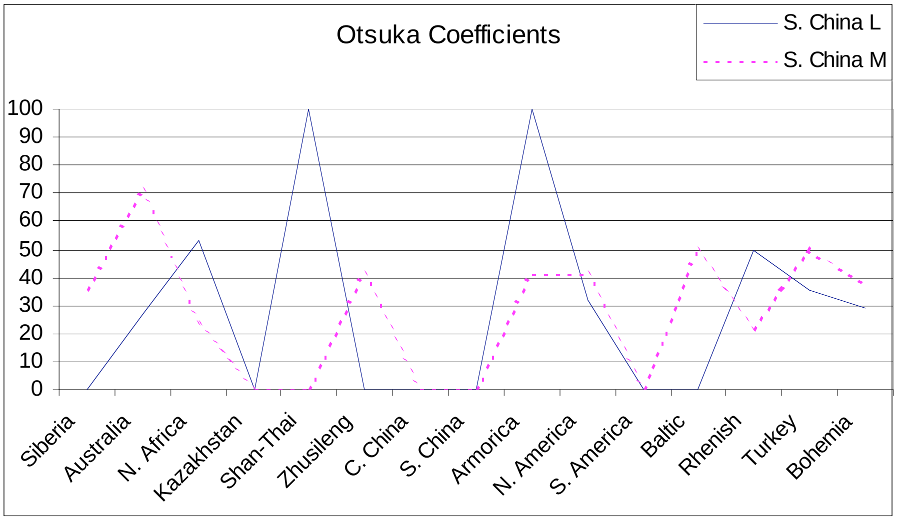
Otsuka Coefficients
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S. China M
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N. Africa
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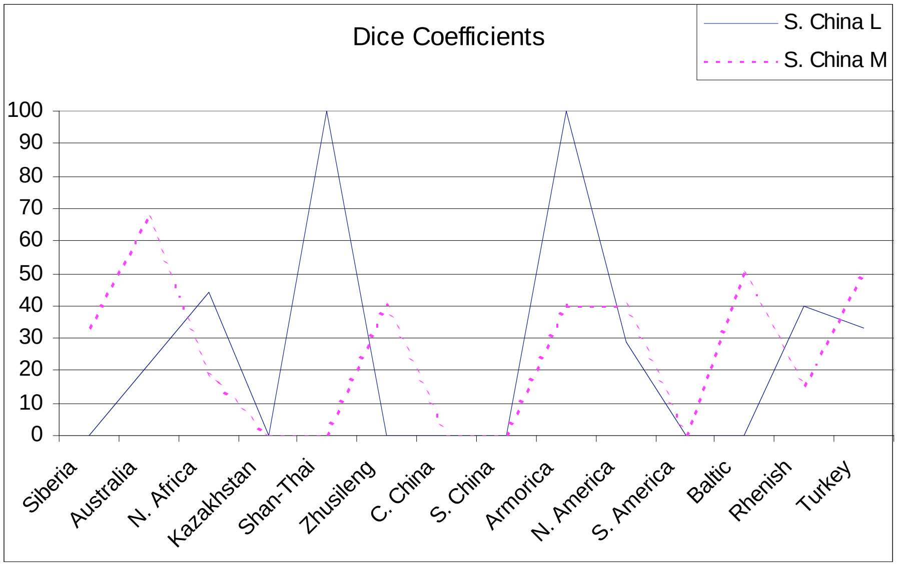
Dice Coefficients
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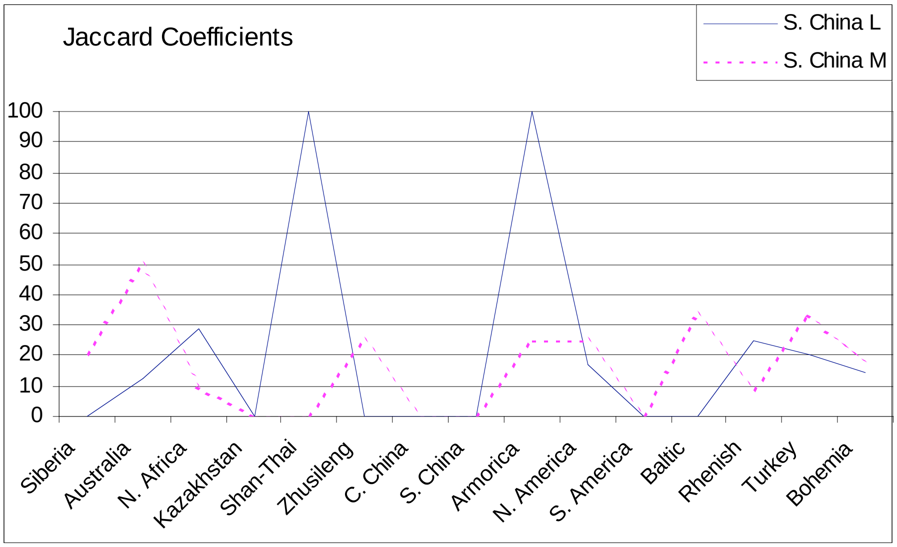
Jaccard Coefficients
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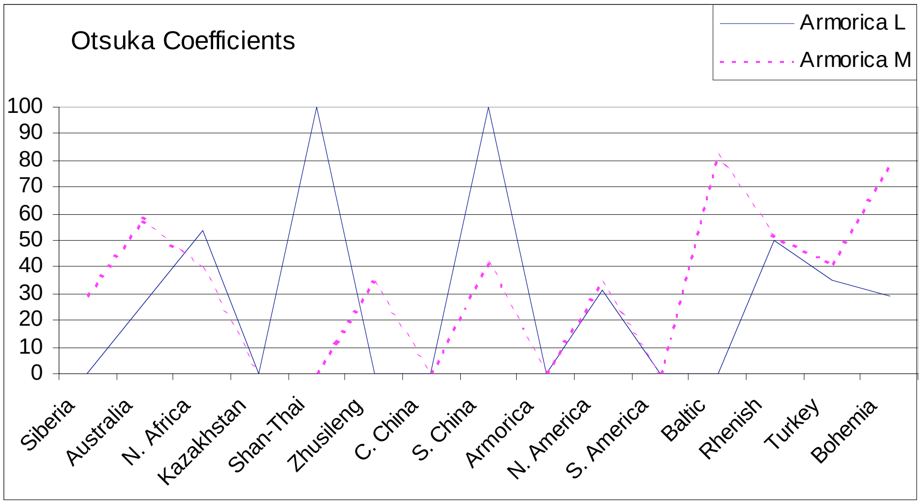
Armorica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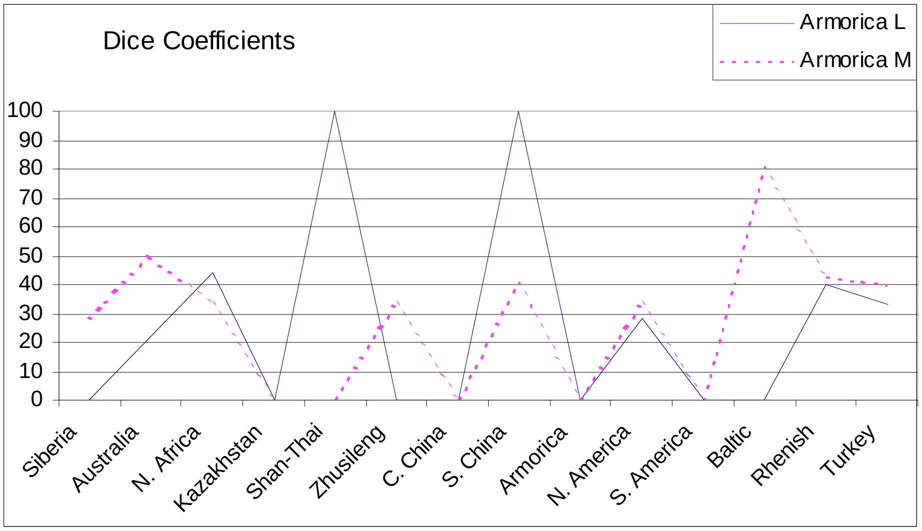
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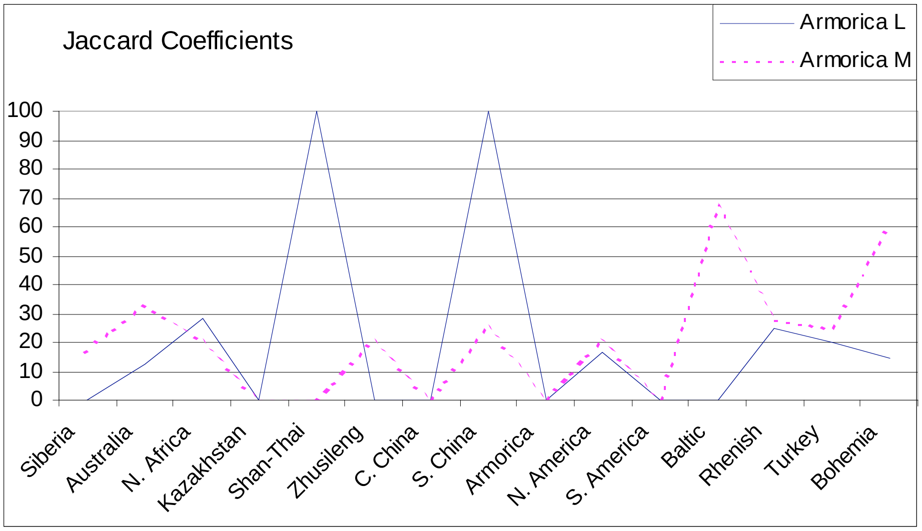
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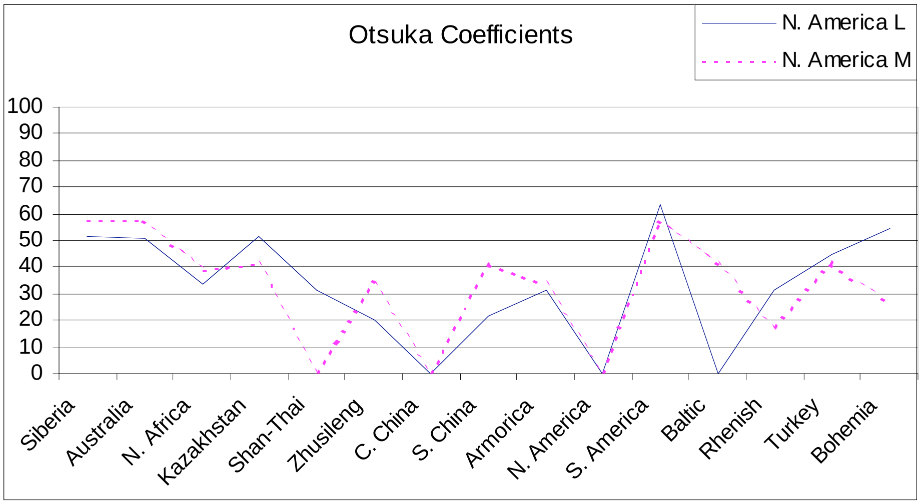
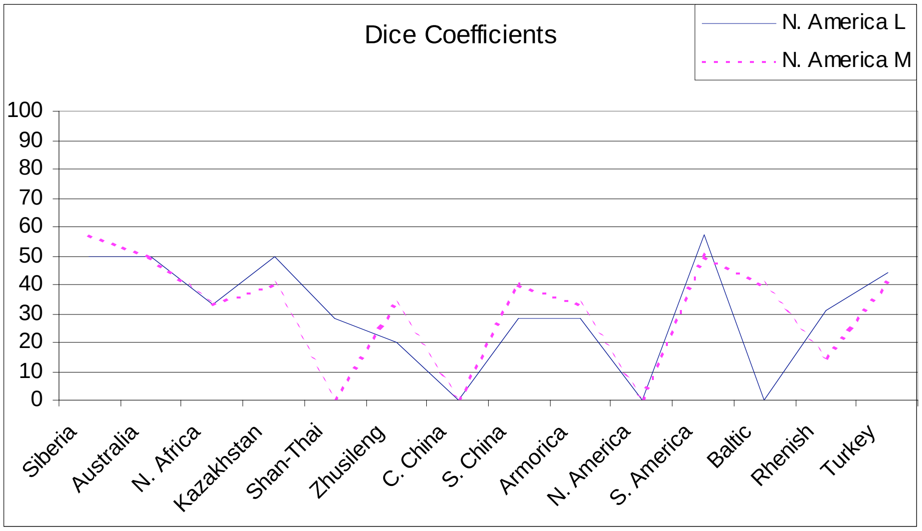
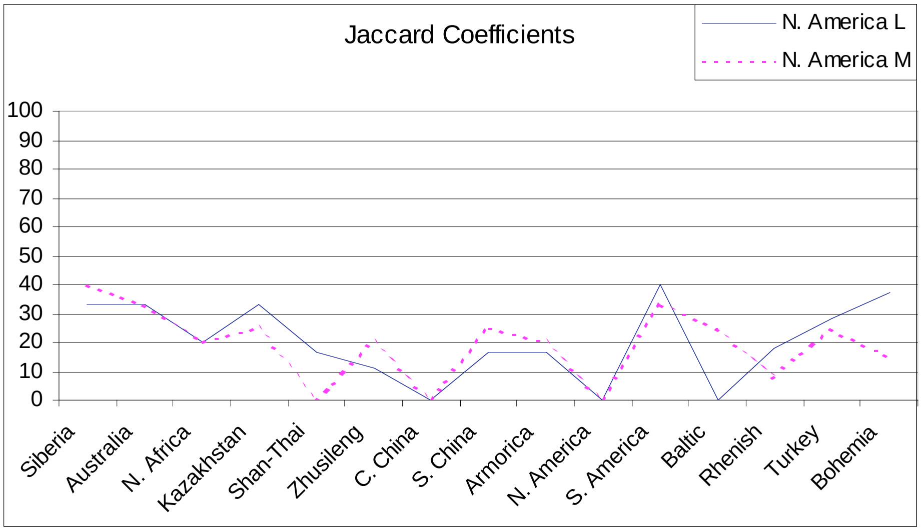
North America







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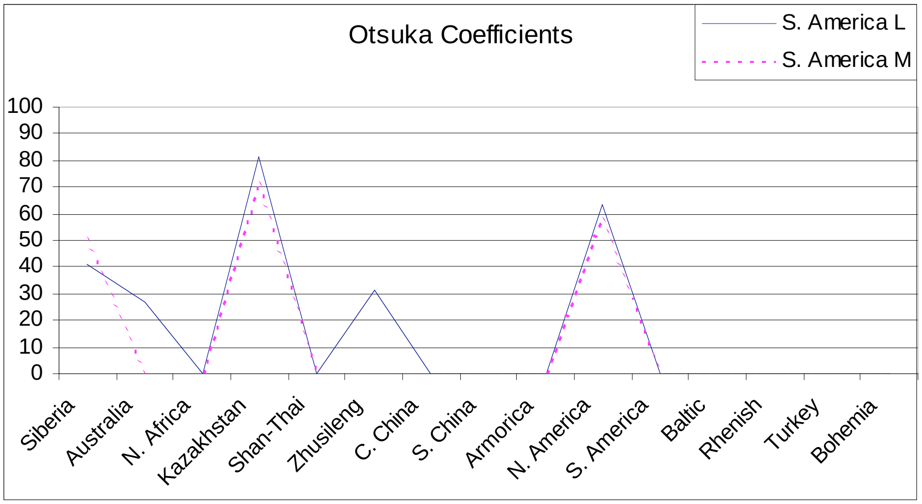

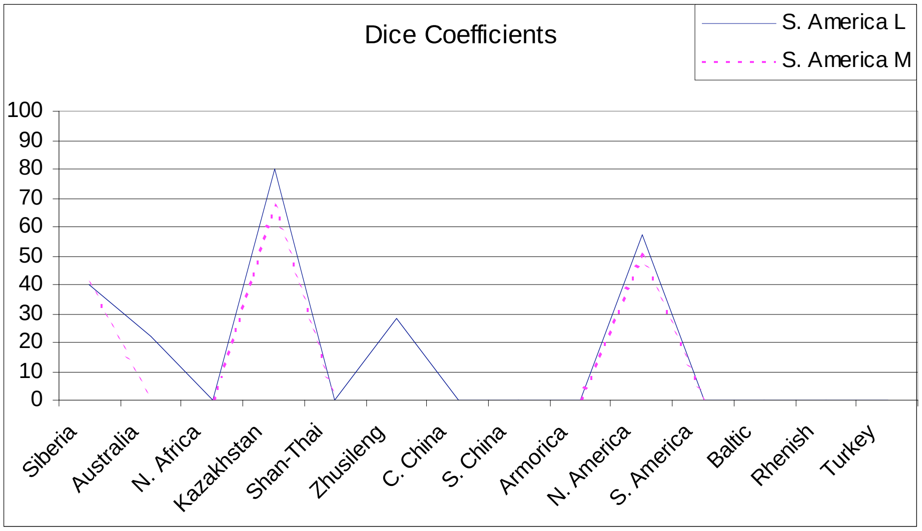

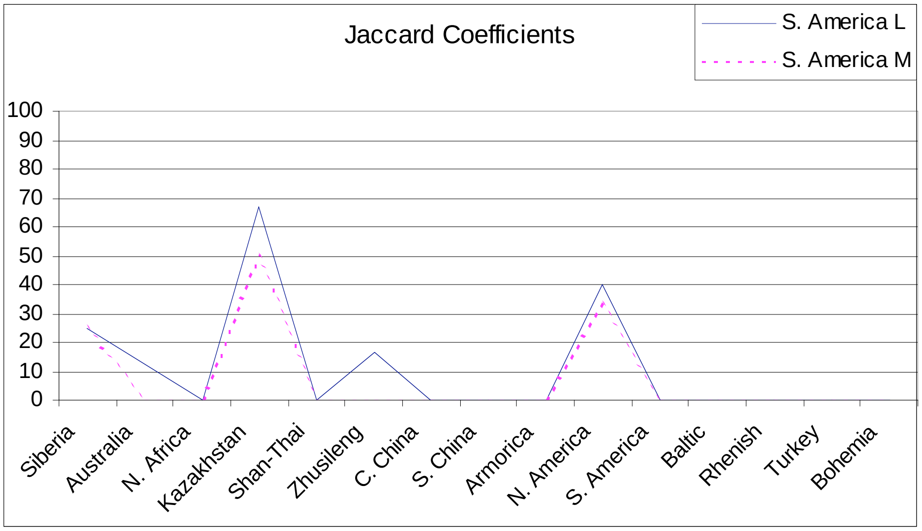

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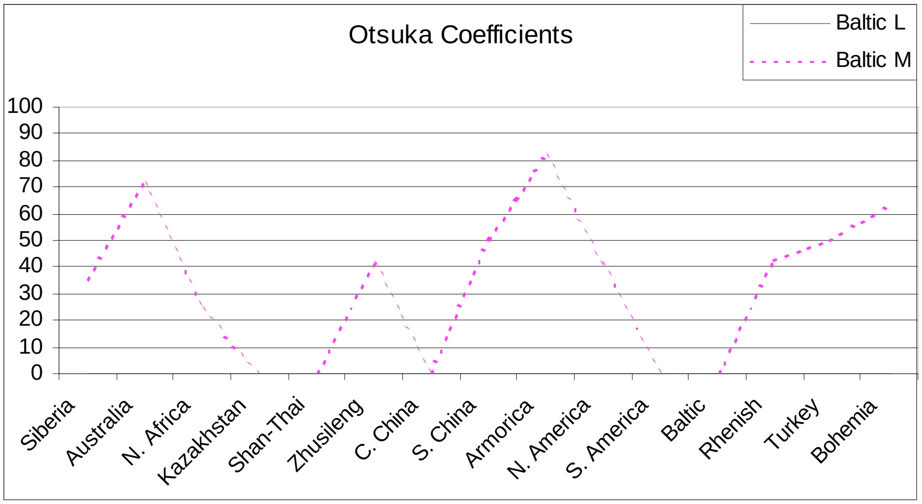
Otsuka Coefficients
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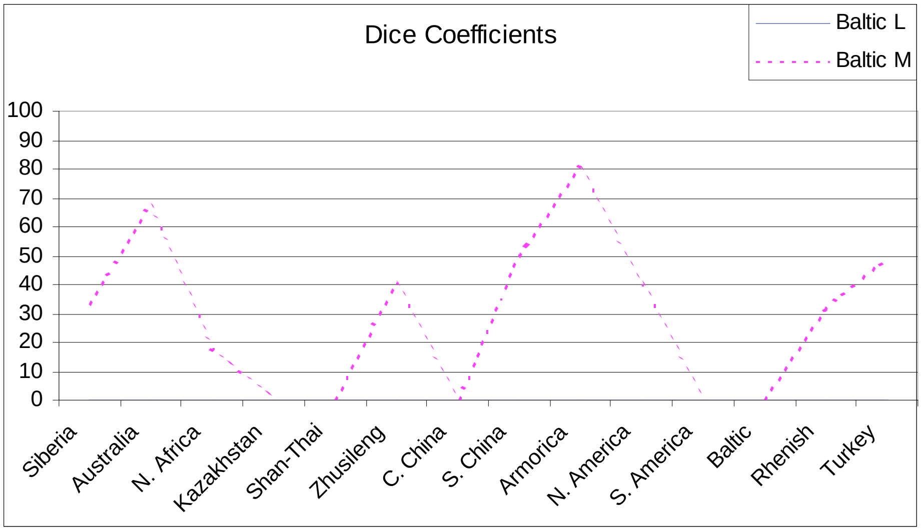
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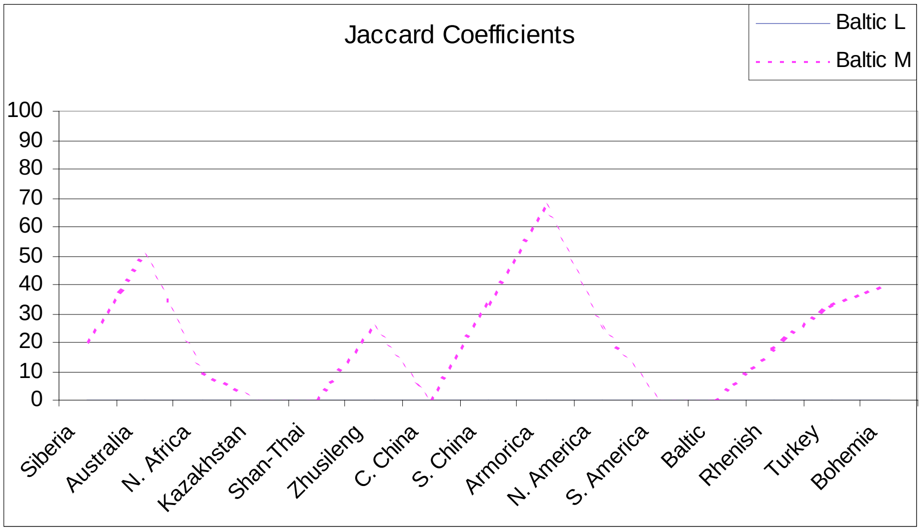
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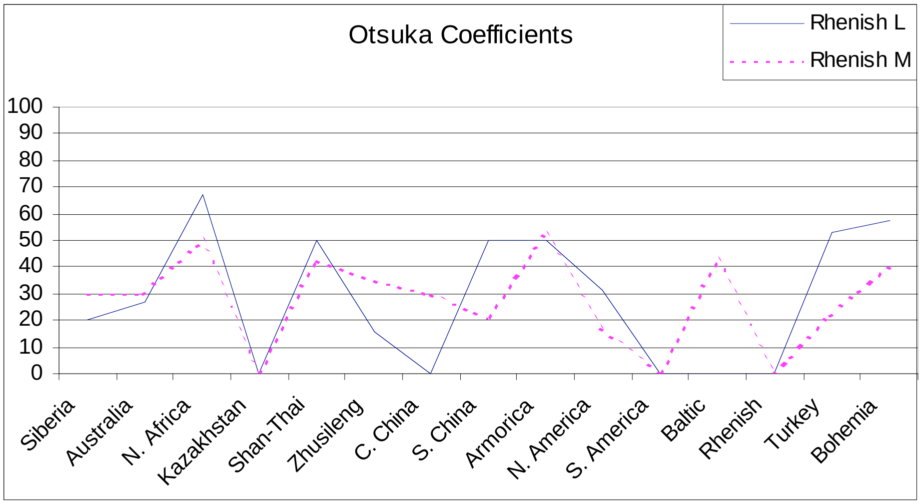
Rhenish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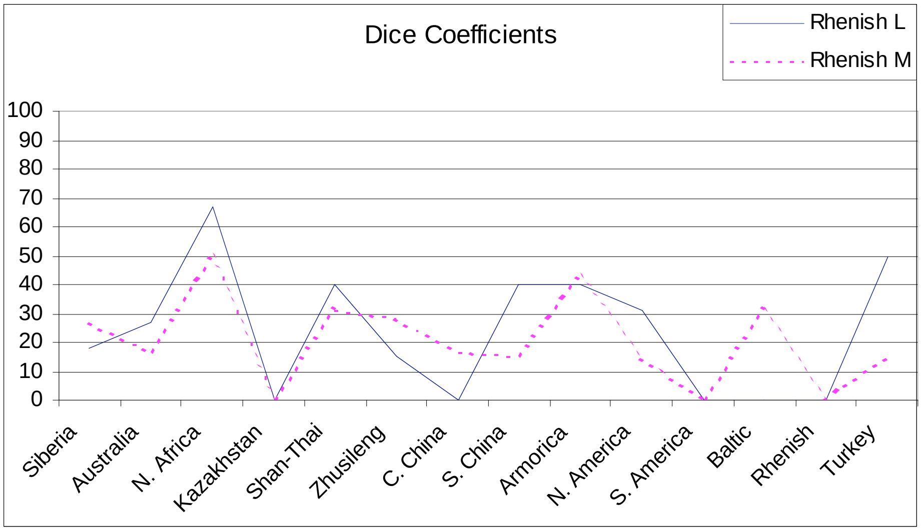
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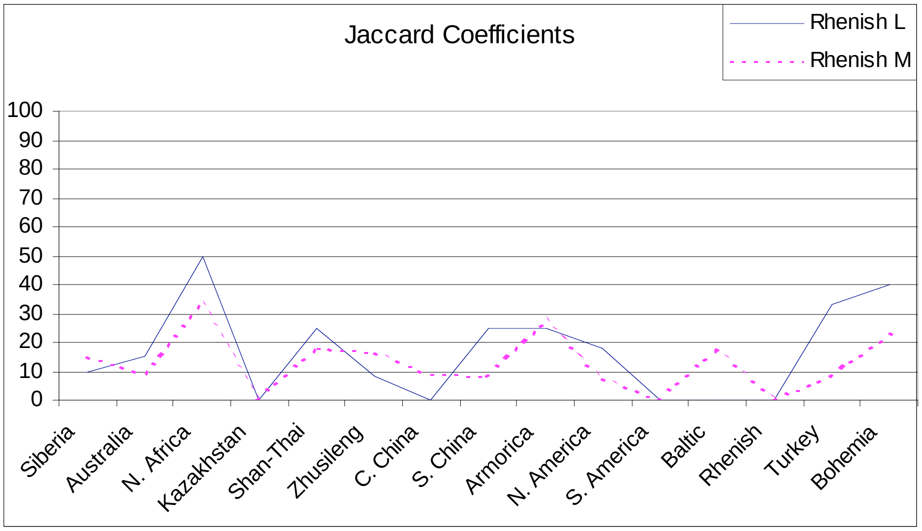
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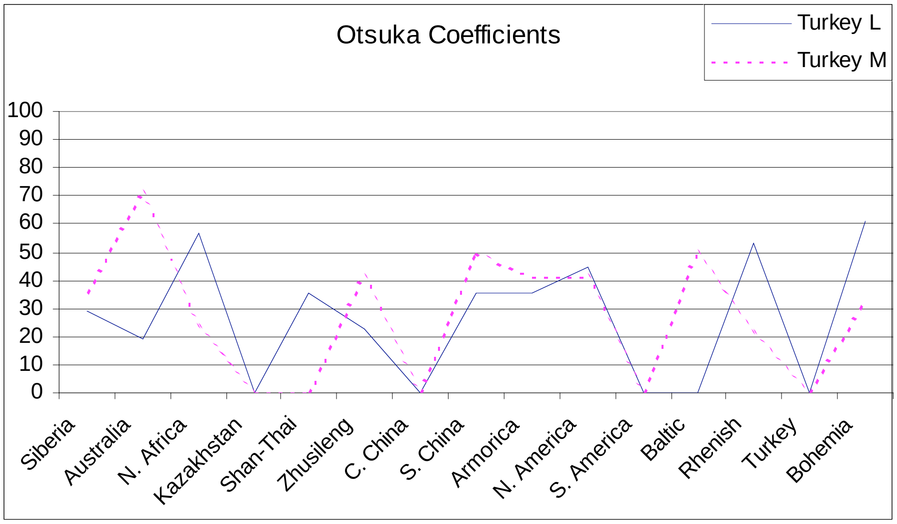
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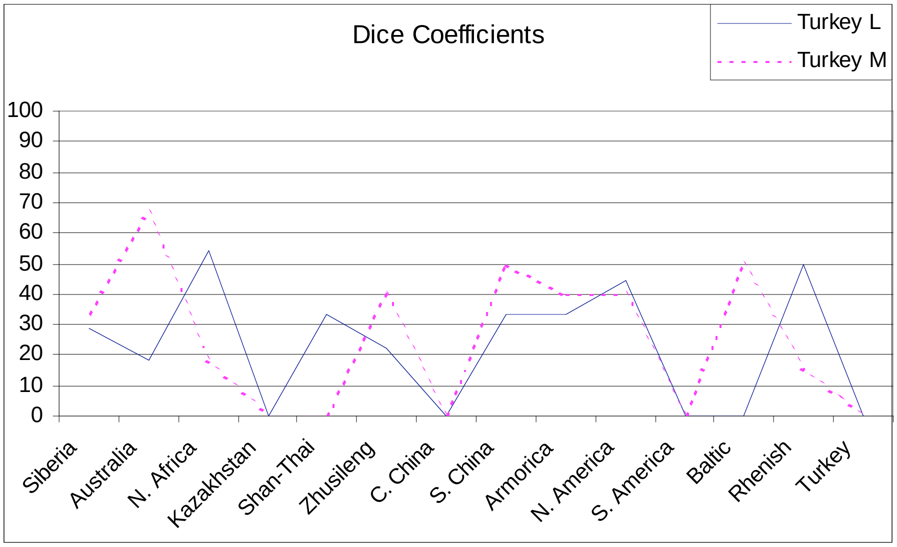
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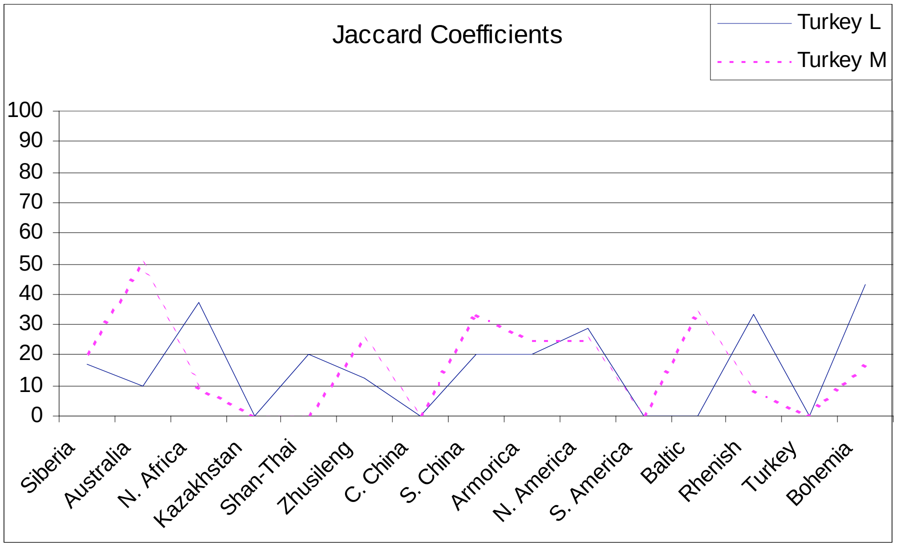
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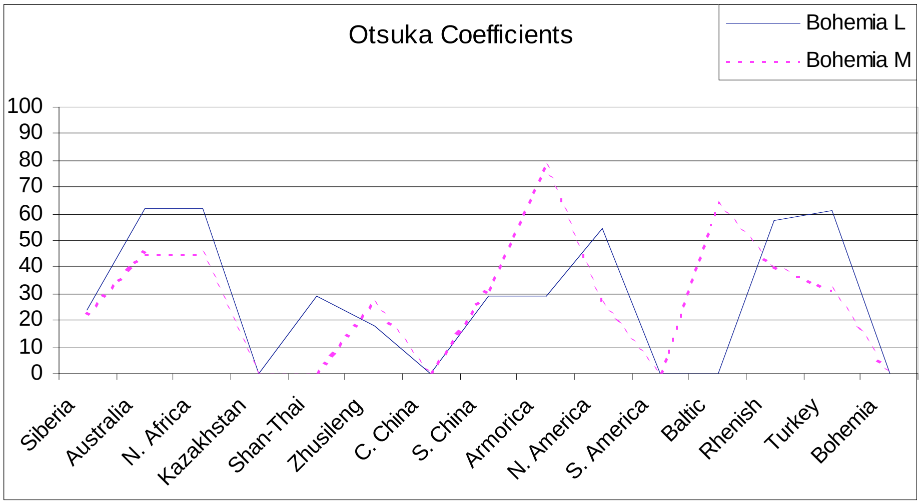
Bohemia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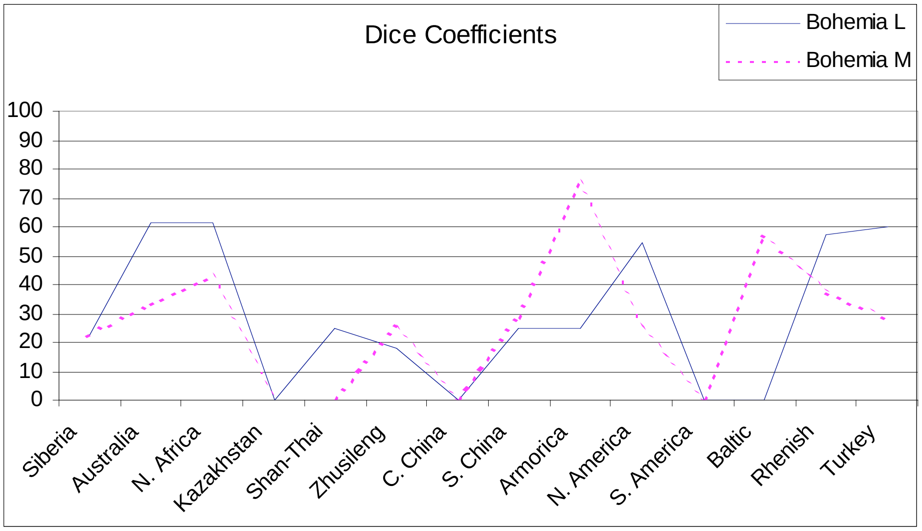
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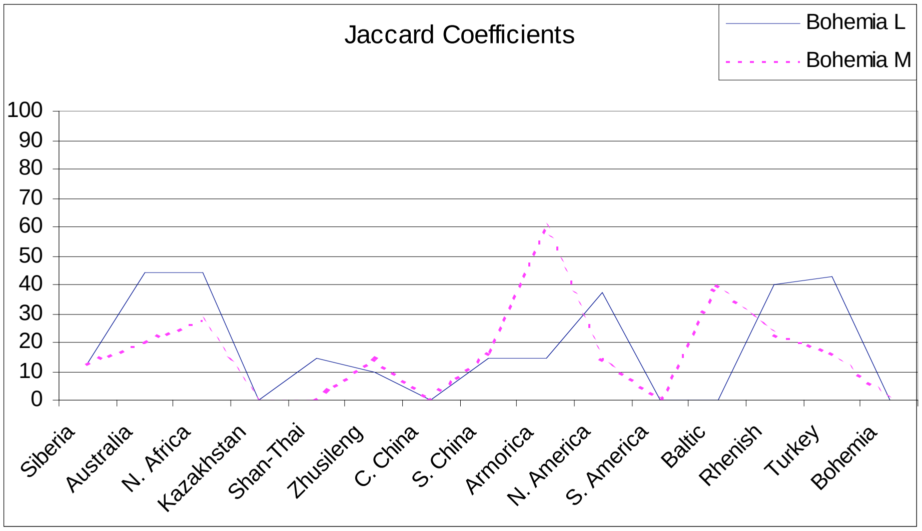
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