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A taxonomic revision of the Early Devonian dalmanitid trilobite *Kasachstania* Maksimova, 1972 from central Kazakhstan

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Abstract.—The dalmanitid trilobite *Kasachstania* Maksimova, 1972, previously reported from the Lower Devonian of Kazakhstan and North America (USA) and the upper Silurian–Lower Devonian of South America (Bolivia and Argentina), is revised. *Kasachstania kasachstanica* (Balashova in Maksimova,1968) and *K. septicostata* (Maksimova, 1968) are regarded as junior synonyms of the type species *K. saryarkensis* (Maksimova, 1960), all from the Lower Devonian of the type locality in central Kazakhstan (northern Balkhash). On the basis of a new diagnosis, *K. ulrichi ulrichi* (Delo, 1940) from the Emsian of the United States, *K. ulrichi asiatica* (Maksimova, 1968), *K. pristina* (Maksimova, 1968), and *K. alperovichi* Pour et al., 2019, from the Lower Devonian of Kazakhstan, *K. andii* (Kozłowski, 1923) from the upper Silurian–Lower Devonian of Bolivia, and *K. gerardoi* Edgecombe and Ramsköld, 1994, from the upper Silurian–Lower Devonian of Bolivia and Argentina are excluded from *Kasachstania*. This genus, represented only by *K. saryarkensis* and *K. kiikbaica* (Maksimova, 1968), is restricted to the Lower Devonian of central Kazakhstan, corresponding to the Balkhash–Mongolo–Okhotsk province in the paleobiogeographic context of the Old World Realm, instead of being nearly cosmopolitan as previously considered. In addition, we provide some remarks about *Saryarkella* Maksimova, 1978b, a monospecific dalmanitid genus largely overlooked although valid from the Emsian of the same area in central Kazakhstan.

Introduction

The dalmanitid trilobite *Kasachstania* Maksimova, 1972 was originally recognized from the Lower Devonian of Kazakhstan (Fig. 1) and coeval strata in the Great Basin from Nevada, USA. Later, this genus was reported from the Silurian and Lower Devonian of southern South America (Pek and Vaněk, 1991; Edgecombe and Ramsköld, 1994) and thus considered of nearly cosmopolitan distribution (Fig. 2).

In South America, the genus was recognized in the Andean region through two endemic species. The first, *Kasachstania andii* (Kozłowski, 1923) was reported from the upper Silurian and Lower Devonian of Bolivia (Swartz, 1925; Braniša, 1965; Wolfart, 1968; Pek and Vaněk, 1991; Edgecombe and Ramsköld, 1994). The second, *Kasachstania gerardoi* Edgecombe and Ramsköld, 1994 was recognized from the upper Silurian of Argentina to the lowermost Devonian of Bolivia (Waisfeld et al., 1988; Edgecombe and Ramsköld, 1994).

The very wide geographic distribution of *Kasachstania* contrasts with the mostly endemic trilobite faunas known from the Early Devonian of Southwestern Gondwana (faunas of the Malvinokaffric Realm), where entire families, such as the calmoniids, were restricted and diversified (Eldredge and Braniša, 1980; Boucot and Racheboeuf, 1993; Abe and Lieberman, 2009, 2012; Carbonaro et al., 2018). In fact, the diversification of Southwestern Gondwana dalmanitids was identified with a minor intensity relative to calmoniids, rapidly radiating during the Devonian in the Malvinokaffric basins from previous cosmopolitan Silurian stocks (Eldredge and Ormiston, 1979). *Kasachstania,* widely distributed since the late Silurian, initially supported this hypothesis.

As a result of preliminary revisions of this genus from the Lower Devonian of Argentina (Rustán, 2011, 2016), we revisit and test this proposal, focusing on Malvinokaffric records. Hence, a profound revision of some poorly defined taxa appeared necessary to better understand biostratigraphic, phylogenetic, and paleobiogeographic patterns of dalmanitids in the middle Paleozoic of Southwestern Gondwana and particularly from South America.

Here we provide a taxonomic reappraisal of *Kasachstania*. Some concerns regarding the original material of Maksimova from the type area of the Lower Devonian of central Kazakhstan are addressed. Nomenclatural issues that involve the correct spelling of the genus are also dealt with. Species previously included in *Kasachstania* are revised, focusing on new illustrations, the original material, and new taxonomic criteria to improve the accuracy of its diagnosis and to recognize biostratigraphic and biogeographic implications of reassignments.

In addition, some insights on the largely overlooked valid dalmanitid genus *Saryarkella* Maksimova, 1978, described from the same type locality and age of *Kasachstania,* are provided. This genus drew our attention during the revision as it was never mentioned after the original publication and has a particular distribution of marginal spines that is uncommon for dalmanitids.

Geological settings

The area where *Kasachstania* was defined corresponds to the Lower Devonian marine deposits from northern Balkhash in

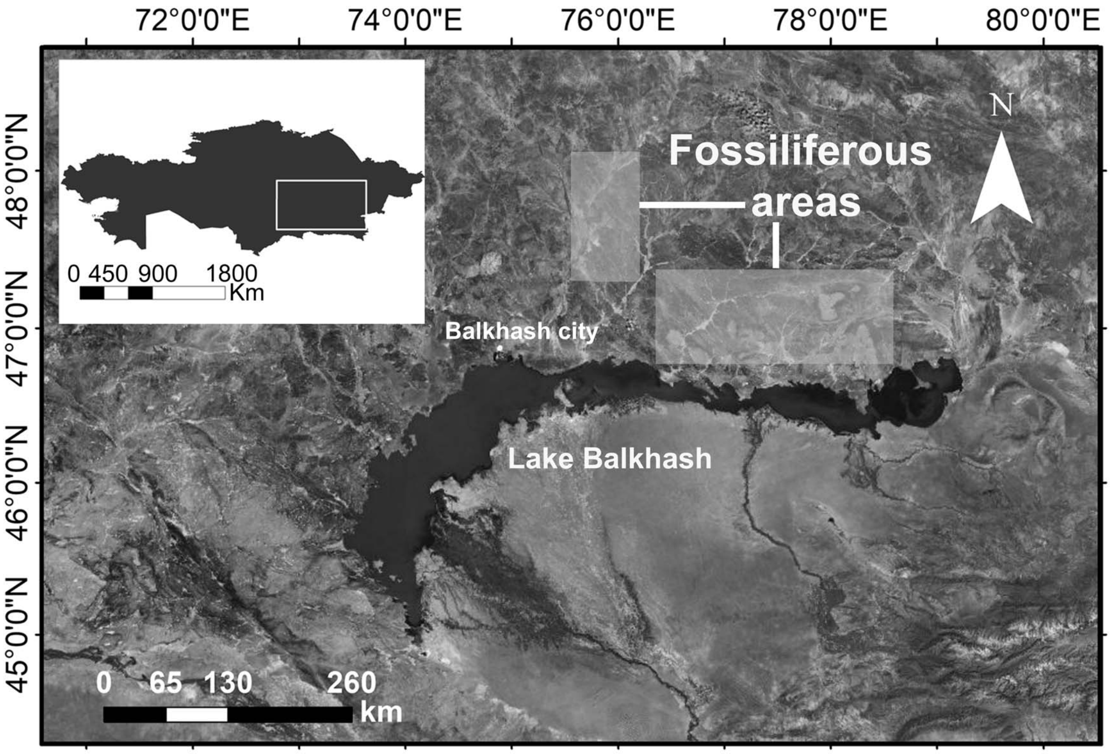

Figure 1. Map of the Devonian fossiliferous area of Balkhash, in central Kazakhstan, showing areas recording *Kasachstania* Maksimova, 1972 and related taxa (based on Maksimova, 1968, 1978b).

central Kazakhstan (Fig. 1). The stratigraphy and age of this region are mainly based on the paleontological reports of Bublichenko (1945) and Maksimova (1968, 1978a). Sedimentary successions consist mainly of siltstones and sandstones, with subordinate interlayers and lenses of limestones.

The stratigraphic scheme of the Lower Devonian of central Kazakhstan has been classically described through several informal divisions that include, from base to top, the Aynasu, Kockbaital, Pribalkhash, and Sardzhal horizons, which would span from the Silurian–Devonian boundary through the Emsian (Kaplun and Senkevich, 1978). However, more precise works are necessary to resolve the complex stratigraphy of central Kazakhstan. Indeed, the Aynasu and Kockbaital horizons are considered a single cycle of deposition (the Karazhirik horizon according to Kaplun and Senkevich, 1978), making the correlation between different layers difficult. The presence of the graptolite *Monograptus uniformis angustidens* Přibyl, 1940, at the base of the Aynasu horizon, indicates the lowermost Lochkovian (Maksimova, 1978a). However, no other index fossil was identified in the Kockbaital horizon, and late Silurian ages should not be rejected in some localities (see Budil et al., 2014).

The Karazhirik horizon is represented by green-colored various-grained sandstones, siltstones, argillites, shales, bluish-gray ashy tuffs, and lens-like layers of light reef-related limestones of very uneven thickness. The total thickness of the Karazhirik horizon ranges from 500 to 2,400 m.

The Karazhirik horizon bears several dalmanitids type species such as *Kasachstania saryarkensis* (Maksimova, 1960), *K. kasachstanica* (Balashova in Maksimova, 1968), and '*Odontochile*' *pristina* Maksimova, 1968. Species restricted to the Aynasu horizon include *Kasachstania septicostata* (Maksimova, 1968) and several species of the subgenus *Odontochile* (*Pacifina*) Maksimova, 1978b (see Kaplun and Senkevich, 1978).

Kasachstania kiikbaica (Maksimova, 1968) occurs in the Kockbaital horizon, and in the lower levels of the overlying Pribalkhash horizon. This horizon is represented by different-grained sandstones, tuff sandstones, siltstones, and ash tuffs of greenish and brownish color with thin layers of limestone. The thickness reaches 280–600 m. It is widely distributed in central Kazakhstan and abundantly fossiliferous. It is considered to be upper Lochkovian to Pragian in age (Kaplun and Senkevich, 1978).

The Sardzhal horizon is regarded as lower Emsian (Kaplun and Senkevich, 1978) and sharply differs from the underlying Pribalkhash horizon on the basis of the trilobite content. Dalmanitids recorded include '*Odontochile*' *asiatica* Maksimova, 1968, '*O.*' (*Pacifina*) *arcuata* Maksimova, 1968, '*O.*' (*P.*) *carinata* Maksimova, 1968, and *Saryarkella radiata* Maksimova, 1978b.

The determination of the precise paleogeographic position and environmental settings of this basin in central Kazakhstan is hindered by the complex geological history of the different tectonic terranes involved (Li et al., 2018) and contrasting models of reconstruction (Wang et al., 2013; Dowding and Ebach, 2018). Bazhenov et al. (2012), focusing on western Kazakhstan, proposed that Kazachstania and other terranes were involved in a huge subductive margin, located approximately at 30°N during the Early Devonian. These terranes, in temperate water settings, rotated, bent, and moved from north to south and were linked to the Siberian plate (Fig. 2). The subduction of the Junggar plate is

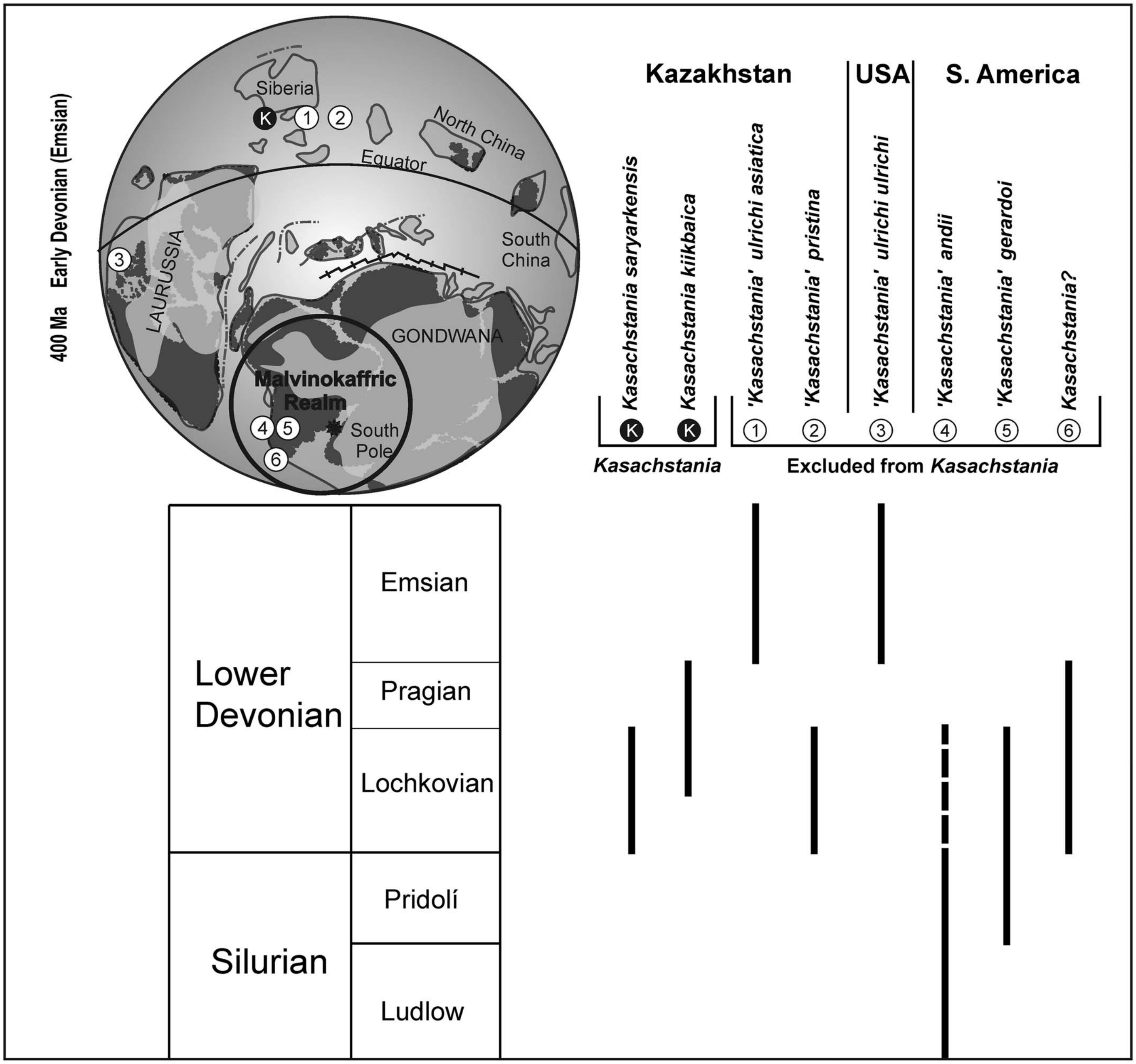

Figure 2. Occurrence of the taxa assigned to *Kasachstania* Maksimova, 1972. Temporal distributions in doubt are shown with dashed lines.

associated with the development of a Devonian Volcanic Belt, representing an Andean-type volcanic arc at the margins of Kazachstania (Li et al., 2018).

In North America, by contrast, the only *Kasachstania* species recognized by Maksimova (1972) is ‘*Odontochile*’ *ulrichi* Delo, 1940, described from the ‘Devonian of Eureka District, Nevada, USA’ (p. 63) without any additional information. The specimens were found specifically near Combs Peak and Brush Peak in central Nevada (M. Florence, personal communication, 2017). This Emsian area corresponds with the McColley Canyon Formation (Johnson, 1962). This unit is divided into three members (Yigit and Hofstra, 2003); the only one bearing trilobites is the Bartine Member (Schalla, 1978). Hence, ‘*Odontochile*’ *ulrichi* probably occurs in this member.

In South America, *Kasachstania* was recorded from the Silurian and Lower Devonian of Bolivia and Argentina. In Bolivia, it was reported from the Cordillera Real and Catavi formations of the Central Andean region (Steinmann and Hoek, 1912; Kozłowski, 1923; Braniša, 1965; Edgecombe and Ramsköld, 1994). The Cordillera Real Formation refers to a fossiliferous succession containing ‘*Dalmanites*’ *andii* (Suárez–Soruco, 1992), considered to be of Silurian age (Braniša, 1969). Nevertheless, an Early Devonian age for some of the fossiliferous deposits has been suggested (Suárez–Soruco, 1992; Edgecombe and Ramsköld, 1994). The siliciclastic Catavi Formation, where ‘*D.*’ *andii* was also reported (Braniša et al., 1972), starts with an important sandstone bank deposited during the upper Silurian (Pridoli). This formation is topped by a pelitic horizon called

Ventilla, where '*Kasachstania*' *gerardoi* was identified (Edgecombe and Ramsköld, 1994), which is referred to the base of the Devonian (Suárez–Soruco, 2000).

In Argentina, scarce dalmanitids provisionally identified as *Kasachstania*? sp. (Rustán 2011, 2016) were recorded from siliciclastic outcrops of the Lower Devonian Talacasto Formation in the central Precordillera Basin. Fossils come from Lochkovian to Pragian lower muddy intervals (see García Muro et al., 2018), preserved in nodules.

Hence, considering the three major marine paleobiogeographic realms recognized for the Early Devonian (see an update in Dowding and Ebach, 2018), *Kasachstania* was considered present in two of them: the Balkhash–Mongolo–Okhotsk Province and the Nevada Province of the Old World Realm (in temperate–warm carbonatic settings) and in the Malvinokaffric Realm (in cold-water siliciclastic settings).

Materials and methods

Repositories and institutional abbreviations.—Figured and cited specimens are housed in the Alexander Petrovich Karpinsky Russian Geological Research Institute in St. Petersburg, Russia (VSEGEI), the Smithsonian National Museum of National History in Washington, DC, USA (UNSM), the Muséum national d'Histoire naturelle in Paris, France (MNHN.F.B), and the Národní Muzeum in Prague, Czech Republic (NM–S).

In addition to other published illustrations, we particularly consulted specimens published by Waisfeld et al. (1988) and Edgecombe and Ramsköld (1994) assigned to *Kasachstania gerardoi* from the Silurian of the Los Espejos Formation of Argentina, housed in the paleontological repository of the Centro de Investigaciones Paleobiológicas (CIPAL) at the CICTERRA (Centro de Investigaciones en Ciencias de la Tierra: CONICET–University of Córdoba), numbered with the prefix CEGH–UNC (Cátedra de estratigrafía y Geología Histórica–Universidad Nacional de Córdoba) and in the collection of the Museo de Paleontología of the University of Córdoba numbered with the prefix CORD–PZ (Córdoba– Paleozoología).

Systematic paleontology

Terminology.—Technical terms are abbreviated as traditionally in trilobite descriptions: transversal/transversely (tr.), sagittal/sagittally (sag.), exsagittal/exsagittally (exsag.). In the description of the pygidial terminal piece, we counted any furrow that indicates segmentation, including those barely impressed (see discussions in Campbell, 1977). Open nomenclature follows criteria by Bengtson (1988). Morphological structure denomination follows Whittington and Kelly (1997).

Family Dalmanitidae Vogdes, 1890
Subfamily Dalmanitinae Vogdes, 1890

Remarks.—The recognition and definition of subfamilies within Dalmanitidae have been long discussed, and currently several genera particularly challenge the valid concept of Dalmanitinae (see Carvalho and Fonseca, 2007; Holloway and Carvalho, 2009). Since we cannot broach further discussions herein, we provisionally follow taxonomic proposals given by Campbell (1977) and Holloway (1981), together with additional taxonomic criteria drawn by Holloway and Carvalho (2009) to retain *Kasachstania* as a member of Dalmanitinae.

Genus *Kasachstania* Maksimova, 1972

Type species.—*Dalmanites saryarkensis* Maksimova, 1960 from the Lochkovian (Kockbaital horizon) of Kotanbulac mountains, Northeast Balkhash, central Kazakhstan by original designation. Holotype: isolated pygidium VSEGEI 9112 No. 18, figured by Maksimova (1960), table 55, fig. 9.

Other species.—*Kasachstania kiikbaica* (Maksimova, 1968).

Emended diagnosis.—Cephalic margin approximately parabolic without processes or crenulations, barely less convex anteriorly to axial furrows in dorsal view. Short preglabellar area (sag.), no more than 10% of the cephalon total length (sag.). Glabellar frontal lobe with an evenly curved anterior side (in dorsal view), slightly flattened dorsally toward its central and anterior region, with an elongated (sag.) posteromedial and two rounded anterolateral shallow depressions. Anterior branch of facial suture running closely to the frontal lobe. S3 oriented at 50°–65° from sagittal line, widening (exsag.) and shallowing near junction with axial furrow. S2 and S1 approximately parallel and oriented slightly backward, both short (tr.), bearing apodemal pits adaxially, and nearly effaced in contact with axial furrows. Large eyes, length (exsag.) equal to 50% of cephalic total length (sag.). Lateral and posterior border furrows separated by a posterolaterally directed ridge in the genal area. Pygidium heart–shaped to widely subtriangular (length-to-width index approximately 0.61–0.8), with rounded anterior sides of the pleural fields, widely rounded anterolateral corners, evenly convex lateral margin that becomes barely concave posterolaterally before a wide-based (tr.) and short (sag.) terminal spine. Pygidial axis narrow, 0.21 of maximum pygidial width (tr.), with 11–15 rings, fading posteriorly at level of the interior margin of pygidial doublure. Pygidium with 8–11 pleurae, concave adaxially and then progressively more convex, posteriorly deflecting abruptly close to the margin (pleural bands not reaching the pygidial margin); anterior pleural bands convex dorsally (in lateral view), narrower (exsag.) adaxially, then widening near the margin; posterior pleural bands wider (exsag.), slightly concave dorsally (in lateral view); pleural furrows deep and wide (exsag., tr.), interpleural furrows incised. Wide (exsag., tr.) and stout doublure, up to 15% of total pygidial width (tr.).

Occurrence.—Lower Devonian (Lochkovian to Pragian), Northeast Balkhash, central Kazakhstan.

Nomenclatural note.—Regarding the use of the nominal taxon, Pek and Vaněk (1991, p. 84), Edgecombe and Ramsköld (1994, p. 397, 398, 401, 403, 405, 407, 409), and Rustán (2016, p. 5, fig. 6) cited the genus as *Kazachstania*. Nevertheless, the original spelling is *Kasachstania* as defined by Maksimova (1972), and it is used here as such.

In 1967, Maksimova (1967) named several new dalmanitids entirely on the basis of illustrations and provided the descriptions afterward (Maksimova, 1968). They were later assigned to *Kasachstania* (Maksimova, 1972; Edgecombe and Ramsköld, 1994). According to the International Code of Zoological Nomenclature (1999, art. 13), all these species should be interpreted as formally erected in 1968, when illustrations together with descriptions were provided. These taxa, revised herein, include *Dalmanites kasachstanicus* Balashova in Maksimova, 1968, *Dalmanites septicostatus* Maksimova, 1968, *Odontochile kiikbaica* Maksimova, 1968, and *Odontochile ulrichi asiatica* Maksimova, 1968.

Moreover, *Dalmanites kasachstanicus* has been also cited as *Dalmanites kazachstanicus* in the text of the original publication (Balashova in Maksimova, 1968) and posterior works (e.g., Lespérance, 1975). The correct spelling is *Dalmanites kasachstanicus* in accordance with the first mention of this species, posteriorly to the original publication, by Maksimova in 1972.

Remarks.—*Kasachstania* was originally erected as a subgenus of *Odontochile* Hawle and Corda, 1847, also including several species assigned to *Dalmanites* Barrande, 1852. *Kasachstania* was defined mainly on the basis of pygidial characters, particularly a broader doublure, rounded anterior pleural sides, and less-developed segmentation compared to *Odontochile*. In the original work (Maksimova, 1972), most species referred to *Kasachstania* occurred in the Lower Devonian of northern Balkhash in central Kazakhstan: *Odontochile ulrichi asiatica* Maksimova, 1968, *Dalmanites saryarkensis* Maksimova, 1960, *Dalmanites septicostatus* Maksimova, 1968, and *Dalmanites kasachstanicus* Balashova in Maksimova, 1968. *Odontochile ulrichi ulrichi* Delo, 1940 from the Lower Devonian of Nevada, USA, was also included. Meanwhile, some other species from the United States were assigned with doubts: *Dalmanites lingulifer* Delo, 1940 from the Devonian of Oklahoma, *Dalmanites illinoisensis* Weller, 1907 from the Silurian of Illinois, and *Dalmanites rutellum* Campbell, 1967 from the Silurian of Oklahoma. Subsequently, *Odontochile pristina,* from the Lower Devonian of Balkhash, was also included in *Kasachstania* (Maksimova, 1978b).

Dalmanites andii Kozłowski, 1923 from the Silurian of Bolivia was assigned to *Kasachstania* by Pek and Vaněk (1991). In that work, *Kasachstania* was interpreted as a subgenus of *Dalmanites* without further justifications. Then, Edgecombe and Ramsköld (1994) interpreted *Kasachstania* as a distinct genus for the first time. They described the new species *Kasachstania gerardoi* from the lowermost Devonian of Bolivia and upper Silurian of Argentina (Waisfeld et al., 1988). Moreover, they reassigned *Odontochile kiikbaica* Maksimova, 1968 from the Devonian of northern Balkhash to *Kasachstania*.

Some of these assignments lacked a solid taxonomic justification due to the relatively vague terms of the original diagnosis of *Kasachstania* and the poorly preserved and scarce type material (Maksimova, 1972). In addition, Campbell (1977) questioned particularly the doublure and number of pygidial rings as main diagnostic characters of *Kasachstania*. He attributed these characters to sexual dimorphism and advised using them carefully in systematics. Despite this assumption, we considered such characters as taxonomically meaningful, supported by the fact that sexual dimorphism in trilobites is still a somewhat controversial issue even in cases of well-preserved assemblages apparently including supposedly mating pairs (Hughes and Fortey, 1995).

Taking all this into account, we included additional characters to clarify the diagnosis of *Kasachstania*. Hence, *Kasachstania* is distinguished from *Odontochile,* following Budil et al. (2009), on the basis of the anterior branch of the facial suture running next to the frontal lobe instead of anterior to the preglabellar furrow (Fig. 3.1) and the presence of a short preglabellar area that is absent in many species of *Odontochile* (Figs. 3.1, 4.1, 4.2). In addition, the pygidium of *Kasachstania* is heart-shaped while in *Odontochile* it is more elongated (sag.) and with a higher number of axial rings (16–20) and pleurae (13–14).

Kasachstania has also been considered close to *Dalmanites* (Pek and Vanêk, 1991). According to the diagnosis of *Dalmanites* (Richter and Struve in Harrington et al., 1959), *Kasachstania* differs in having a very short preglabellar area, a very wide hearth-shaped pygidium, and a higher number of pleural segments, about 8–11 in *Kasachstania* versus 6–7 in *Dalmanites* (Figs. 3.3–3.6, 4.3–4.6). Nevertheless, a clear separation is not possible since the diagnosis of *Dalmanites* has been heavily questioned (Ramsköld, 1985), and its revision is beyond of the scope of this work. Campbell (1977) stated that *Odontochile* and *Dalmanites* deserve further taxonomic work, focusing especially on the number of pygidial axial rings, location of facial suture, and doublure width. Until such revision, the relation between *Dalmanites* and *Kasachstania* remains unclear.

Recently, Pour et al. (2019) considered *Zlichovaspis* Přibyl and Vaněk, 1971 related to *Kasachstania*. *Zlichovaspis* could be clearly distinguished by a subtriangular instead of parabolic cephalon, the presence of a short precranial median process, a more subtriangular pygidium with a higher number of axial rings (16–20) and pleurae (12–17), and sculpture of fine to large granules and spines. With these important differences, there is no reason to establish *Kasachstania* as more similar to *Zlichovaspis* than any other dalmanitid.

The morphologically closest genus to *Kasachstania* is probably *Reussiana* Šnajdr, 1987a, originally defined as *Reussia* Maksimova, 1972 and later replaced due to a secondary homonymy with *Reussia* M'Coy, 1854, a Cretaceous crustacean from England (Šnajdr, 1987a). Original diagnostic characters for *Reussiana* were similar to *Kasachstania*, including rounded anterior sides and wide doublure of the pygidium. An emended diagnosis was provided by Šnajdr (1987b); accordingly, *Reussiana* can be distinguished from *Kasachstania* on the basis of pygidial characters, including more than 15 axial rings strongly elevated medially, a keel-like postaxial ridge, a dorsally concave pygidial border developed after a steep distal inclination of the dorsal convexity toward the border, and more than 11 pleurae that are less curved. *Reussiana reussi* (Barrande, 1846), the type species and the only species of the genus known from a complete cephalon, shows a rounded and deep posteromedial depression of the frontal lobe and a long (sag.) preglabellar area that clearly differs from *Kasachstania*.

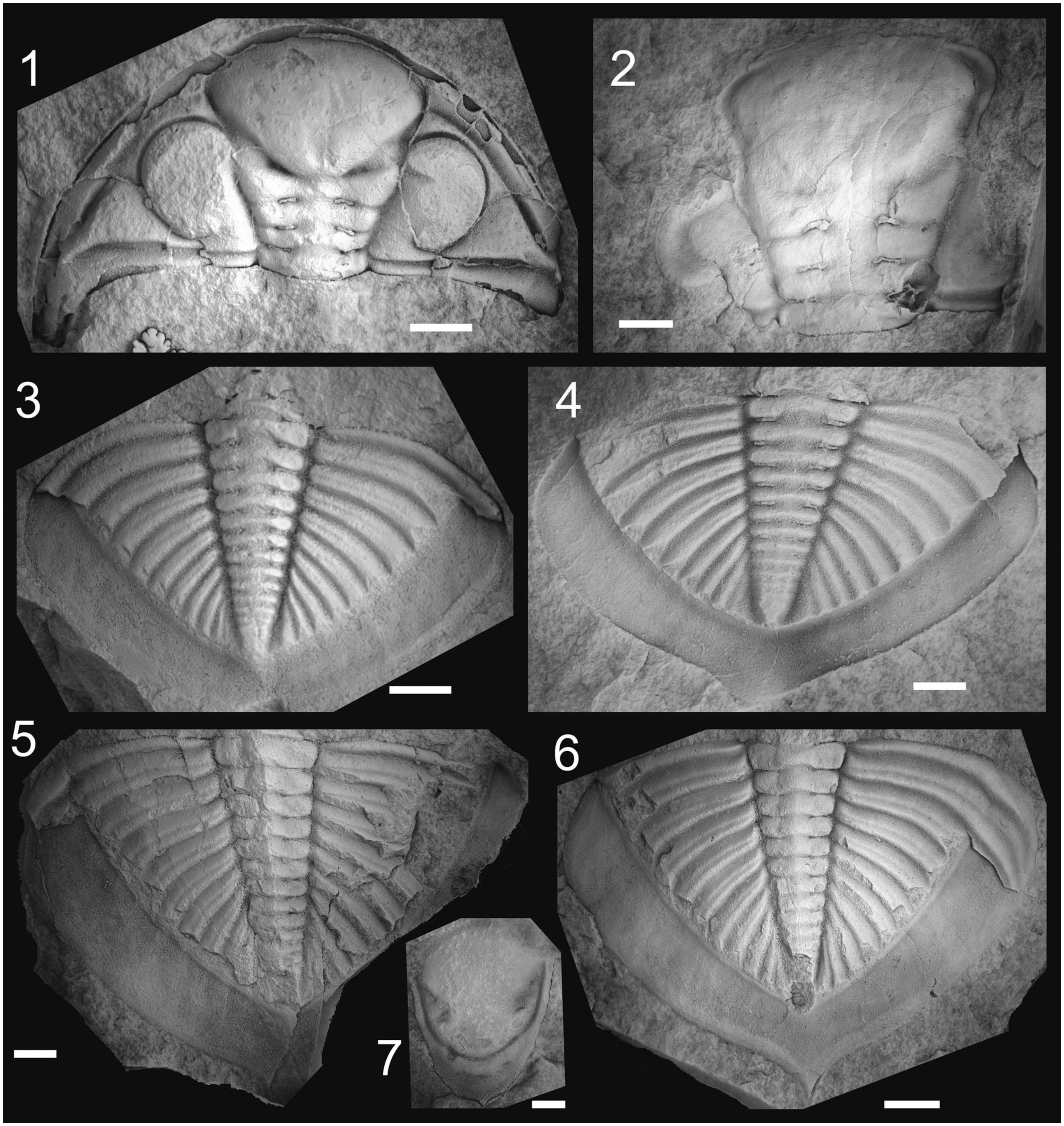

Figure 3. *Kasachstania* Maksimova, 1972 from the Lochkovian of Balkhash, central Kazakhstan. All from the Kockbaital horizon except (**6**), from the Pribalkhash horizon. (**1, 3, 4, 7**) The type species *Kasachstania saryarkensis* (Maksimova, 1960): (**1**) internal mold of cephalon, VSEGEI 8597/144, near Sary–Oba mountains; (**3**) internal mold of pygidium, VSEGEI 8597/145, Kotanbulac Mountains; (**4**) internal mold of pygidium, VSEGEI 8597/147, Kotanbulac Mountains; (**7**) internal mold of hypostome, from the same sample of the pygidium in (**4**). (**2, 5, 6**) *Kasachstania kiikbaica* (Maksimova, 1968): (**2**) internal mold of cephalon, VSEGEI 8597/177, Kiikbai mountains; (**5**) internal mold of pygidium, VSEGEI 8597/175, Kiikbai mountains; (**6**) lectotype, internal mold of pygidium, VSEGEI 8597/173, Kiikbai mountains. Scale bars = 5 mm.

According to our diagnosis, a number of species previously assigned to *Kasachstania* should be excluded from this genus.

Kozłowski (1923) erected *Dalmanites andii* on the basis of material originally assigned to *Dalmanites maecurua* Clarke, 1890 by Steinmann and Hoek (1912). The illustrations of this material consisted of drawings of a complete specimen and a pygidium. Kozłowski (1923) interpreted the complete specimen as extremely deformed and therefore based the description of *D. andii* on pygidial characters, including illustrations of two additional pygidia. The illustrated pygidia in these publications

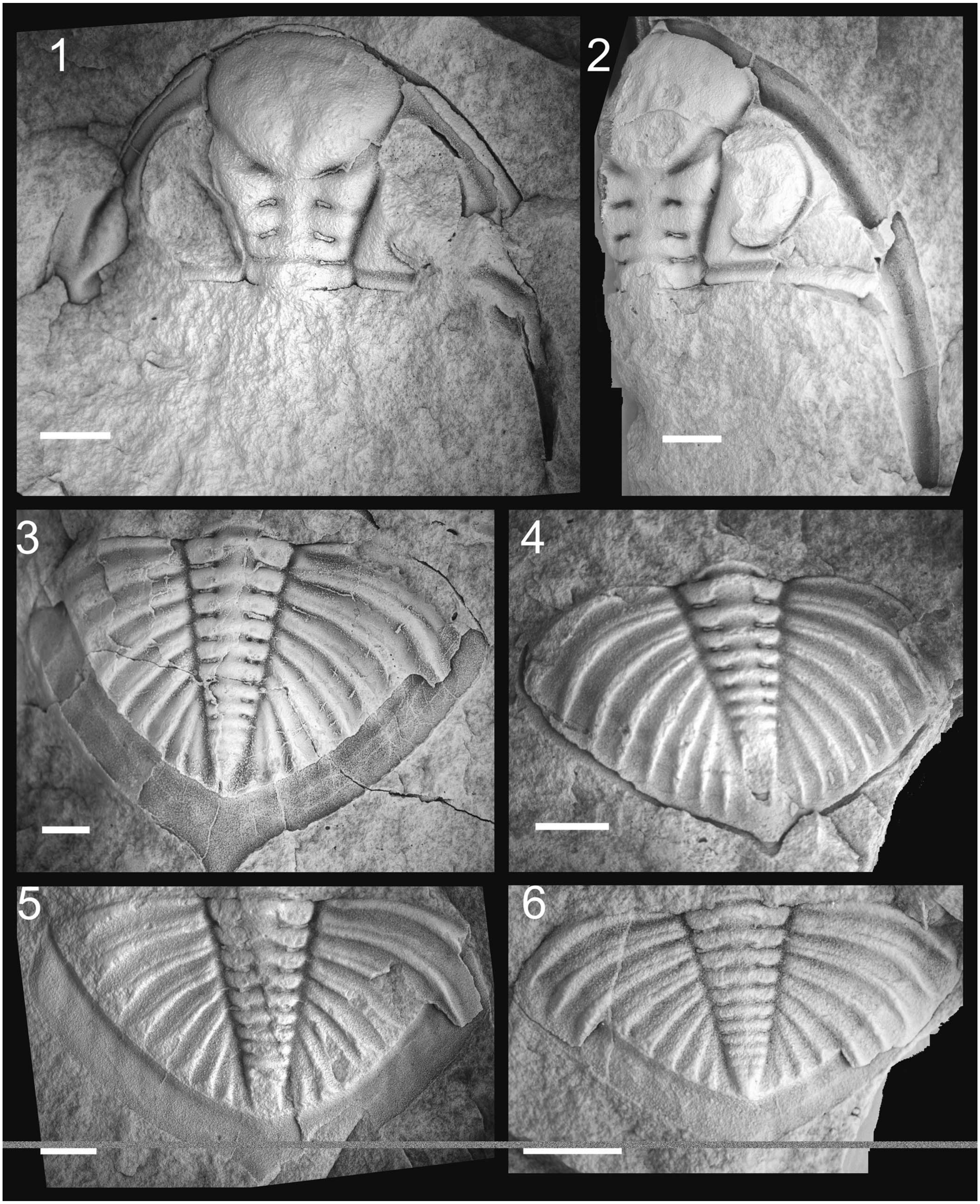

Figure 4. Some specimens of taxa synonymized with *Kasachstania saryarkensis* (Maksimova, 1960), from the Lochkovian of the Kockbaital horizon, Balkhash, central Kazakhstan. (**1–3**) Specimens originally considered *K. kasachstanica* (Balashova in Maksimova, 1968): (**1**) internal mold of cephalon, VSEGEI 8597/156, near Sary–Oba mountains; (**2**) internal mold of incomplete cephalon, VSEGEI 8597/157, near Sary–Oba mountains; (**3**) internal mold of pygidium, VSEGEI 8597/158, Kotanbulac mountains. (**4–6**) Specimens originally considered *K. septicostata* (Maksimova, 1968): (**4**) internal mold of pygidium, VSEGEI 8597/149, Kiikbai mountains; (**5**) internal mold of pygidium, VSEGEI 8597/150, Kotanbulac mountains; (**6**) internal mold of pygidium, VSEGEI 8597/153, Kiikbai mountains. Scale bars = 5 mm.

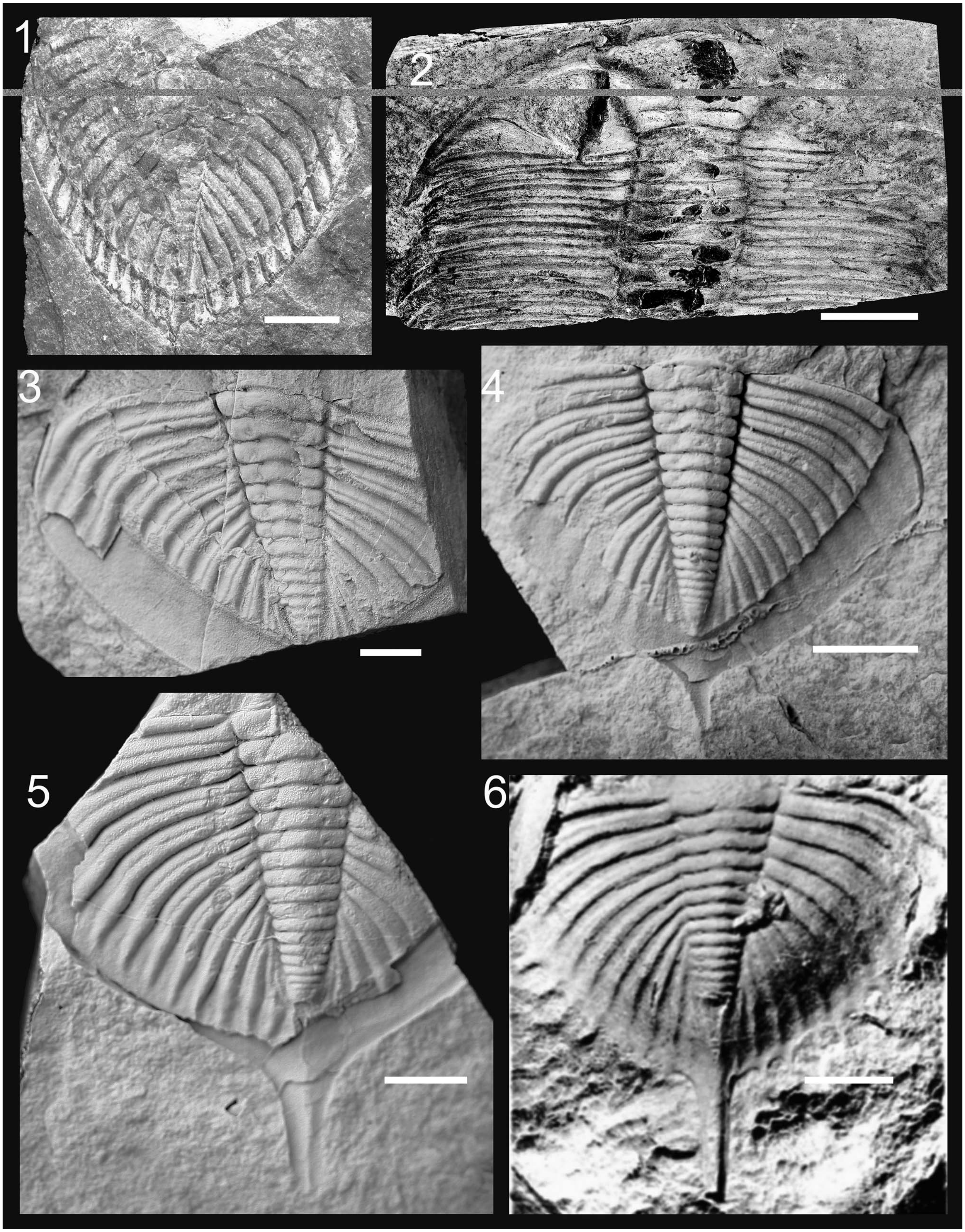

Figure 5. (**1–5**) Taxa excluded from *Kasachstania*: (**1, 2**) *Dalmanites andii* (Kozłowski, 1923) from the upper Silurian of Viloco, schistes de la Cordillera Royale, Bolivia: (**1**) internal mold of a slightly flattened pygidium, USNM PAL 373947; (**2**) internal mold of a cephalon and seven thoracic segments, USNM PAL 373946. (**3–5**) *Odontochile pristina* Maksimova, 1968 from the Lochkovian of the Kockbaital horizon, Balkhash, Kazakhstan: (**3**) internal mold of incomplete pygidium, VSEGEI 8597/159, northwest of the Kiikbai mountains; (**4**) internal mold of pygidium, VSEGEI 8597/160, near mount Sary–Oba; (**5**) internal mold of incomplete pygidium, VSEGEI 8597/161, near mount Sary–Oba. (**6**) *Saryarkella radiata* Maksimova, 1978: latex of external mold of pygidium, VSEGEI 11091/3, Emsian of the Sardzhal horizon, Sayak mine area, Kazakhstan. Scale bars = 1 cm.

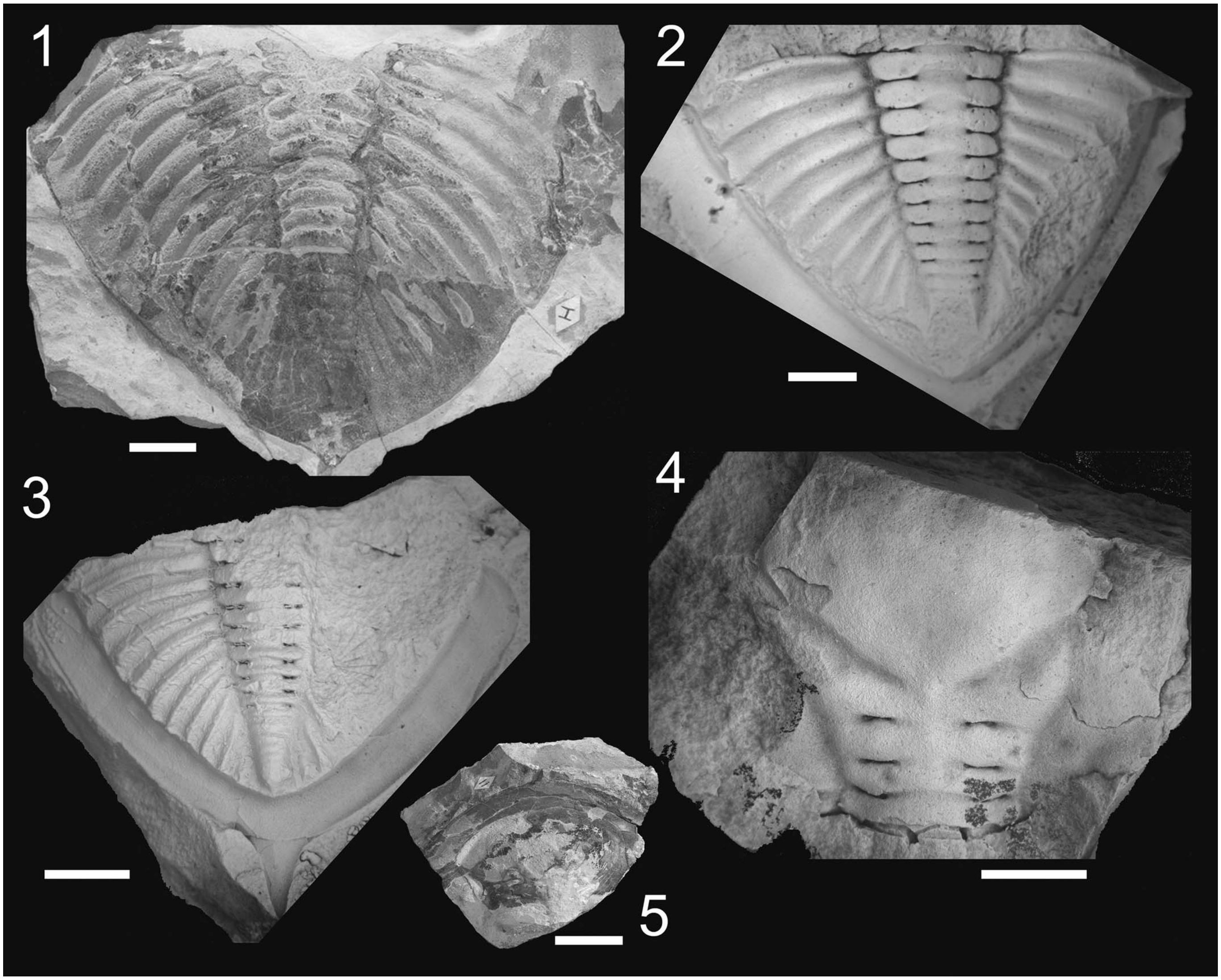

Figure 6. Taxa excluded from *Kasachstania*: (**1, 5**) *Odontochile ulrichi* Delo, 1940 from south slope of Brush Peak, Eureka District, Nevada, USA, USNM PAL 13996, Emsian: (**1**) internal mold of pygidium; (**5**) internal mold of frontal lobe and margin; (**2–4**) *Odontochile asiatica* Maksimova, 1968, from Sardzhal horizon, Balkhash, Kazakhstan, Emsian: (**2**) internal mold of a damaged pygidium, VSEGEI 8597/182, near the Akkuduk well; (**3**) internal mold of pygidium, VSEGEI 8597/180, the area of the Bala well; (**4**) internal mold of incomplete cephalon, VSEGEI 8597/181, Sayak mine area. Scale bars = 1 cm.

present several differences in shape (tr.), curvature and width (exsag.) of pleural bands and furrows, and curvature of the posterior margin, which may indicate tectonic or taphonomic deformation or interspecific variability. The first description of cephalic characters was provided by Swartz (1925), who assigned an isolated cephalon found among several pygidia apparently similar to those described by Kozłowski. However, Swartz did not provide illustrations of the pygidia, making it impossible to validate the supposed association between cephalon and pygidia. In addition, no repository number was included in any of these publications, and the cephalon was illustrated through a drawing. After that, an isolated cephalon housed at the Smithsonian National Museum of Natural History in Washington, DC, USA (Fig. 5.1, 5.2), was illustrated by Braniša (1965, plate 9, figs. 1, 2). Pek and Vaněk (1991) determined two new cephala and one pygidium but illustrated only one isolated cephalon (NM–S2111). The Národní Museum of Prague, Czech Republic, provided pictures of a nearly complete unpublished specimen (NM–S4688). The poor preservation does not allow a formal taxonomic identification; moreover, we are not aware that it was revised by Pek and Vaněk (1991). Hence, the only complete specimen of *D. andii* available is the original drawing of Steinmann and Hoek (1912). Unfortunately, it is extremely deformed. However, it highlights an ovoid glabellar frontal lobe different from any other cephala assigned. As a result, it is not possible to link the described pygidia of *D. andii* to any other cephala.

Without the holotype defined, Wolfart (1968) selected as lectotype the pygidium of Kozłowski (1923, plate 2, fig. 3); unfortunately, he did not specify repository number.

To shed light on this problem, we looked for the type specimens of Kozłowski in main institutions that might house material of *D. andii* in their catalogs. The Museo Nacional de Historia Natural de Bolivia in La Paz, Bolivia; the Sorbonne Université in Paris, France; the Université de Rennes 1 in Rennes, France; the Národní Museum in Prague, Czech

Republic; the Geozentrum Hannover in Hanover, Germany; the Instytut Paleobiologii Polska Akademia Nauk in Warsaw, Poland; the Smithsonian National Museum of Natural History in Washington, DC, USA; and the American Museum of Natural History in New York City, USA, confirmed that they do not house the type material. An incomplete pygidium (MNHN.F.B05830) housed at the Muséum national d'Histoire naturelle in Paris, France, is cataloged as a paralectotype of this species. However, this pygidium was not mentioned or illustrated in any publication. Because of these statements, the original type material of Kozłowski (1923) is herein considered probably lost.

Hence, the assignment of *D. andii* to *Kasachstania* by Pek and Vaněk (1991) is poorly supported, being based only on the 'similar structure of its exoskeleton' and a comparison between *D. andii* and *K. saryarkensis*. Besides the issues hindering the definition of *D. andii*, all assigned specimens differ from *Kasachstania* in having a pointed glabellar frontal lobe (described as 'subpentagonal' by Swartz, 1925); an S1 particularly deep, close to the axial furrow (Fig. 5.2); a subtriangular pygidium instead of a heart-shaped outline; 18–19 pygidial axial rings (versus 11–15); 13–14 pleural segments (versus 11–12); pleural bands nearly straight; and a moderately wide doublure, as was pointed out by Edgecombe and Ramsköld (1994) and inferred by Braniša (1965; Fig. 5.1). We therefore exclude *D. andii* from *Kasachstania*. A revision of Bolivian collections and new material would be necessary to definitely solve the taxonomy of *D. andii*. Presently, the original drawings (probably idealized in part) and a poorly preserved cephalon that cannot be reliably linked to a pygidium do not allow such study.

The assignment of '*Kasachstania*' *gerardoi* from the lowermost Devonian of the Catavi Formation of Bolivia and the upper Silurian of Argentina, by Edgecombe and Ramsköld (1994), was based on pygidial similarities with *Kasachstania kiikbaica* and cephalic similarities with *D. andii.* However, '*Kasachstania*' *gerardoi,* in contrast with *D. andii,* is based on well-preserved original material. '*Kasachstania*' *gerardoi* differs from *Kasachstania* by a pointed anterior cephalic margin; a subrhombic glabellar frontal lobe; a depressed area of the pygidium approximately coincident with the interior margin of the doublure; pleural bands becoming progressively less expressed distally, defining a wider pygidial border; and narrower pygidial doublure (tr.). In addition, the shape of the pygidium is more elongated (sag.) and without a clear heart-like shape. This species is therefore also excluded from *Kasachstania*.

Dalmanites andii and '*K.*' *gerardoi,* in turn, were considered similar, with their main differences at the pygidium (Edgecombe and Ramsköld, 1994). They consist of fewer pygidial rings and pleurae, more sinuous pleural bands, and wider doublure in '*K.*' *gerardoi*.

These similarities suggest that '*K.*' *gerardoi* and at least some specimens assigned to *D. andii* might belong to the same (and undescribed) genus, closely related to *Kasachstania*. However, *D. andii* is extremely difficult to define, as stated previously, and its eventual inclusion in a new genus depends on a complete revision of the assigned specimens.

Odontochile ulrichi and *Odontochile asiatica* do not conform to the proposed diagnosis of *Kasachstania* in having a proportionally longer pygidium, subtriangular instead of heart-shaped in outline; pleurae that tend to be evenly curved instead of having a sinuous shape; anterior pleural bands nearly reaching the pygidial margin showing a gentle sinuosity; and more than 15 axial rings (Fig. 6.1–6.3). In particular, *O. asiatica* has nearly no pygidial interpleural furrows expressed and exhibits a much longer (sag.) terminal spine than *Kasachstania* (Fig. 6.2, 6.3), while *O. ulrichi* has more than 11 pygidial pleurae and a much longer (sag., exsag.) preglabellar area (Fig. 6.1, 6.5). As a result, these taxa are excluded from *Kasachstania.* Both subspecies were grouped solely on the basis of a similar pygidial axis width (tr.) and pygidial pleural shape. Differences between *O. ulrichi* and *O. asiatica* previously reported include the near absence of interpleural furrows and a distinct number of pygidial pleurae in *O. asiatica* (Maksimova, 1968). In addition, we observed that the pygidium of *O. asiatica* is proportionally longer, with deeper and wider intrapleural furrows and a delicate ridge-like dorsal surface on the anterior margins of the anterior pleural bands, which is completely absent in *O. ulrichi*. Thus, *O. asiatica* and *O. ulrichi* are interpreted here as two different species. Furthermore, they might belong to distinct genera. *O. ulrichi* would conform to the taxonomic concept of *Odontochile* (Fig. 6.1, 6.5). However, *O. asiatica* most closely resembles the subgenus *Odontochile* (*Pacifina*), registered in the same stratigraphic interval and area. In particular, *Odontochile* (*Pacifina*) *arcuata* Maksimova, 1968 is the most similar species of this subgenus according to the pygidial shape, pleural bands, and furrow curvature, the number of axial rings, and the strongly straight S1 (Fig. 6.4). However, despite these similarities, *O. asiatica* does not match all the requirements of the subgeneric diagnosis of *Odontochile* (*Pacifina*), as defined by Maksimova (1978b), in having a terminal spine and fewer axial rings (Fig. 6.2, 6.3). Furthermore, there appears to be a problem with the definition of *O.* (*Pacifina*) since at least two other species of this subgenus, *O.* (*Pacifina*) *carinata* and *O.* (*Pacifina*) *pratteni* (Roy, 1933), clearly show a caudal spine. Hence, a revision and emended diagnosis of *O.* (*Pacifina*) is necessary to reassess its subgeneric status and resolve its taxonomic relationship with *O. asiatica*.

Odontochile pristina is distinguished from *Kasachstania* by the presence of a large caudal spine, higher number of pygidial rings (18 versus 11–15), a proportionally elongated (sag.) pygidium (not heart-shaped) with abrupt changes of curvature in the anterolateral sides (not rounded), a wider (tr.) axis, and pleurae strongly curved posteriorly (Fig. 5.3–5.5). Consequently, *O. pristina* is excluded from *Kasachstania*. Despite differences in size and scarcity of material, we believe that it might belong to *Odontochile*. Recently, Pour et al. (2019) considered material of *O. pristina* insufficient to justify a formal generic assignation.

Some specimens from the Lower Devonian of Argentina were reported as *Kasachstania*? sp. by Rustán (2011, 2016, p. 5, fig. 6). A preliminary revision of this material suggests clear differences from *Kasachstania*, and therefore they are excluded from this genus. The taxonomic study of such specimens is in progress to be reported in a forthcoming work.

Dalmanites lingulifer was revised in detail by Campbell (1977) and reassigned to *Huntonia* Campbell, 1977, an endemic genus of North America. Later, this genus was found to be a

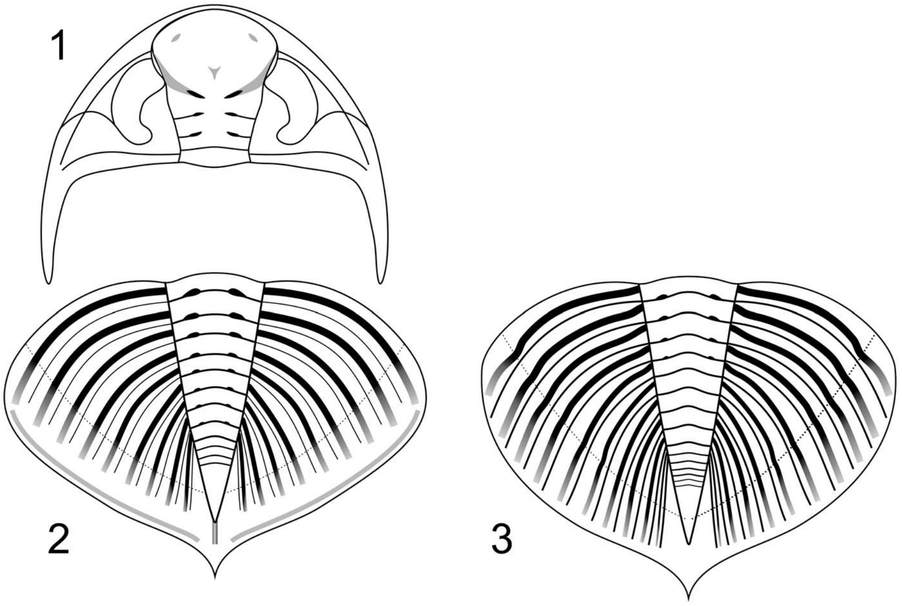

Figure 7. Schematic drawings of the two species of *Kasachstania* Maksimova, 1972 based mainly on their type specimens: (**1, 2**) *Kasachstania saryarkensis* (Maksimova, 1960): (**1**) cephalon after VSEGEI 8597/144; (**2**) pygidium after VSEGEI 9112/18. (**3**) *Kasachstania kiikbaica* (Maksimova, 1968): pygidium after VSEGEI 8597/173. Terminal part of pygidial axis idealized because of incomplete specimens. Dashed line indicates inner margin of pygidial doublure. Slight differences in shape of pygidia might reflect different orientation of specimens in the original photographs.

junior homonym of the isopod *Huntonia* Vandel, 1973 and was replaced with *Huntoniatonia* Jell and Adrain, 2003. On the basis of new material, Campbell (1977) rejected any relationship with *Kasachstania*, as was suggested before by Maksimova (1972), due to the long, simple anterior cephalic process, which Campbell considered as a diagnostic character of *Huntoniatonia*. Additional differences with *Kasachstania* involve the presence in *Huntoniatonia* of a subrhombic glabellar frontal lobe, deeper S1 and S2 at the contact with the axial furrow, a more elongated (sag.) pygidium, a wider (tr.) pygidial axis, and a long (sag.) terminal spine, twice as long as the pygidium. On the basis of these features, we agree with Campbell that *H. lingulifer* is excluded from *Kasachstania.*

Dalmanites illinoisensis is known only from its pygidium. Characters distinguishing it from *Kasachstania* include a tendency to be subtriangular, proportionally smaller and rounded anterolateral sides, a wide (tr.) and well-defined pygidial border, and a longer (sag.) caudal spine with a dorsal postaxial ridge. We agree with Delo (1940), who stated that the generic assignment of *D. illinoisensis* needed further study because its wide (tr.) border, elongated (sag.) spine, and larger size differentiate it from all other North American dalmanitids.

Dalmanites rutellum can be distinguished from *Kasachstania* on the basis of an extended preglabellar area, an anterior cephalic margin interrupted by a slight, well-rounded anterior protuberance, S1 in clear contact with the axial furrow where it is deeper, an elongated (sag.) pygidium, and pygidial pleurae strongly curved posteriorly.

Recently, Pour et al. (2019) erected *Kasachstania alperovichi* from the Early Devonian of west Balkhash, Kazakhstan. This species does not conform to the proposed diagnosis of *Kasachstania* in having a subpentagonal glabellar frontal lobe, a distinct and longer (exsag.) postocular area, a more subtriangular pygidium, and fewer axial rings and pleurae. They made a comparison with *Odontochile pristina*, and '*K.*' *alperovichi* differs in having a more subtriangular outline, narrower pygidial pleurae, faint interpleural furrows, and longer caudal spine with a robust base. '*Kasachstania*' *alperovichi* most closely resembles *Dalmanites* as it shares the facial suture running very close to the frontal lobe of the glabella.

Kasachstania saryarkensis (Maksimova, 1960)
Figures 3.1, 3.3, 3.4, 3.7, 4.1–4.6

1960 *Dalmanites saryarkensis* Maksimova, p. 272, 376, pl. 55, figs. 8, 9.
1968 *Dalmanites kasachstanicus*; Balashova in Maksimova, p. 90, pl. 9, fig. 2, pl. 22, figs. 6–8, pl. 27, figs. 5, 6.
1968 *Dalmanites kazachstanicus*; Balashova in Maksimova, p. 89 [Lapsus calami]
1968 *Dalmanites septicostatus*; Maksimova, p. 88, pl. 22, figs. 1–5.
1972 *Odontochile* (*Kasachstania*) *saryarkensis*; Maksimova, p. 81.
1972 *Odontochile* (*Kasachstania*) *kasachstanica*; Maksimova, p. 81.
1972 *Odontochile* (*Kasachstania*) *septicostata*; Maksimova, p. 81.
1975 *Odontochile* (*Kasachstania*) *kazachstanica*; Lespérance, p. 100. [Lapsus calami]
1975 *Odontochile* (*Kasachstania*) *septicostata*; Lespérance, p. 99.
1991 *Dalmanites* (*Kasachstania*) *saryarkensis*, Pek and Vaněk, p. 85.
1994 *Kasachstania saryarkensis*; Edgecombe and Ramsköld, p. 403.

Holotype.—An incomplete pygidium, VSEGEI 9112, No. 18. Figured by Maksimova (1960, table 55, fig.9).

Diagnosis.—*Kasachstania* with 11–12 pygidial axial rings and 8–9 pleural furrows; pleural sinuosity barely expressed, pleurae tending to be evenly curved. Pygidial inter-ring furrows wide (sag., exsag.) with deep adaxial apodemal pits. Interpleural furrows slightly impressed.

Occurrence.—Lochkovian, Northeast of Balkhash city, Karazhirik horizon, Kotanbulac mountains, area of the Bala Well and Kiikbai mountains, central Kazakhstan.

Remarks.—Only one hypostome (Fig. 3.7) is considered to possibly belong to *K. saryarkensis* (Maksimova, 1968) although without attachment to any cephalon. Therefore, its characters are not included in the diagnosis. This hypostome is elongated (length-to-width index approximately 1.36), tending to be sub-oval. The anterior part is incompletely known, so the wings could not be described. The middle furrow is deep anterolaterally up to a strong posteromedial macula. The lateral margin is slightly concave anteriorly, converging gently backward up to a distinct lateral projection near the macula, then again concave up to the other lateral projection in the posterior part of the lateral border, and finally converging gently toward the spiny posterolateral junction with the posterior margin. The outline of the posterior margin is convex, and a conspicuous median spine is directed backward. The posterior border furrow is convex with a slightly pointed middle part. The posterior border has a medial convex depression. Five denticles in the posterior part are mentioned in the original description (Maksimova, 1968), but only one can be observed and two might be inferred.

Several described species are herein considered synonyms of *Kasachstania saryarkensis*. The differences mentioned by Maksimova (1968) between *K. saryarkensis* and *K. kasachstanica* are related mainly to the pygidium. *Kasachstania kasachstanica* has a wider axis (approximately 0.25 times the maximum pygidial width versus 0.23–0.24 in *K. saryarkensis*) and a shorter pygidium (length-to-width index approximately 0.63 versus 0.68) with fewer axial rings (11 versus 12) and pleurae (8 versus 9). Maksimova (1968) stated her concerns about these differences, which might be intraspecific. We also consider them too subtle to support a specific distinction. In addition, one pygidium assigned to *K. kasachstanica* (VSEGEI 8597 No. 158; Fig. 4.3) has a length-to-width index of approximately 0.8 compared to the 0.63 index of the type material, supporting an intraspecific variation. Additional differences mentioned by Maksimova (1968) include the maximum width (tr.) of the pygidial doublure in *K. kasachstanica* (which should occur at the level of the seventh–eighth ring, while at the fifth–sixth in *K. saryarkensis*), a transition between posterior border and genal spines more angulated than in *K. saryarkensis*, and S1 and S2 in contact with axial furrows. In our opinion, these additional differences might be explained by taphonomy since the maximum width of pygidial doublure (as specified by Maksimova, 1968) might depend on preservation, and the illustrated cephalon of *K. saryarkensis* (Fig. 3.1) is probably deformed, modifying the proportions of the glabella and making it look wider. In addition, no significant differences are recognizable in S1 and S2. Considering that all specimens come from the same locality and layers, we consider *K. kasachstanica* a junior synonym of *K. saryarkensis.*

Kasachstania septicostata is known from 24 pygidia (five illustrated). It is also very similar to *K. saryarkensis* but with narrower (exsag.) pleurae and wider and deeper pleural furrows (Fig. 4.4–4.6). However, all specimens assigned to *K. septicostata* are small-sized and share locality and bearing layers with *K. saryarkensis*. Hence, we interpret them as probable juveniles of this species, differences being ontogeny-based. Preliminarily, we report the specimens formerly assigned to *K. septicostata* as *K. saryarkensis*?. Such specimens might eventually shed light on the ontogeny of these dalmanitids, an aspect greatly overlooked.

Kasachstania kiikbaica (Maksimova, 1968)
Figure 3.2, 3.5, 3.6

1968 *Odontochile kiikbaica* Maksimova, p. 97, pl. 24, figs. 1–5.
1972 *Odontochile* (*Reussia*) *kiikbaica*; Maksimova, p. 82.
1975 *Odontochile* (*Reussia*) *kiikbaica*; Lespérance, p. 100.
1994 *Kasachstania kiikbaica*; Edgecombe and Ramsköld, p. 403, 405, 407.

Holotype.—An incomplete pygidium, VSEGEI 8597, No. 173, figured by Maksimova (1968, table 24, fig. 1) and herein (Fig. 3.6).

Diagnosis.—*Kasachstania* with 15 pygidial axial rings tending to be inflated medially and 10 pleural furrows; pleural sinuosity well expressed. Pygidial inter-ring furrows narrow (sag., exsag.) with shallow adaxial apodemal pits. Interpleural furrows well expressed. Anterior pleural bands inflated at level of inner margin of doublure.

Occurrence.—Lochkovian–Pragian, Northeast of Balkhash city, Kockbaital and Pribalkhash horizons, Kiikbai and Kockbaital mountains, and the area of the Bala Well, central Kazakhstan.

Remarks.—A diagnosis is provided for this species for the first time. *Kasachstania kiikbaica* was originally assigned to *Reussiana* by Maksimova (1972). However, in the revision of this genus, Šnajdr (1987b) did not discuss *K. kiikbaica*. Later, Edgecombe and Ramsköld (1994) assigned *K. kiikbaica* to *Kasachstania* based mainly on similarities with ‘*Kasachstania*’ *gerardoi*. Here the taxonomic assignment to *Kasachstania* is supported but on the basis of the emended diagnosis and comparisons with the type species.

Kasachstania kiikbaica is distinguished from *K. saryarkensis* by the presence of 15 axial rings (versus 11–12), 10 pleurae (versus 8–9), more sinuous pleurae, narrower inter-ring furrows (sag.) with shallower apodemal pits, deeper interpleural furrows, axial rings that tend to be inflated, and anterior pleural bands with a distal inflation (Figs. 3.5, 3.6, 7). *Kasachstania kiikbaica* appears to have a narrower pygidial axis, but scarce and poorly preserved material hinders further precisions.

Genus *Saryarkella* Maksimova, 1978b
Figure 5.6

Type species.—*Saryarkella radiata* Maksimova, 1978b, from the Lower Devonian, Emsian, Sardzhal horizon of Northeast Balkhash city, Sayak mine area, central Kazakhstan.

Diagnosis.—Translated and adopted from Maksimova (1978b): pygidium flat, almost semicircular. Axis rapidly narrowed back, with 16 rings, behind which an undifferentiated tail passes into a rounded keel, ending with a long spine. Pleurae with 10 pairs of posteriorly directed ribs; the first pairs bear weak traces of pleural furrows; their posterior pleural bands vanish near the pygidial margin. The narrow pygidial margin has flat, posteriorly directed spines, corresponding to the width of the pleurae.

Remarks.—The monospecific genus *Saryarkella* was not mentioned in any publication after its original erection. It is known only from one pygidium (VSEGEI 11091, No. 3; Fig. 5.6), which shows a robust caudal spine and conspicuous marginal spines, a combination that differentiates it from any other mature dalmanitid holaspid. Marginal pygidial spines are rare among dalmanitids. They are present in *Coronura* Hall and Clarke, 1888 and *Chacomurus* Braniša and Vaněk, 1973, but these closely related taxa are characterized by a median embayment in the posterior margin of the pygidium (without a caudal spine), developed between two lateral spines. *Saryarkella*, by contrast, is unique in having a typical dalmanitid pygidial shape with well-developed lateral and caudal spines located at the same (dorsoventral) level of the pygidial margin. Equivalent marginal spines were found in some meraspids and early holaspids of different dalmanitids such as *Odontochile*, *Dalmanites*, *Zlichovaspis*, and *Songxites* Lin, 1981 (Whittington and Campbell, 1967; Vaněk, 1996; Budil et al., 2009). *Erbenochile* Alberti, 1981, a genus considered related to Dalmanitids (Bignon and Crônier, 2014), has marginal spines that continued from the posterior pygidial pleural bands. This kind of marginal spine is not found in any dalmanitids, being larger and more robust than *Saryarkella*, *Coronura*, and *Chacomurus*. The evolutionary context, morphofunctional, and ecological implications of spinosity in dalmanitids remain unclear. It might be assumed that this spinosity is driven by heterochrony, and it probably plays a defensive role, particularly in early ontogenetic stages. The striking pygidial spines of *Saryarkella* would suggest a defensive function also in mature holaspids.

Discussion

The Devonian trilobites from central Kazakhstan appeared to be cosmopolitan, according to the first-reported taxonomic lists, since the bulk of them (reported mainly by Maksimova) were included in classic genera reported virtually worldwide (*Dalmanites*, *Odontochile*, *Phacops* Emmrich, 1839, and so on). However, after a number of taxonomic reappraisals, these classic genera were separated into several new taxa with a more restricted distribution. Similarly, all species from Kazakhstan previously assigned to *Reussiana* and the phacopid *Paciphacops* Maksimova, 1972 were questioned in their generic assignment because of the poor original material and absence of diagnostic characters. As a result, the presence of these two widely distributed genera is currently putative in Kazakhstan (Šnajdr, 1987b; Ramsköld and Werdelin, 1991; Budil et al., 2009). In the case of *Kasachstania*, the material was considered enough to support the genus, conformed with two endemic species.

Hence, these new insights suggest that trilobites from the Devonian of Kazakhstan support a more endemic signature than previously thought. This pattern coincides with the clearly endemic Early Devonian brachiopod fauna from Balkhash, which share only a few genera with the Siberian plate, the main paleogeographic neighbor with similar climatic settings (Wang et al., 2013). Nevertheless, recently Pour et al. (2019) commented on the presence of shared homalonotid trilobites between west Balkhash and Australia. They related the two faunas with *Kasachstania* in Balkhash and *Zlichovaspis* in Australia, considered by them as related dalmanitids. This similarity is discussed before in this current work and is not considered well supported. In addition, they remark on a relation of the brachiopods of west Balkhash with the Rhenish–Bohemian Province. Dowding and Ebach (2019), however, commented that a faunal relation between the Ural region as a whole and the Gondwana basins was a novelty of Middle–Late Devonian.

It is worth mentioning that the complex paleogeographic history of the basins in the Early Devonian paleogeographic evolution of the tectonic terranes involved in the present central Kazakhstan, as commented on previously, could certainly have favored isolation and speciation, promoting rising biogeographic barriers and vicariance.

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